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Effects of Grazing by Wild Ungulates in Yellowstone National Park

Technical Report NPS/NRYELL/NRTR/96-01

United States Department of the Interior • National Park Service
Yellowstone National Park

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The cover photograph depicts giant wild rye, big sagebrush, and Douglas fir near Rescue Creek in the Yellowstone Northern Range (photograph by Norman A. Bishop, July 1984).

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Edited by
Francis J. Singer

United States Department of the Interior
National Park Service
Natural Resource Program Center
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Foreword

The Northern Range of Yellowstone National Park is an internationally significant and ecologically unique area that comprises one-third of the park in Wyoming and Montana. Ecologists have referred to it as "America's Serengeti." The range and its renowned wildlife populations have been the subjects of increasingly intensive ecological research for a half-century. As a result, more scientific journal articles about research in the Northern Range were published in the last decade than in all previous years. Our understanding of this range evolved rapidly, and, as research continues, the complexity of the Northern Range ecology is continually revealed to researchers and students in new ways.

This volume consists of 28 reports of research by university and government scientists from across the nation. The studies were conducted under the Northern Range Research Program from 1986 to 1991. The program addressed the population dynamics and ecological effects of native ungulates (elk, bison, moose, pronghorn, bighorn sheep, mule deer) on the soil, vegetation, and watersheds of the Northern Range. Most studies were funded through the Natural Resource Preservation, Post-Fire, and Wolf Study Programs by the U.S. Department of the Interior, National Park Service (NPS). Additional funding was supplied by the U.S. Fish and Wildlife Service, the U.S. Forest Service, the University of Wyoming, the Utah State University, the Colorado State University, the Montana State University, the Rob and Bessie Welder Wildlife Foundation, and the Montana Riparian Association.

This volume does not present an exhaustive synthesis of the more than 50 years of study on the Northern Range. It contains only a compilation of reports of research conducted during the 6-year Northern Range Research Program. Many of the authors have continued their studies and published additional scientific reports elsewhere. Some of the reports in the publication were published previously and are included by special arrangement with the respective publishers. Advanced students of the ecological relations reported here may want to review the references cited at the end of each paper and those published since 1991.

To ensure objectivity in the Northern Range Research Program, several administrative elements were included in the program design. First, substantial participation was sought from peer scientists and natural resource managers outside the National Park Service. Scientists with long-term involvement in the Greater Yellowstone Ecosystem were asked to participate in several forums to identify and prioritize needed research. Second, program managers sought substantial collaborative participation by non-NPS scientists in projects managed or coordinated by NPS scientists. Third, many of the studies conducted with funds from the Northern Range Research Program were administered by the University of Wyoming-National Park Service Research Center. The competitive cooperative research program proposals for these studies were subjected to national competition, a peer review, and ranking in priority order to determine funding.

Each report was extensively peer reviewed before acceptance by the National Park Service. Every previously published report had been subjected to peer review by the respective journal. Peer review was conducted of all unpublished reports in this volume. Thus, most of the reports were subjected to at least two and occasionally three separate reviews.

In addition to the steadfast authors of this volume, who endured more extensive scrutiny than they expected, many people must be thanked and acknowledged for contributions. Yellowstone Superintendent R. Barbee had the foresight to see the need for the research and to seek agency support for it. Project coordinators J. Varley of the National Park Service and F. Singer and D. Despain of the National Biological Service deserve much credit for managing the 5-year program. Study designs were based on extensive problem analyses by S. McNaughton, J. Detling, L. Wallace, D. Houston, E. Garten, and D. Goodman; these able people helped us ask the right questions. For the competitively selected research cooperators, M. Boyce and colleagues of the University of Wyoming reviewed submitted proposals. Logistical, editorial, and graphic support was contributed by N. Bishop, S. Broadbent, J. Cox, R. Evanoff, K. McElwain, M. Nelson, M. Nichols, D. O'Leary, P. Opler, P. Schullery, J. Selleck, and P. Vohs. D. Huff supervised the administration of several program projects and A. Miller and J. Selleck facilitated the final stages of production of this document.

This compilation received peer review equal to or beyond that required for National Park Service Monograph Series publications. However, because it was determined necessary to include previously published reports to include all reports of the Northern Range Research Program in a single compilation, this document was published as part of the National Park Service Technical Report Series instead. The reports provide the basis for a Report to the NPS Director on Grazing on Yellowstone's Northern Range that is being prepared concurrently by the National Park Service for transmittal to appropriate congressional committees this year.

MICHAEL SOUKUP, PH.D.

Associate Director, Natural Resource Stewardship and Science
National Park Service

Reprint of Chapter 15, pages 209–230 *in* R. B. Keiter and M. S. Boyce, editors. The Greater Yellowstone Ecosystem: Redefining America's Wilderness Heritage.

The Concept of Overgrazing and Its Application to Yellowstone's Northern Winter Range

Michael B. Coughenour and Francis J. Singer

Overgrazing can be defined simply as an excess of herbivory that leads to degradation of plant and soil resources. The excess of herbivory must be induced and defined by humans, however. The concept of overgrazing has no meaning in ecosystems where there are no humans to alter or evaluate natural processes.

Concern is widespread that man has altered natural processes in Yellowstone National Park and that overgrazing is, consequently, a valid possibility. In line with the goal of preservation of natural processes, Yellowstone National Park embarked in 1968 on an experimental program of natural-regulation management of the large ungulates of the park's northern range (Cole 1971; Houston 1971). Some believe that natural regulation is impossible and that uncontrolled herbivore numbers can result only in overgrazing and ecosystem degradation. In 1986 Congress directed the National Park Service to "start a study on Yellowstone to see whether there is evidence of overgrazing [and] what should be done to avoid that... ." (Congressional Record—Senate, S 12613, September 16, 1986). National Park Service policy states that "natural processes will be relied upon to control populations of native species to the greatest extent possible. Unnatural concentrations of native species caused by human activities will be controlled if the activities causing the concentrations cannot be controlled" (U.S. Department of the Interior 1988).

Unfortunately, the demarcation between proper grazing and overgrazing is not sharp, as grazing severity varies along a continuum. Moreover, recognition and definition of overgrazing depends on understanding plant and soil responses to climate and herbivory, as well as natural interactions between plants, herbivores, and predators over both short and long time scales. Application of the concept in Yellowstone or any national park depends upon our ability to correctly identify natural processes and mechanisms of natural population regulation. The ability to assess overgrazing, therefore, depends greatly on the state of ecological science.

Our objectives in this chapter are to examine the concept of overgrazing in general and as applied in Yellowstone—to reveal how the concept has evolved in relation to changes in natural conditions, changes in human influence on the system over time, and scientific advances. We compare concepts of overgrazing as used by a range manager, a wildlife manager, a model of natural regulation (Caughley 1976), the Yellowstone natural-regulation hypothesis, and a model of natural regulation that is less dependent on equilibrial assumptions.

HISTORY OF THE CONCEPT OF OVERGRAZING IN YELLOWSTONE

The concept of overgrazing may have first been introduced to Yellowstone in 1887 when Lt. Elmer Lindsley estimated there was enough summer range for forty thousand elk, but only enough winter range for one-fourth that number. In 1895 Acting Superintendent George S. Anderson remarked that a series of mild winters could make elk more numerous than the food supply could support (Houston 1982). The perception was that too many elk were confined to too small an area (Graves and Nelson 1919). Later, however, Ranger James Depuis observed in the 1910s and early 1920s that range grass was plentiful and that the northern range was not overgrazed (Edwards 1931).

High wintering densities were viewed as unnatural (Skinner 1928; Cahalane 1943). This view may have arisen for three reasons. First, elk within the park had been protected from hunting since 1883. The last park wolf was eliminated in 1926 (Weaver 1978).

Thus it seemed clear that elk would seek refuge from hunters and wolves by remaining within the park. Second, few elk were believed to have wintered in the park prior to 1878. Instead, the elk herd presumably had migrated out of the park area and far down the Paradise Valley every winter. Winter elk censuses were not conducted in those early days, however (Houston 1982). It is unclear what part of the herd may have moved down the valley, what the total herd distribution was, or how this would have varied in response to winter severity. Third, ranching development outside the park was assumed to have excluded elk from using these traditional winter ranges while unrestricted hunting eliminated the migration.

The summer of 1919 was very dry and that winter "there was no forage on the winter range at all" (Rush 1932). Park staff estimated that six thousand animals starved that season (Grimm 1945). Houston (1976, 1982) later questioned the accuracy of this number. However, a significant winterkill clearly did occur. Assertions that the mortality was an indirect result of an elk population eruption was never substantiated (Houston 1979, 1982)

Dry conditions greatly influenced perceptions of overgrazing. George Whittaker, an army scout, stated that "during those years of plentiful moisture, no depletion of the range was noticed, but generally dry conditions since 1926 caused the ranges to have a look of apparent overgrazing" (Edwards 1931). Like the summer of 1919, those of 1921 and 1926 were very dry (Edwards 1931). The drought continued and intensified through 1936. Rush (1932) subjectively assessed changes since 1914. To him it appeared that one to two inches of topsoil had eroded and that the grass was badly disturbed. Browse species were being heavily used. In 1933 there was a serious grasshopper infestation (Wright 1934). LaNoue (1936) noted soil erosion, disappearance of herbaceous cover, damage to tree growth, elk in poor physical condition at winter's end, and periodic large elk winter kill. Grimm (1935) reported erosion and denudation of plant cover aggravated by elk. Willows were dying at Slough Creek. The first scientific studies using grazing exclosures indicated that the decrease in plant density from 1930 to 1937 was 43 percent inside exclosures and 59 percent outside exclosures (Grimm 1937).

Growing conditions improved in 1937 (Grimm 1937), and grass production nearly doubled by 1941 (Gammill 1941). Gammill (1940) reported a significant increase in plant density, but only 50 percent recovery from the drought. In spite of the wetter conditions aspen and willow continued to decrease, and in 1943 Grimm noted that the amount of browse from willow and aspen was too small to even factor into elk forage requirements.

Later observations suggested a dramatic decline in big sagebrush on the part of the northern range (near Gardner) preferred by antelope (Grimm 1945). Aspen sprouts were reportedly heavily browsed and suffered a net decline in shoot height (Kittams 1949, Barmore 1968), and willows greatly declined in abundance (Kittams 1948; Wright 1934). Sparse vegetative cover and the degree of bare soil was attributed to soil erosion from overgrazing (Wright 1934; Cahalane 1941). Competition between elk and other ungulates (Mills 1935; Gammill 1941), and some grasslands retrogressed from bluebunch wheatgrass to bluegrasses (Kittams 1948). Jonas (1955) found that trees failed to regenerate on sites that had been harvested by beaver. Jonas observed that elk browsed on the regrowth and this seemed to inhibit tree recovery.

Superintendent Lemuel (Lon) Garrison decided in 1956 that a balance had to be restored between ungulates and the range. In 1962 the elk cull was increased dramatically, and elk numbers had been reduced to less than 3,200 by 1968.

NATURAL REGULATION

Artificial reductions of elk, bison, and pronghorns in Yellowstone were terminated in 1968. The object was to test the hypothesis that park elk populations would be naturally regulated (Cole 1971; Houston 1976). This Yellowstone natural-regulation hypothesis demands acceptance of the following assertions (1) that the Yellowstone area elk existed in an ecologically complete habitat; (2) that hunting by Indians could not have been sufficient to control these large elk populations (Houston 1982, based on Lahren 1976); (3) that predation by wolves and other predators was not essential for regulation of populations (Houston 1971; Cole 1971). Potential bases for rejection of the hypothesis included: (1) eruption of the elk population; (2) retrogressive plant succession; (3) competitive exclusion of previously sympatric ungulates; (4) population eruptions among sympatric ungulates; (5) a significant effect of natural predation on elk population fluctuations (Houston 1976).

Ecological theory provided additional reasons for testing the natural-regulation hypothesis. Caughley (1981) pointed out that culling to prevent overgrazing, especially during a population eruption, would weaken the system's feedback mechanisms and could delay the ultimate equilibrium between ungulates and plants. He argued further that culling could destabilize the system.

Some studies in the 1960s and 1970s supported the natural-regulation hypothesis. Cayot, Prukop, and

Smith (1979) concluded from historical photographs and literature that most of the traditional winter range seemed intact and that vegetative conditions on zootic climax sites were natural. Barmore (1980) observed after his northern range field studies (1964–1967) that "vegetation on the winter range has either changed little since primeval times or measured changes primarily reflect factors other than natural impacts of native ungulates." Houston (1982) attributed the decline of sagebrush on the antelope winter range to removal of heavy livestock grazing, and that of willow to drier climate. He found no real evidence for widespread soil erosion and surmised that fluctuations in abundance of perennial grasses were mostly the result of precipitation variability.

Peek (1980) concluded that a test of natural regulation in Yellowstone and the existence of a natural zootic climax vegetation could not be realized as long as fire and wolves were excluded from the system. Kay (1984), however, judged that elk in Yellowstone were not being naturally regulated because he felt that willow and aspen declines were evidence of retrogressive succession and because the elk population had not stabled even in the 1980s. Kay (1987) also argued that since no experimental control for the natural-regulation experiment had been identified, the hypothesis was not falsifiable.

RANGE MANAGEMENT VIEWS

When President Theodore Roosevelt first recommended scientific management of Yellowstone elk in 1915, the science of range ecology was just emerging (Barnes 1913). Range science arose out of necessity after decades of open range livestock exploitation. Natural revegetation of degraded range lands was studied on the bases of plant growth requirements and life histories (Sampson 1914). Concepts of a natural succession of plants toward a climax equilibrium were developed (Clements 1916), and these concepts were implemented to determine the degree to which grazing had caused retrogression from a presumed equilibrium state (Weaver and Clements 1938; Dyksterhuis 1949).

Although succession-based classification may measure departure from theorized climax equilibrium, it does not necessarily provide a relationship between current stocking rate and the direction or rate of departure (trend). Determination of overgrazing is based on observing the effects of stocking rate on range trend, as determined through trial and error (grazing trials). Stocking rates are designed to achieve a balance between retrogressive effects of grazing and natural tendencies of succession toward climax (Stoddart and Smith 1955).

These concepts of overgrazing can be difficult to implement in the context of the natural-process mandate for national parks. First, such concepts presume that an ideal balance between vegetation and herbivores will be maintained by human control. If climate change shifts the appropriate balance, the manager must try to adjust stocking rate. Human mis-manipulation of stocking rate may result in retrogression or range deterioration, which has no parallel in natural systems. Therefore, as stocking rate is not truly within human control in a natural system, this concept of overgrazing is ambiguous. Second, these concepts assume that the plant–herbivore equilibrium will always shift continuously and reversibly. As Westoby, Walker, and Noy-Meir (1989) have argued, this may not be a valid assumption. A third problem is that there is no allowance for temporary, but natural, imbalances that arise from imperfect adjustments of herbivores to changes in climate and vegetation.

INFLUENCE OF POPULATION AND COMMUNITY ECOLOGY

While the term *carrying capacity* was used by early range managers in reference to an appropriate stocking rate, ecological usage is more accurately traced back to Thomas Malthus's work in 1798, and Pierre-François Verhulst, who in 1838 formulated the logistic population model with a parameter (K) representing the maximum sustainable population. This theory led to the concept of intrinsic balance between the size of a consumer population and its food resources (Nicholson 1933). Nicholson argued that the controlling factor on population must ultimately be some process that acts proportional to population density, particularly by increasing competition for limited food. Mathematical analysis (Lotka [1924]; Volterra 1926) predicted that damped cyclic population fluctuations or stable limit cycles would occur about a theoretical equilibrium between predators and prey. The mathematical conditions leading to stable oscillations, dampened oscillations, or divergent oscillations in predator–prey systems were graphically developed by Rosensweig and MacArthur (1963). Equilibrial predator–prey theory significantly influenced the formulation of the Yellowstone natural-regulation hypothesis. Caughley's (1970, 1976) equilibrial analyses of ungulate population eruptions following their introduction into new habitat predicted damped oscillations resulting in a new equilibrium, with subsequent minor eruptions due to disturbance. Sinclair (1977) found this body of theory useful in his studies of population control in African buffalo following release from Rinderpest disease. Caughley's eruption model seemed relevant for Yellowstone because of the potential effect of release of elk from decades of artificial regulation.

An earlier, different school of thought (Uvarov 1931) theorized that climate ultimately controls population size, but acceptance of this theory waned as Nicholson's (1933) hypothesis was more widely embraced (Krebs 1972). An accumulation of empirical data later led Andrewartha and Birch (1954) to support a climate-control theory once again. The new theory proposed that population sizes could be determined primarily by extrinsic abiotic controls affecting the time that growth rate remains positive, and by density-independent mortality.

POST-NATURAL REGULATION ECOLOGY

Using equilibrial predator–prey theory, Noy-Meir (1975) found that range vegetation could be forced to extinction, achieve a low-production equilibrium with livestock, or achieve a high-production equilibrium with livestock, depending on the responses of plant growth and herbivore intake to plant abundance. Sudden transitions from the high to the low equilibrium were predicted, and these have since been interpreted in the light of catastrophe theory (May 1977). Holling (1973) and Peterson, Clark, and Holling (1979) developed a theory of multiple stability domains. As long as a system remains in a given stability domain, it will tend to move toward the equilibrium in that domain. Shifts among the domains (catastrophes) result in new equilibria. The theory also allowed for continual shifting of domain boundaries due to processes of natural selection. Caughley's models also recognized multiple stability domains (Caughley 1976, 1979). Walker et al. (1981) found multiple stability domains in analyses of savanna grazing systems. Multiple equilibrial (catastrophe) theory has recently been suggested as one explanation for sudden transitions among vegetation states (Westoby, Walker, and Noy-Meir 1989). These authors maintain that it is best to acknowledge the likelihood of such changes, and to identify the sets of conditions or rules that govern the transitions.

An evaluation of the evidence needed to judge ecological stability (Connell and Sousa 1983) indicated a continuum of dynamic variability, with no clear boundary between equilibrial and nonequilibrial systems. The authors concluded that there were few examples of stable periodic oscillations, and no evidence of multiple stability domains. They suggested that long-term persistence with bounded stochastic variation was a more meaningful concept than stability about an equilibrium point.

A more recent theory is that many nonlinear feedback systems exhibit chaotic behavior (Gleck 1987). Quite different system trajectories may result from small differences in the initial state of the system. Chaotic behavior may also be induced by strong periodic forcing (for example, climatic oscillation). Predators and prey may exhibit seemingly unpredictable dynamics about an underlying "strange attractor" (Schaffer and Kot 1985). Although populations fluctuate chaotically, the dynamics are still confined to the attractor domain.

Equilibrial assumptions have come under scrutiny because abiotic density-independent population controls are often more significant than biotic interactions (Weins 1977, 1984). Weins suggested that is a gradient from nonequilibrium to equilibrium systems spans the range from climatically variable habitats, which are unsaturated with competing organisms to predictable habitats, which are nearly saturated with competing organisms. Ellis and Swift (1988) argued that assumptions of strong density-dependent feedback between livestock and plants, and resulting equilibria, have often resulted in ineffective or adverse range-management policies. They found that periodic drought inevitably reduces plant and herbivore populations irrespective of density, but that compensatory response mechanisms promote endurance, recovery and long-term persistence.

A thorough review (DeAngelis and Waterhouse 1987) has shown that simple deterministic equilibrial models do not sufficiently explain the instabilities caused by nonlinear feedbacks and time lags in biological interactions, stochasticity and density-independent effects, and forcing by fluctuating environments. Persistence under nonequilibrium may be facilitated by herbivore movement from grazed to ungrazed areas, or by an ability of plant populations to survive at low densities (DeAngelis and Waterhouse 1987) or as an ungrazeable reserve (Noy-Meir 1975).

Nonequilibrial concepts are relevant to overgrazing in Yellowstone for several reasons. First, elk populations may be affected by density-independent variables, and by climate in particular. Winter severity affects elk (Houston 1982) and bison (Meagher 1973, 1976). Exceptionally severe winters (for example, in the mid to late 1800s, 1919–1920, 1989–1990) or mild winters (for example, 1986–1988) may cause large shifts in the number of animals per unit of plant production. Climate may act directly, or it may modify effects of density dependence (Sauer and Boyce 1983). Elk populations were affected by climate only when near carrying capacity (Picton 1984). Second, short-term climatic changes determine forage availability. Long-term climate and fire histories may have caused long-term changes in vegetation species that are not limiting to elk (or involved in density-dependent feedback) but nevertheless heavily utilized by elk (that is, browse). Third, time-lags in herbivore responses to sudden decreases in plant growth are possible; for example, drought may have reduced the ability of plants to withstand grazing in 1919–1936, before elk numbers declined. Finally, migration patterns are labile rather than immutable (Meagher 1989); increases in use of certain areas therefore may cause localized, but significant vegetation changes.

When the Yellowstone natural-regulation hypothesis was formulated, local seasonal movements were known to be important as a means of regulating animal density in relation to local spatial and temporal variability of plant resources. An ecologically complete habitat thus "provided contingencies for ungulates to obtain food and maintain relatively stable populations in variable and periodically harsh environments" (Cole 1971). Further, "interspersion of different habitats" provided a carrying capacity that was "greater than the sum of the parts" (Cole 1969, 1971).

Stable equilibrium states should not be viewed as a fundamental property of ecological systems except by extrapolation to large spatial scales (DeAngelis and Waterhouse 1987). As spatial scale increases, more local instabilities are averaged, dampened, or compensated for—the idealized level of stability may be achieved only at large spatial scales. Brown and Allen (1989) similarly pointed out that although negative effects may accrue to individual plants, effects at community or ecosystem levels may be neutral or positive.

Now ecologists hypothesize that persistence of small-scale ecosystems may depend on the states of and interactions with surrounding small-scale systems to achieve stability at the larger scale. Although intermixing of regional herds in the Yellowstone-Teton region may normally be minimal (Cole 1969; Houston 1982), infrequent local population increases can result in dispersion. It may become advantageous for individuals to avoid competition through emigration. Thus we might posit that the northern range plant–herbivore system is nonequilibrial, but that the larger scale-system of regional herds as a whole is stable.

The question of whether herbivore populations are food limited or predator controlled has not been resolved. This question is critical to the natural-regulation hypothesis, which assumes that food limitation is critical, and predation an unnecessary adjunct (Cole 1971). Food seems to limit herbivore populations in many grazing ecosystems (Bobek 1977; Sinclair 1977; Sinclair and Norton-Griffiths 1982; Sinclair, Durbin, and Borner 1985; Fryxell 1987), but predators seem to be more limiting in other systems (Caughley 1976; Smuts 1978; Bergerud, Wyett, and Snider 1983; Messier and Crete 1985; Borner et al. 1987; Fryxell, Greever, and Sinclair 1988). Multiple equilibrium theory predicts that herbivores can be held near a lower steady state by predation, but that if herbivores escape predator control, they become limited instead by food at a higher equilibrium. Predators may hold prey into the lower "predator pit" (Walker and Noy-Meir 1982; Messier and Crete 1985), but periodic eruptions may occur if herbivore intrinsic rates of increase are high and if herbivore reproduction responds rapidly to favorable climatic variation.

Whether predators do, in fact, control large mammals is a topic of debate at present (Sinclair n.d.; Bergerud, Wyett, and Snider 1983; Messier and Crete 1985). Evidence of true regulation seems to be lacking (Sinclair n.d.). Yet there is some supporting evidence. Bear predation on newborn caribou *(Rangifer tarandus)* (Singer 1986), moose (*Alces alces*) Franzman, Schwartz, and Peterson 1980), and elk (Schlegal 1976; Singer and Harting unpubl. data) can be significant. Unregulated wolf increases coupled with severe winters and in some cases harvesting by man have resulted in decreased ungulate populations (Gasaway et al. 1983; Bergerud, Wyett, and Snider 1983; Messier and Crete 1985). Finally, significant inverse relations have been observed between wolf density and caribou recruitment rates (Bergerud 1988).

COMPARISON OF DIFFERENT HYPOTHESES RELEVANT TO OVERGRAZING

A comparison of the concepts of overgrazing employed by an idealized range manager, a wildlife manager, the Caughley model (Caughley 1970, 1976, 1979), and by the Yellowstone natural-regulation hypothesis (YNRH) (Houston 1971; Cole 1971) illustrates the effects of varying underlying assumptions and management objectives on assessments of overgrazing (Table 15.1). We also consider what might be termed the persistence model, which emphasizes population persistence in the face of natural instability. This model considers the effects of climatic variation, intrinsic population instability, and spatial scale (Connell and Sousa 1983; DeAngelis and Waterhouse 1987; Ellis and Swift 1988; Westoby, Walker, and Noy-Meir 1989). We will consider only the effects induced by herbivory. The direct effects of climate and fire on vegetation are not considered, and none of the

Table 15.1 Comparison of Yellowstone's natural-regulation experiment with other concepts of overgrazing

	Concept Employed to Determine Overgrazing				
Ecological Observation	Range Manager	Wildlife Manager	Natural Regulation	Caughley Model	Persistence Model
Effects on plant (standing crop and production)					
Reduced vegetation biomass	accept	accept	accept	accept	accept
Reduced vigor of preferred species (flower no., stem ht.)	accept	accept	accept	accept	accept
Reduced primary production	limited	limited	limited	limited	limited
Heavy browsing, severely reduced growth of shrubs and plant death	cond.	reject	reject	cond.	cond.
Plant species shifts (deaths of some individuals of some species)					
Zootic climax	rej.–n.c.p.	cond.	accept	accept	accept
Zootic climax					
(a) herbivore production maximal	accept	cond.	reject	accept	reject
(b) herbivore production submaximal	reject	reject	reject	accept	reject
Trend of declining range condition					
(a) irreversible	reject	reject	reject	reject	reject
(b) transient, anthropogenic	reject	reject	reject	cond.	reject
(c) transient, natural	rej.–n.c.p.	accept	rej.–n.c.p.	accept	accept
Extinction of a plant species	cond.	reject	reject	reject	reject
Effects on ungulates					
Eruption and re-equilibriation after release from artificial control					
(a) predators can control herbivores but they are absent	rej.–n.c.p.	reject	rej.–n.c.p.	accept	reject
(b) predators cannot control herbivores	rej.–n.c.p.	accept	accept	accept	accept
Immigration or reduced emigration					
(a) anthropogenic	rej.–n.c.p.	cond.	rej.–n.c.p.	accept	reject
(b) nonanthropogenic	rej.–n.c.p.	cond.	rej.–n.c.p.	accept	accept
Competitive displacement of other ungulates	accept	reject	reject	cond.	cond.
Submaximal size, health, and fertility of individual herbivores	reject	reject	accept	accept	accept
Effects on soils					
Increased runoff, reduced infiltration	reject	reject	reject	limited	limited
Increased erosion	reject	reject	reject	reject	rare cond.

Note: Specific responses to changes in herbivory level or pattern may either be accepted or rejected relative to goals and assumptions that underlie each definition of overgrazing. Responses may also be accepted under certain conditions (cond.), accepted to a limited degree, or rejected because the model does not consider the event possible (rej.–n.c.p.).

criteria can be applied without removing their confounding effects. More specifically, changes in browse species abundance due to climate or fire, changes in range plant abundance and composition, and resultant soil erosion due to drought are presumed to be accounted for. Whether these affects have been disentangled in Yellowstone is beyond the scope of this paper.

1. *Reductions of vegetation biomass* by grazing would inevitably be accepted by the YNRH and all other models over intraseasonal time periods. Over longer time periods, a range manager would try to maintain maximum sustainable yield, which is achieved at a higher vegetation biomass than under food limitation.

2. *Decreased vigor of preferred grasses* induced by grazing would have to be accepted by the YNRH and all other hypotheses to some degree because this is the most sensitive indicator of grazing impact and can arise before reductions in basal area or production (Pond 1957; Mueggler 1975), and certainly before species shifts. Thus it may be a stable condition and an unavoidable consequence of light to moderate grazing.

3. *Reduced plant productivity* would be accepted by the YNRH and all others to a limited degree. A range or wildlife manager might find that animal production is maximized with a small reduction in plant

growth. Larger decreases in plant production could be acceptable to other hypotheses because stable equilibria between plants and herbivores probably occur significantly below submaximal plant production (Caughley 1979). Browsing that results in some highlining (browse lines) and some reduced tree and shrub growth, though often more apparent than herbaceous responses, would be similarly viewed.

4. *Plant mortality due to browsing* would not be accepted by the YNRH because this would represent a deviation from the assumed pristine plant–herbivore balance. If browse is heavily foraged, but is not the limiting food, then browse survival must depend on some other limitation of herbivore populations. A wildlife manager might reject browsing induced mortality to maintain other species that depend on browse for food or habitat. The Caughley model would accept some browse mortality if it is an inevitable consequence of equilibration. The persistence model would accept this nonequilibrial mortality if it is not a consequence of human activity. The persistence model would not necessarily require duplication of conditions in the late nineteenth century, because the plant–herbivore equilibrium may have shifted, may have been unstable, or may never have occurred.

Reductions in growth eventually lead to plant death and to replacement by other species that are more tolerant or better able to avoid herbivory. A resultant species composition that has naturally equilibrated with herbivores is a zootic climax (Daubenmire 1968; Cole 1971; Cayot, Prukop, and Smith 1979). If the equilibrium composition is human induced such as through disruptions of migration patterns, it may be viewed as a zootic disclimax (Beetle 1974).

5. *A zootic climax* would be acceptable to the YNRH and most other models. The concept of a zootic climax has no meaning for a range manager because any equilibrium that is attained is the result of human manipulation. A wildlife manager might find a zootic climax acceptable, but not if it results in submaximal herbivore production or nondesired habitat quality.

6. *A zootic disclimax* would be rejected by the YNRH because it is unnatural. A disclimax would be accepted by a range manager, provided the new equilibrium does not decrease herbivore production. The wildlife manager would likely reject a disclimax if it conflicted with other management objectives, and he or she would clearly reject it if it reduced game productivity. The Caughley model would find a disclimax tolerable because it does result in re-equilibration. The persistence model would reject disclimax in the spirit of natural-process preservation.

7. *An irreversible trend* toward vegetal denudation due to grazing would be unacceptable to all the models, including the YNRH (Houston 1976). *A human-induced, transient (reversible) trend* in species composition would be rejected by all the models except the Caughley model, which might accept this if the trend was actually reversed or stabilized. *A natural transient change* in species composition brought about by herbivory is not considered possible by the YNRH because there should be no natural grazing-induced departures from equilibrium. Transient trends are acceptable to the Caughley model, if they are part of re-equilibration. The Caughley model also allows for minor ungulate suberuptions that must produce transient vegetation trends. A natural transient decline might be accepted by the persistence model, if an equlbrium is ruled out.

8. *Plant species extinction* would be unacceptable to any management trying to sustain the integrity of natural systems. This might exclude some strictly production oriented range managers. Even this criterion may be deemed arbitrary in very rare cases, however, because species extinction is also a natural process. Species disappearance from local areas may also be a rare natural process, as range shifts have certainly been documented over paleoecological time.

9. *Herbivore population eruption.* The YNRH assumes no predator control of herbivores, so an eruption due to lack of predation would be considered impossible. The YNRH also assumes that eruptions should not occur in populations that are at a stable equilibrium with an ecologically complete habitat (Houston 1976). Range managers would not consider release from artificial control. Wildlife management would probably view an eruption as a sign of ineffective management for a stable system. The Caughley model would accept an eruption followed by re-equilibration. The persistence model would not accept an eruption due to lack of predation because the new equilibrium would be unnatural. If, however, predator control is unlikely, then the persistence model would allow that an eruption could be a form of natural instability.

10. *Herbivore immigration or reduced emigration.* Acceptance would depend on whether these changes in movement were human-induced. The YNRH does not consider natural variability in movement patterns. The YNRH also assumes that movement patterns are not affected by humans, so there should be no artificial concentrations along park boundaries (Houston 1976). Range managers, of course, would not accept any uncontrolled animal (livestock) movement in or out of the system. Acceptance by wildlife managers would depend on effects on plants and other game. The Caughley model would

accept a change in herbivore movement if it is accompanied by gradual system re-equilibration. The persistence hypothesis accepts altered movement only if it can be explained in terms of natural variability. The persistence model might accept, for instance, an immigration due to natural vegetation decline in another grazing area.

11. *Competitive displacement of sympatric ungulate species* would be unacceptable to equilibrial views, including the YNRH (Houston 1976), because concepts of equilibrial community structuring through competition and niche differentiation would be violated. Communities may also be structured by predation (Sinclair 1984), but this would not be considered by the YNRH. A range manager might find competitive displacement acceptable provided the displaced animals were of no potential use. The wildlife manager might reject competitive displacement because he or she is probably trying to maximize diversity and minimize fluctuation. The Caughley model would accept a community restructuring if it is part of reequilibration. The persistence hypothesis would accept competitive displacement if it results from natural nonequilibrial processes.

12. *Smaller, thinner, and less healthy ungulates* would be accepted by the YNRH and the Caughley hypotheses as an inevitable result of food limitation. These two would also recopize that this may be the effect of climate on carrying capacity. The persistence model would also allow that this may result from climatically induced disequilibrium. The persistence model, however, also allows for the possibility of predator control, in which case food stress would be unacceptable. Reduced herbivore production would be unacceptable to wildlife or range managers.

13. *An increase in runoff* would reflect change and constitute departure from equilibrium. This would have to be determined by establishing the level of runoff that occurs at plant–herbivore equilibrium, which might include some grazing-induced runoff. Increased runoff would be unacceptable to all but the Caughley and the persistence model. These two would accept transient changes during re-equilibration and natural disequilibration, respectively.

14. *Accelerated erosion* due to grazing would represent departure from equilibrium and would be rejected by all equilibrial hypotheses. The Caughley hypothesis would probably find increased erosion unacceptable because this would be evidence that feedback mechanisms were unsuccessful in preventing system degradation. A very limited increase in grazing-induced erosion would be accepted by the persistence model if rare and extreme climatic events increased susceptibility to grazing.

The possibility that man has disrupted a persistence mechanism (migration) at a larger scale than Yellowstone has been a concern since the inception of overgrazing concepts in Yellowstone and long before the natural-regulation experiment. To establish this as a valid cause of overgrazing would require firm support of the hypotheses that emigration has been inhibited, that immigration has increased, that nondisrupted movements once enhanced persistence, and that disrupted movements now endanger ecosystem persistence. Arguments that some or all wintering grounds were formerly outside the park only shift the location, not the fact that populations are somehow naturally controlled. Whether animals winter in or out of the park, some natural mechanisms that limit population size must be advanced. It is conceivable, however, that the overall ratio of winter to summer range has been altered by human activities outside of Yellowstone Park, as has been shown for the Jackson Hole herd (Cole 1969). In this situation, large elk population sizes may be supported by large summer range, but the limits are set by the size of the winter range. It has been suggested that there should be a balance between summer and winter range in an ecologically complete habitat (Cole 1971). The probability of perfectly stable winter–summer range ratio has not been calculated, however. The role of this ratio for plant-herbivore balance, the degree of its disruption, and the potential effects of such a disruption also have not been established in a quantitative fashion for the northern range.

If natural conditions have changed because of climate shift, long-term cycles of vegetation or fire, or non-equilibrial dynamics, then it may prove impossible to conclude that elk are either a natural or an unnatural part of the system based solely on their abundance just prior to human settlement. The assumption that the presettlement state (1800–75) was static and thus represents an appropriate experimental control cannot be accepted at face value; steady states are not necessarily expected in climatically variable environments or where biotic interactions are intrinsically unstable. If climate, fire, herbivores, and large predators, or interactions among them are changing, then there may be no control treatment for either a natural-regulation or an artificial-regulation experiment. Similar problems arise in control of confounding variables at large spatial scales and in comparisons with other land areas, even those abutting the park. To address overgrazing criteria that involve herbivore population responses or movements would require experimentation on a scale that is larger than the Yellowstone northern range. A single control treatment, much less replicate treatments, would be very difficult to find. Other methods of strong inference

(Platt 1964) may be necessary to attempt falsification of hypotheses of natural regulation.

A number of steps can be taken, nevertheless, to improve understanding of the northern range grazing ecosystem:

1. Falsifiable hypotheses should be added to the list proposed by Houston (1976). Some of the 1976 hypotheses may need refinement. It is important to define nonambiguous evidence for falsification. Hypotheses that can be falsified through manipulative experimentation on plants and soils are the least likely to be ambiguous. Paleobotanical records of plant species composition, paleoecological evidence of predator abundance, and long-term changes in climate and fire can be used to attempt falsification of hypotheses of past ecosystem dynamics. Such nonmanipulative analyses should rely, however, upon established understanding of ecosystem processes rather than correlative relations.

2. Hypothesized mechanisms of interaction between predators, prey and plants should be quantitatively formulated (for example, through numerical simulation) so they are clearly stated and related to other ecological processes. This formulation should consider (a) consistency with observed historical changes in range condition, (b) spatial effects and heterogeneity, particularly herbivore movements, effects of landscape heterogeneity on plants, and significance of balance between summer and winter range areas, (c) food quality and quantity distributions in time and in space, (d) ability of herbivores to endure periods of little or no food, (e) effects of food supply on herbivore mortality and natality, (f) effects of predation, (g) direct effects of climate on herbivores, (h) mechanisms of plant responses to herbivory, fire, and climate and interactions between these effects over both short and long temporal scales, and (i) effects of herbivory, fire, and climate on nutrient cycling among plants, soil and herbivores. Multiple approaches and sets of working hypotheses would be desirable (Platt 1964) and would provide an opportunity for corroboration among models.

3. Concepts of natural regulation should be refined to be consistent with current ecological knowledge. Formulation of a natural-regulation hypothesis generally appears to be an appropriate framework for detecting departures from natural processes that may be occurring on the northern range. The strict comparability to pristine conditions demanded by Cole (1971) and Houston (1976) is rigorous. However, certain of their assumptions about natural conditions need to be reexamined.

(a) Although it has yet to be verified theoretically or experimentally, the possibility that wolves, combined with other predators including native Americans, may have reduced herbivore numbers needs to be seriously considered rather than dismissed as unimportant.

(b) Natural regulation should not be predicated on an assumption that the upper winter range is a self-contained system (Houston 1976, 1982). Migratory elk from the northern herd apparently do not clearly separate into an upper and lower herd (Singer, unpubl.), although an elevational gradient of hunting pressure probably occurs.

(c) Natural regulation should not assume that density-independent effects only occur in unusually severe winters, or especially, that density-dependent mortality is necessarily more consistent, and therefore important (Cole 1971). Density-independent effects of winter severity on both mortality and reproduction should be considered. Hypothesized effects of variability in forage due to climatic fluctuation should be stated much more explicitly and precisely.

(d) The possibility that natural systems are not precisely regulated through homeostasis and therefore do not attain static equilibrium should be considered. Although the existence of an equilibrium would make it far easier to specify a management goal, this may be unrealistic.

4. There should be a short-term evaluation of current understanding of population dynamics, the role of predation, and responses of plants to herbivory in recent and ongoing studies in Yellowstone.

Conclusions should be related to historical claims of overgrazing.

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The Parker Transects Revisited—Long-term Herbaceous Vegetation Trends on Yellowstone's Northern Winter Range

Michael B. Coughenour[1]

Francis J. Singer[1,2]

James J. Reardon[2,3]

Abstract. A method to rapidly assess range condition and trend from line transect measurements of basal area and species composition was first applied in Yellowstone in 1958 in association with 2-ha grazing exclosures established on the northern winter range. Transects in and out of the exclosures were resampled in 1962, 1967, 1974, 1981, 1986 and 1989. Total live plant frequencies increased significantly both in and out of exclosures between 1967 and 1981 and decreased from 1981 to 1986. Changes in plant frequencies between 1958 and 1989 were much more significant than changes because of exclosure from grazing. Precipitation variability was the most probable cause of these temporal changes, as suggested by correlations between precipitation and plant frequencies. Exclosure had no effect on total live plant frequencies. The increase in total plant frequency until 1981 implied a converse decrease in bare ground. The decrease in plant frequency after 1981 was climatically driven, as evidenced by parallel changes outside and within exclosures. Dominant perennial grasses either maintained their relative abundance or increased until 1986. Forbs decreased in relative abundance until 1986 and increased after 1986 in response to drought. On the basis of these trends obtained by application of Parker transects, we conclude that elk winter grazing has not degraded the herbaceous component of the Yellowstone northern winter range. We recommend, however, that the Parker data be converted to basal area using a recent algorithm and that the technique be dropped in favor of less problematic methodologies.

Yellowstone National Park's (YNP) management of ungulates requires reliable long-term monitoring of trends in vegetation cover and plant species diversity (Beetle 1974; Cayot et al. 1976; Houston 1982; Coughenour and Singer 1991). Rangeland measurements date back to the 1930's on the northern range (W. H. Gammill, Range studies of 1939–41, Yellowstone National Park, unpublished data; R. L. Grimm, Range studies of 1935–38 and 1943–47, Yellowstone National Park, unpublished data). The park's current range monitoring program was initiated in 1958–62 (Denton 1958; Bergstrom 1962; Barmore 1980). Eight 2-ha exclosures were constructed in 1958 and 1962 along with a series of permanently marked Parker transects (Parker 1954; Francis et al. 1972). Vegetation intercepts within 1.9-cm loops were measured along the transects. These transects have constituted the principal long-term sampling program of herbaceous vegetation on the Yellowstone northern winter range.

The Parker transect methodology may be outdated and may be inadequate for detecting vegetation change. Parker transect data are obfuscated by differing effects of plant density, shape, size, and size class distribution of plants. As a result, Parker transects are difficult to interpret (Francis et al. 1972; Houston 1982). The data cannot be analyzed in a straightforward, mechanical manner (Francis et al. 1972; Risser 1984). Computer algorithms have only recently been developed to convert Parker frequencies to basal area (Brady et al. 1991; Cook et al. 1992). Parker transect frequencies often overestimate the most common plant species (Cook and Box 1961). A positive bias towards higher frequency in comparison to cover of smaller plants has been reported (Francis et al. 1972). Therefore, Parker frequencies should not be expected to be correlated with estimates of plant cover (Risser 1984). Parker frequencies showed poor relations with plant cover, herbaceous weight, and plant density (Francis et al. 1972). As a result, the

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[1] Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, Colorado 80523.

[2] Formerly of Research Division, Box 168, Yellowstone National Park, Wyoming 82190.

[3] Aerial Fire Depot, Box 6, Airport Terminal, Missoula, Montana 59802.

northern regions of the U. S. Forest Service dropped Parker transect readings in 1982 (D. Tyers, U.S. Forest Service, Gardiner, Montana, personal correspondence). Small sample sizes limit the power of statistical tests, particular for tests of individual species abundances. Species data have necessarily been pooled together to conduct statistical tests (Barmore 1980; Houston 1982). Yet, comments on YNP's ungulate management program have expressed concern over possible species increases or decreases because of possible excessive grazing of the range (Beetle 1974; Chase 1986).

The purpose of this investigation is to reexamine the Parker transect results. We report on more recent trends on Parker transects during 1981–89 which have not been reported following Houston's (1982) report. We attempt to correlate the plant frequency to weather and ungulate population trends. We also compare Parker frequencies to measures of plant cover and biomass from the same sites, and evaluate the Parker transect method.

Methods

Study Sites

The lower winter range study site was located below Mammoth and near the park boundary at Gardiner, Montana. Elevations of the lower winter range are 1,500–2,000 m. The growing conditions are relatively xeric. Precipitation averages 20 cm/year. Less snowfall, faster melting and wind removal of snow from the slopes relative to the upper winter range result in easy access to forage and high use by wintering elk.

The higher elevation (2,000–2,400 m) grassland study sites on the upper winter range were located near Mammoth, Blacktail Creek, Junction Butte, and the Lamar Valley. The upper winter range grasslands tend to be more mesic and more productive than those of the lower winter range; precipitation ranges from 30 cm/year at Mammoth to 55 cm/year at the Lamar ranger station.

Weather Data

Monthly precipitation data were obtained for Mammoth (YNP), Tower Ranger Station, Lamar Ranger Station, Gardiner, and Cooke City. Precipitation data were summarized by site and season. Fall included September–October. Winter precipitation included that in November–March. Spring included April–May. Summer included June–August. Precipitation from September of the preceding year through August of a given year was summed to yield water year precipitation because fall and winter precipitation are manifested in plant growth measurements the following summer. Precipitation for Gardiner was used for the lower winter range site whereas precipitation data for Mammoth, Tower, and Lamar were averaged for correlations with plant growth measurements made on the upper winter range.

Vegetation Sampling

Parker transects were established in 1957 and 1962 in conjunction with 2-ha grazing exclosures on the northern winter range (Barmore 1980; Houston 1982). Six exclosures were established on the four sites of the upper winter range and two exclosures were established on the lower winter range site. Transects were sampled in 1958, 1962, 1967, 1974 (Barmore 1980; Houston 1982), 1981, 1986, and 1989. The original intent of the method was to monitor trends in range condition, primarily by detecting changes in relative species abundances and changes in total vegetated soil surface relative to nonvegetated soil surface. The transects were part of the Parker three-step method: step one—establish transects and record data; step two—analyze the data; step three—establish permanent photopoints (camera location and azimuth) on the range. Permanent line transects 32.8 m (100 feet) in length were established. A 1.9-cm (3/4-inch) loop was lowered to the ground at 30.5-cm (1-foot) intervals, and contacts with plant tissues were recorded. Contacts were classified by species, litter, or type of abiotic material. Data comprised total contact counts for each species and material. Perennial grasses and forbs must have had their root crown within the loop to have been recorded. Transects were organized in paired clusters of one to three—but normally two, with one cluster inside and one cluster outside an exclosure. Thus, 2–6 transects were present per site with about half inside and half outside exclosures. Each cluster pair was selected to represent similar topography and soil. Fourteen clusters containing 29 transects were established inside and 9 clusters containing 18 transects were established outside exclosures. Transects within each pair were located on similar soils and topography. Overstory shrub data were also collected (i.e., shrubs with canopies well above the herbaceous vegetation layer) but these data were not used here because few shrubs were located on any of the transects. Results from a parallel belt transect survey (a better methodology for measuring large shrub abundance) are reported elsewhere (Houston 1982). Dwarf shrubs, however, were included in the analyses because their shoots were contained within the herbaceous stratum. Our conclusions are thus restricted to the responses of the predominantly herbaceous understory.

A repeated-measures two-way analysis of variance was performed with year and exclosure from grazing as main effects. Cluster means rather than transects were replications because transects within a cluster are nonindependent by definition and because the low number of transects per cluster (usually 2) prohibits accurate assessment of within-cluster variance. Repeated measures ANOVA was used because the same clusters were read every year. Thus, the analysis corrects for possible correlations of frequencies within a given cluster over time. A univariate repeated ANOVA used data from all sample years. Multivariate repeated ANOVA's were also calculated, but only the years 1974–89 could be included because of high numbers of missing values for clusters in earlier years. Exclosure effects were also tested with t-tests comparing means inside and outside exclosures in individual years. If variances were unequal, a t' statistic was used (Sokal and Rohlf 1981). Proportion data were transformed with the arcsine function before testing. Duncan's multiple range test was used to determine differences among yearly means.

The Parker transect data were correlated against seasonal, annual, and multiannual precipitation data. Data from inside and outside exclosures were pooled at each site for correlations on precipitation because of lack of significant exclosure effects (Barmore 1980; Houston 1982; this study).

Results

Total live plant frequencies (Fig. 1a) increased from 1967 to 1981 (Houston 1982) and decreased from 1981 to 1986, both inside and outside exclosures. Whereas the decrease from 1981 to 1986 reduced lower winter range frequencies to pre-1974 levels, upper winter range frequencies were greater in 1986 than in 1958–67. Lower winter range frequencies were consistently less than those on the upper winter range, probably as a result of a warmer, drier climate near Gardiner. Significant temporal changes occurred only between 1967–74 and 1981–86 (Fig. 1a). In comparison, elk numbers declined from 1956 to 1968, then generally increased from 1968 to 1988 (Fig. 1b).

ANOVA indicated *Koeleria macrantha* and *Poa* spp. were more abundant outside than inside exclosures (Table 1), however, an interaction existed between exclosure and year effects on *Poa* spp. However, t-tests indicated significant differences between inside and outside exclosure frequencies for *K. macrantha* in 1974 only ($P < 0.05$), with marginally significant differences ($0.05 < P < 0.01$) in 1986 and 1989 (Table 2). The exclosure effect on *Poa* spp. was limited to 1989, with a marginally significant effect in 1974. There were no significant differences in plant frequencies inside versus outside lower winter range exclosures (Tables 1 and 2), despite notable changes in elk population numbers (Fig. 1b). Data for means of plant frequencies in each cluster are provided in Appendix Tables 1 and 2 in this report to facilitate potential uses by others in the future.

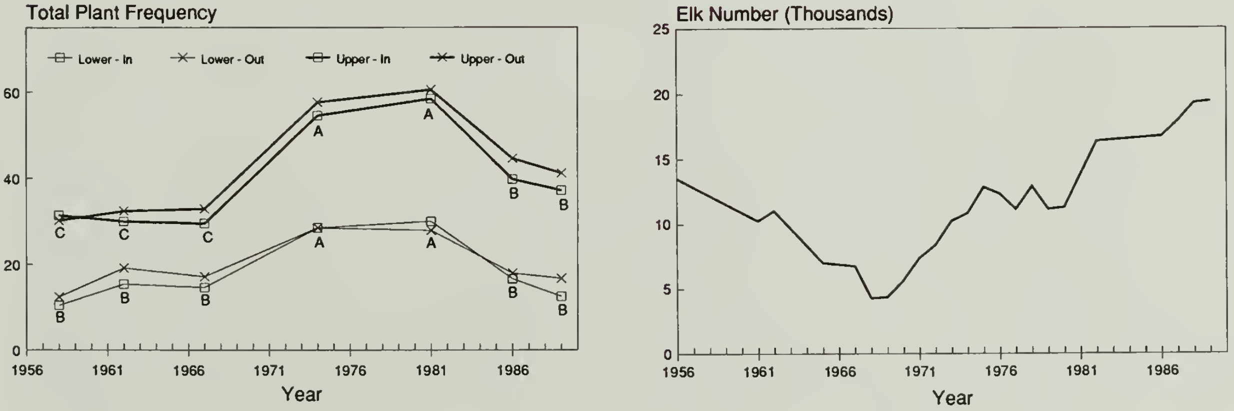

Fig. 1. (*a—left*) Total plant frequency on upper and lower winter range, inside and outside exclosures. There were no significant differences between frequencies in and out of exclosures. Means for years (upper or lower winter range) having the same letter are not statistically different ($P < 0.05$). (*b—right*) Elk numbers on Yellowstone's northern winter range.

Table 1. Significance testing using repeated measures ANOVA (univariate approach) for effects of year and exclosure.[a]

	Upper winter range			Lower winter range
Variable	Year	Exclosure	Year × exclosure	Year
Grass	***[b]			*[b]
Forb		***		m[b]
Dwarf shrub				**[b]
Agropyron spicatum				
Festuca idahoensis	***			
Koeleria macrantha	***	*		***
Poa spp.	***	*	*	**
Total	***			***
Grass (%)	**			
Forb (%)	**			***
Dwarf shrub (%)				m
A. spicatum (%)	m			
F. idahoensis (%)	***			
K. macrantha (%)		**		**
Poa spp. (%)	***	*	**	*

[a] No significant exclosure main effects or year × exclosure interactions on the low elevation winter range were evident.
[b] * = $0.01 < P < 0.05$; ** = $0.001 < P < 0.01$; *** = $P < 0.001$; and m = marginal, $0.05 < P < 0.10$.

Proportions of species and plant functional groups changed over time (Fig. 2). Grass proportion declined during 1958–62, then increased during 1974–81 and declined again during 1986–89. These changes were mirrored by an increase in the proportion of forbs 1958–62, a decrease in 1974–86, and an increase again in 1986–89. Dwarf shrub fraction did not change significantly with time. *Agropyron spicatum* fraction declined in 1958–62. *Festuca idahoensis* fraction increased in 1962–67 and 1981–86, but declined in 1986–89. *K. macrantha* fraction declined in 1958–67, increased in 1974–81,

Table 2. Total grass, forb, and dwarf shrub frequencies.[a]

	Grass		Forb		Dwarf shrub	
Year	In	Out	In	Out	In	Out
			Upper winter range			
1958	25.5(15.0)3	24.2(11.1)3	5.4(4.4)2	5.8(3.1)3	0.6(0.52)3	0.17(0.29)3
1962	19.6(5.7)8	22.4(8.9)5	9.8(4.5)8	9.9(4.5)5	0.69(0.88)8	0.0(0)5
1967	17.3(5.2)8	21.6(10.6)5	11.7(8.6)8	10.9(7.3)5	0.48(0.47)8	0.40(0.55)5
1974	34.1(5.9)10	41.3(10.4)7	19.4(6.3)10	16.1(4.4)7	0.96(1.6)10	0.21(0.29)7
1981	41.5(13.2)10	46.3(10.0)7	16.4(7.1)10	13.2(4.9)7	0.46(1.0)10	1.0(1.2)7
1986	30.9(9.5)10	35.0(8.0)7	8.8(4.0)10	9.4(3.6)7	0.02(0.06)10	0.18(0.24)7
1989	23.7(7.8)10	27.9(6.5)7	13.2(4.9)10	12.8(4.5)7	0.26(0.44)10	0.41(0.72)7
			Lower winter range			
1958	6.8(3.2)2	7.7(3.9)2	2.7(0.35)2	4.7(3.2)2	1.0(0.71)2	0.0(0)2
1962	9.2(4.6)3	11.2(6.1)2	3.8(2.7)3	5.5(0.49)2	2.6(1.8)3	2.5(1.9)2
1967	5.2(1.5)3	9.0(4.9)2	6.2(3.7)	36.7(0.35)2	3.3(2.5)3	1.5(2.1)2
1974	16.8(9.8)4	13.9(8.3)2	3.4(2.5)4	2.3(2.6)2	8.3(3.5)4	11.9(15.4)2
1981	17.8(6.2)4	18.5(17.7)2	3.6(3.6)4	1.6(1.2)2	8.5(1.9)4	7.9(10.4)2
1986	11.5(4.8)4	10.3(2.6)2	0.70(0.77)4	1.6(2.3)2	4.5(2.5)4	6.1(7.2)2
1989	6.0(4.0)4	5.9(2.9)2	5.2(5.5)4	8.5(4.6)	21.3(1.1)4	2.5(1.4)2

[a] Mean(standard deviation)*n*. Here, *n* is the number of clusters sampled each year. For these aggregate plant groups there were no significant differences between inside and outside exclosures (*t*-tests, each year). Units are hits/transect.

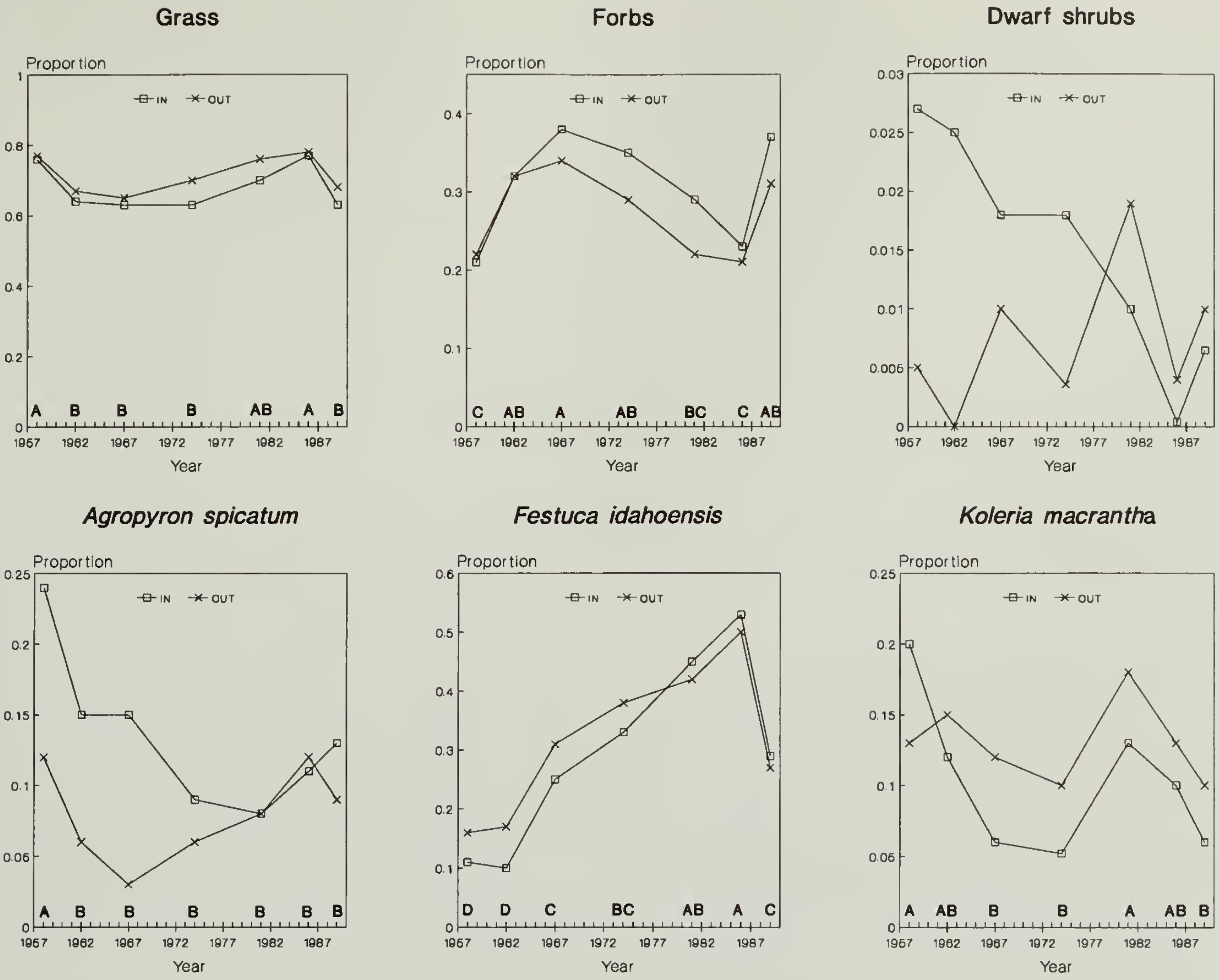

Fig. 2. Proportions of plant groups and major species in the Parker transect data from the upper winter range. Means for years with the same letter above the *X*-axis are not significantly different ($P < 0.05$). The single significant difference between exclosed and nonexclosed proportions in a given year was *Koeleria macrantha* in 1974.

and decreased in 1986–89. *Poa* spp. fraction declined 1974–81, but increased again in 1986–89.

Proportions changed in similar patterns over time on the lower winter range (Fig. 3). No significant changes in the proportion of grass over the years were detectable. Forb proportion declined significantly, however, from 1968 to 1972, and increased from 1986 to 1989. Dwarf shrub fraction increased significantly between 1958 and 1976. The fraction of *A. spicatum* did not change significantly as sample sizes were small relative to variance. *K. macrantha* increased from 1962 to 1976, from 1976 to 1981, then decreased from 1986 to 1989. *Poa* spp. decreased from 1976 to 1981, and increased from 1986 to 1989.

On the upper range, however, the fraction of *Poa* spp. was relatively more abundant outside exclosures in 1989. The fraction of *K. macrantha* was significantly greater outside the exclosure in 1974 only (*t*-test, $P < 0.001$). On the lower range it appeared that *A. spicatum* relative abundance had declined outside exclosures by 1989, however the difference was not significant in any test ($P < 0.1$). In 1989, *A. spicatum* was 0, 12, 24, and 45% of total plant hits in the four clusters inside and 0 and 7% of the two clusters outside the lower range exclosures (refer also to Appendix Tables 1 and 2 for individual cluster data).

The multivariate repeated measures MANOVA for 1974–89 yielded only slightly different results from Table 1. On the upper winter range MANOVA indicated significant year × exclosure effects on *A. spicatum* ($0.01 < P < 0.05$) and percent *A. spicatum* ($0.05 < P < 0.1$). The year × exclosure effects on *Poa* and percent *Poa* were marginal in MANOVA ($0.05 < P < 0.1$). On the lower range, MANOVA indicated no year effects on forb, dwarf shrub, percent forb, or percent dwarf shrub. A significant year × exclosure

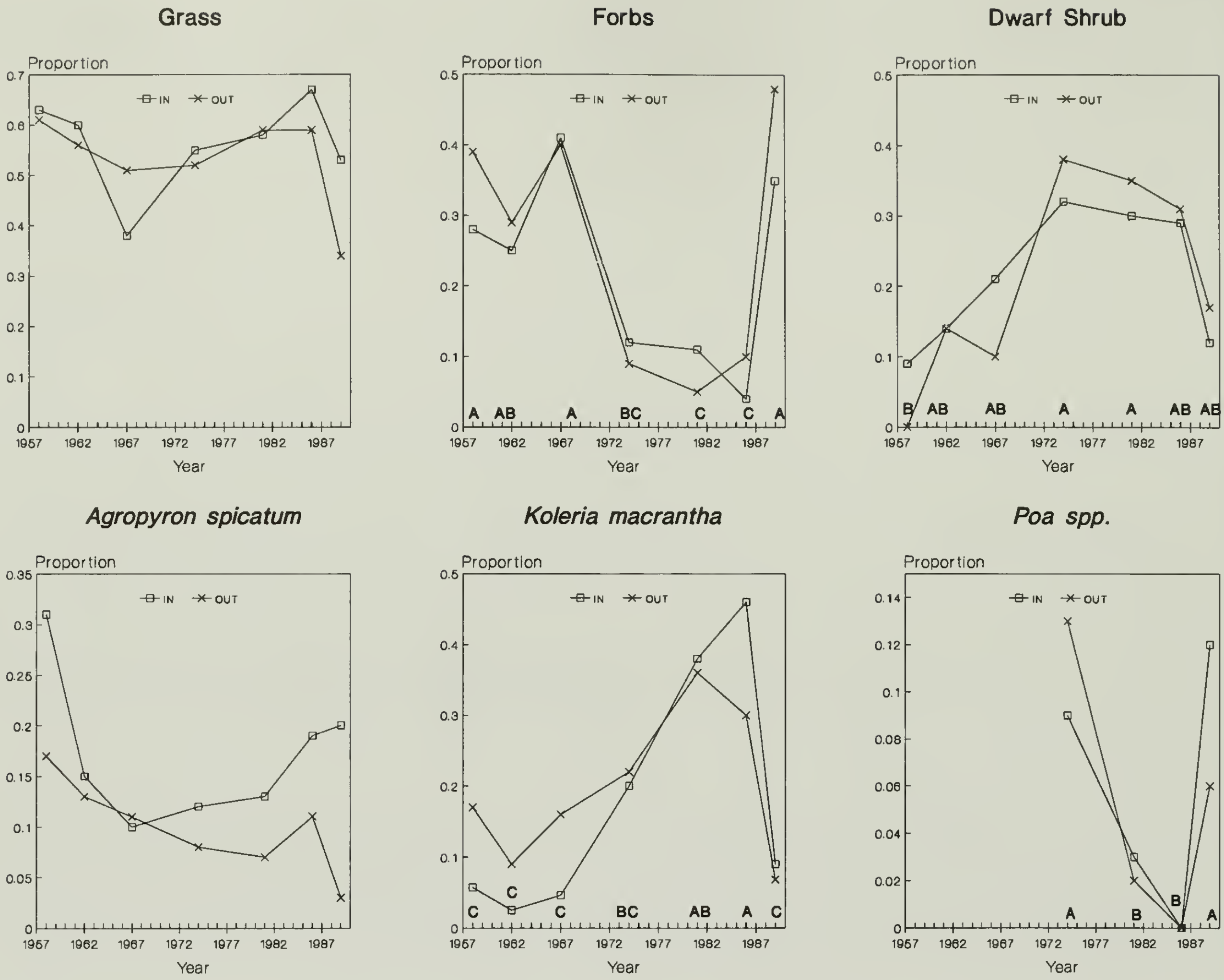

Fig. 3. Proportions of plant groups and major species in the Parker transect data from the lower winter range. Means for years with the same letter above the X-axis are not significantly different ($P < 0.05$). There were no significant differences between frequencies inside and outside exclosures in any given year.

effect on percent *K. macrantha* ($0.01 < P < 0.05$) was present.

Climatic causes of changes in total plant frequencies among years were explored with correlation (Table 3). Correlations were attempted between all vegetation variables and seasonal precipitation in the current year, the previous year, and the mean of all years since the previous Parker sample date. Only correlations that were significant at $P < 0.1$ are displayed in Table 3. On the upper winter range, *K. macrantha* was highly correlated with summer precipitation in the current year. The composition of percent grass versus forb was highly correlated with precipitation in the previous winter; wet winters favored grass over forbs. *F. idahoensis* was highly correlated with summer rainfall over the period since last sampling. Weaker correlations were observed between previous winter precipitation and *A. spicatum* and *K. macrantha*, previous summer rainfall and total grass, and period winter precipitation and dwarf shrub.

On the lower winter range, a significant correlation was observed between period spring rainfall and forb and dwarf shrub abundances (Table 3). Forbs were favored by wet springs whereas dwarf shrubs were disfavored. The percentage of forbs tended to be greater in years with wet springs; *A. spicatum* percentage was greater in years with wet winters in the previous year; grass percentage was greater if previous year's summer was wet and dwarf shrub was greater when fall of the previous year was wet.

Seasonal precipitation data for each year were examined to seek a finer resolution explanation for the rise in Parker frequencies between 1967 and 1974 (Fig. 4). There were no runs of unusually wet falls,

Table 3. Significant correlations with seasonal and total precipitation in the current year, the previous year, and the period between the previous sample date and the current sample date (3–8 years).[a]

Variable	Correlation coefficient (r)
Upper winter range	
Current year—summer	
Koeleria macrantha	0.82[b]
K. macrantha (%)	0.70[b]
Previous year—winter	
Agropyron spicatum	0.66[c]
K. macrantha	0.72[c]
Grass (%)	0.82[b]
Forb (%)	–0.81[b]
Period—summer	
Grass	0.69[c]
Festuca idahoensis	0.87[b]
F. idahoensis (%)	0.95[b]
Period—winter	
Dwarf shrub (%)	0.67[c]
Lower winter range	
Current year—spring	
Forb (%)	0.78[c]
Previous year—winter	
A. spicatum (%)	0.79[c]
Previous year—summer	
Grass (%)	0.65[c]
Period—fall	
Dwarf shrub (%)	0.67[c]
Period—spring	
Forb	0.84[b]
Dwarf shrub	–0.70[c]
K. macrantha	–0.74[b]
Forb (%)	0.90[b]
Dwarf shrub (%)	–0.82[b]

[a] In all cases $n = 7$.
[b] $P < 0.05$.
[c] $0.05 < P < 0.1$.

winters, or springs that would explain the increase. Summer 1968 was exceptionally wet; June and August were both wet and September was moderately wet.

Discussion

Responses to Climate

Changes in plant frequencies between 1958 and 1989 were much more significant than changes because of exclosure (Table 1). Climate, specifically precipitation, was the most probable cause of these temporal changes (Table 3). The marked increases in *F. idahoensis* on the upper winter range and of dwarf shrubs and *K. macrantha* on the lower winter range between 1967 and 1974 (Table 4) were most responsible for the large increases in total plant frequency over that period (Fig. 1).

A plausible explanation for the large increase in total plant frequency on the upper range between 1967 and 1974 was an increase in *F. idahoensis* in response to a favorable year for germination and seedling establishment. This year could have been 1968, when summer rainfall was far above normal (Fig. 4). A single favorable year for germination and establishment would, if not followed by drought, be followed by a steady increase in plant size. The combination of increased plant number and size could explain the increase in Parker frequency. The increase between 1967 and 1974 on the lower range site was in dwarf shrubs and *K. macrantha*. According to the correlations, these plants increase during relatively dry springs. Indeed, there were no wet springs during 1967–74.

Total plant frequency decreased between 1982 and 1986. This roughly paralleled a declining trend in precipitation. In particular, the spring of 1983 was dry, and this was preceded by a relatively dry winter. A dry spring also occurred in 1979, but this was preceded by a wet winter. The dry winter–dry spring pattern could have increased plant mortality in 1983. The dry years of 1987 and 1988 caused an insignificant decrease in frequencies 1986–89, but spring was moist in both years.

Plant community composition proved to be dynamic, rather than static, both inside and outside of the exclosures (Figs. 2 and 3). Changes in relative abundances of species and plant functional groups over time were likely the results of changing weather patterns over the period. Community changes included a decline in the proportion of *A. spicatum* 1958–62 on upper and lower ranges, along with an increase in proportion of forbs on the upper range and in dwarf shrubs on the lower range. The forbs observed here were mostly perennials. As such, their abundances depend on climatic events that affect germination, establishment, and survival. Changes in the abundances of long-lived perennial grasses probably affect the space available for forb and dwarf shrub establishment, as suggested by the inverse relations between forbs or dwarf shrubs and *A. spicatum*.

The increase in the proportion of *F. idahoensis* on the upper winter range over the years 1962–74 was accompanied by decreases in *A. spicatum* and *K. macrantha*, suggesting possible competition between dominant perennial grasses. Correlations suggested that competitive interactions between plant groups are altered by precipitation (Table 3). The percentage of grass was positively correlated and the

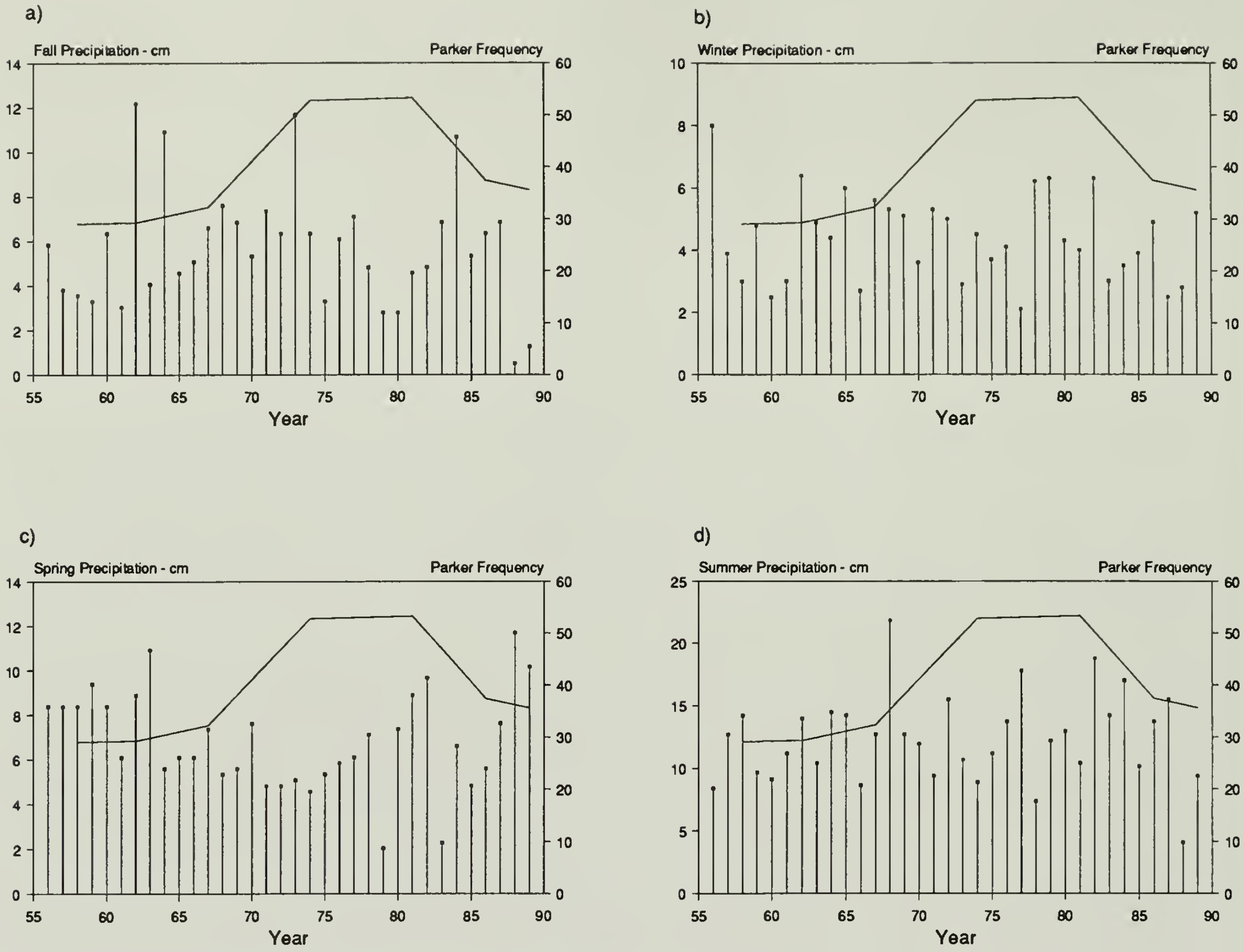

Fig. 4. Seasonal precipitation over the period in comparison to total plant frequency: (*a*) fall; (*b*) winter; (*c*) spring; (*d*) summer. Precipitation is displayed as bars, Parker frequency is displayed as a line.

percentage forb was negatively correlated with winter precipitation on the upper range, suggesting that wet winters shift the competitive balance towards grass. On the lower winter range, *K. macrantha* and dwarf shrubs generally decreased whereas forbs increased, and their correlations with spring precipitation were also opposite. The latter relations suggested that forbs may respond favorably to spring rainfall, and when they do, they become increasingly competitive with perennial grasses.

If climatic events are stochastic, and if plant community composition responds to these fluctuations, then the concept of a singular climax community composition becomes untenable. Rangeland plant community compositions may change in response to weather events and patterns, irrespective of grazing (Westoby et al. 1989; Coughenour and Singer 1991; Friedel 1991; Laycock 1991). Differences among species in their responses to climatic events inevitably cause changes in plant community composition. Temporal changes in composition may simply arise from secondary competitive interactions among plants. For example, a dry year may cause mortality of one perennial grass species, which provides an opportunity for establishment of another species given another climatic event.

Changes are sometimes momentous as environmental thresholds for various plant population events are crossed (Westoby 1991; Friedel 1991; Laycock 1991). Movements across thresholds may or may not be irreversible. There was no evidence for such shifts here. The changes that were observed here, however, point out that the long prevailing, steady-state climatic climax plant community of Clements (1916) should be thought of as dynamic, with responses to short term climatic fluctuations, as Clements originally discussed. Fortunately, an experimental control for the grazing treatment (inside exclosures) showed that plant

Table 4. Major grass species frequencies.[a]

Year	*Agropyron spicatum*		*Festuca idahoensis*		*Koeleria macrantha*		*Poa* spp.	
	In	Out	In	Out	In	Out	In	Out
Upper winter range								
1958	6.8(2.4)3[b]	3.3(.85)3[b]	4.1(6.8)2	5.1(4.5)3	5.4(3.8)3	3.8(1.2)3		
1962	4.9(3.5)8[b]	1.8(1.2)5[b]	3.3(3.8)8	5.8(5.3)5	3.4(3.5)8	4.5(2.6)5		
1967	4.4(6.4)8	1.0(.35)5	6.8(4.4)8	10.6(5.8)5	1.6(2.1)8	3.2(1.6)5		
1974	5.0(3.4)10	3.2(1.8)7	18.6(10.1)10	22.4(7.2)10	2.7(2.1)10[c]	5.9(2.2)7[c]	3.6(1.7)10[b]	5.9(3.2)7[b]
1981	4.1(3.9)10	4.8(2.3)7	28.6(18.8)10	25.3(9.0)7	6.7(4.8)10	11.8(8.0)7	0.62(1.1)10	0.0(0.0)7
1986	4.2(4.4)10	5.3(3.2)7	21.8(11.9)10	22.3(6.4)7	3.1(2.7)10[b]	5.9(3.4)7[b]	0.18(0.33)10	0.0(0.0)7
1989	4.9(3.9)10	3.6(2.4)7	12.1(9.4)10	11.0(3.7)7	2.3(1.9)10[b]	4.4(3.0)7[b]	0.65(1.3)10[c]	4.6(5.2)7[c]
Lower winter range								
1958	4.0(5.6)2	2.2(3.2)2			0.75(1.1)2	2.2(3.2)2		
1962	1.8(1.6)3	3.0(4.2)2			0.80(0.87)3	2.0(2.8)2		
1967	1.3(1.1)3	2.1(2.9)2			0.67(0.76)3	3.0(4.2)2		
1974	3.8(3.3)4	2.0(2.8)2			5.3(1.8)4	5.6(6.5)2	2.5(0.6)4	3.9(2.9)2
1981	4.5(5.2)4	2.2(3.2)21			1.0(4.7)4	11.2(10.9)2	1.0(0.7)4	0.8(1.0)2
1986	3.6(3.4)4	1.8(2.5)2			7.7(2.0)4	5.5(2.1)2	0.0(0)4	0.0(0)2
1989	2.4(2.7)4	0.8(1.1)2			1.0(0.82)4	1.1(0.14)2	1.6(1.4)4	1.0(0.0)2

[a] Mean(standard deviation)*n*. Here, *n* is the number of clusters sampled each year. Significant differences between inside and outside exclosures were tested with *t*-tests in each year. Units are hits/transect.

[b] $0.01 < P < 0.05$.

[c] Marginal, $0.05 < P < 0.1$.

community changes that otherwise might have been ascribed to grazing were, instead, the result of climate.

Responses to Elk Grazing

The ANOVA indicated that there was more *K. macrantha* and *Poa* spp., outside exclosures in certain years. Similarly, the only grazing related differences detected by Barmore (1980) were slightly, but significantly higher graminoid frequencies outside exclosures and this was interpreted as spurious. There were no significant exclosure effects on frequencies on the lower winter range (Table 1).

The only significant exclosure effects were increases in *K. macrantha* and *Poa* spp. the result of grazing, and consistent parallel changes in frequencies inside and outside exclosures, indicating that elk grazing has not impaired herbaceous plant growth on the northern winter range in spite of fluctuations in elk numbers (Fig. 1b). Houston (1982) also concluded from his analysis of Parker transect data 1958–74 that grazing had no significant effect on perennial grasses, forbs, shrubs, total perennial vegetation, bare ground, or litter. Pavement decreased inside exclosures, probably because of increases in dead plant material. Direct sampling of plant biomass (Coughenour 1991) also revealed no differences in total root biomass inside versus outside exclosures. No differences in aboveground plant biomass inside versus outside were observed in 1987. Grass biomass was reduced outside exclosures in 1988, but elk remained on the winter range longer that spring (D. Vales, University of Idaho, personal communication). Frank (1991) documented increases in plant growth due to grazing.

Two differences in species composition were observed between the inside and outside of the upper winter range exclosures. *K. macrantha* and *Poa* spp. were relatively more abundant outside exclosures, but only in certain years. *K. macrantha* was significantly more abundant (relative and absolute) outside exclosures only in 1974. *Poa* spp. was more abundant outside exclosures only in 1989. These differences in composition are limited but positive responses to grazing (Figs. 1–2).

On the lower winter range there seemed to be progressively decreasing relative abundance of *A. spicatum* outside exclosures, particularly from 1986 to 1989 (Fig. 3). Variances among clusters, however, were high, the number of clusters was small, thus the differences were not significant. The trend of increasing divergence between relative *A. spicatum* abundances in and out of exclosures was most pronounced during the drought year of 1988. Elk used the lower winter range heavily during the severe winter of 1988–89 when much of the herd died. The combined effect of drought and increased elk use could have been particularly stressful, but the response was inconsistent among clusters.

A widespread method for assessing rangeland condition is that derived from Dyksterhuis (1949). The method evaluates condition with respect to changes in cover of plant species which typically either increase or decrease in response to overgrazing. Most often, overgrazing will cause decreases in dominant perennial grasses, increases in weedy forbs and increases in bare ground. On the Yellowstone winter range, total plant frequency increased until at least 1981. By definition, this was necessarily accompanied by a converse decrease in bare ground. The decrease in plant frequency after 1981 was climatically driven, as evidenced by parallel changes outside and within exclosures. Dominant perennial grasses either maintained relative abundance, or increased. Forbs decreased until 1986, and increased after 1986 in response to declining grass during drought. On the basis of these trends, we cannot conclude that elk grazing has degraded the Yellowstone northern winter range.

Elk use the winter range during a time of year when most plants are dormant and after seasonal production has already occurred. Thus, elk grazing would not be expected to have large effects on the plant community except through responses to trampling, removal of dead leaves, and increased rates of nutrient recycling (see also Coughenour 1991). Although herbaceous plants are largely snow-covered, herbaceous plants comprised 90% of the diet of elk wintering in 1985–99 (Singer and Norland 1991).

The Method

Parker transect data primarily reflect, but overestimates, basal cover rather than aboveground standing crop; the protocol requires that plant bases are within the sampling loop. Basal cover is primarily affected by the number of plants and the size of the perennating root crown of bunch grasses. Frequencies of forbs are more strongly affected by the numbers of plants and their stem diameters. Basal area of perennial bunch grasses changes more slowly than, and is not necessarily correlated with, annual variations in peak aboveground standing crop. For example, a large basal area may have accumulated because of previous wet years, but a subsequent dry year may cause low grass production without reducing basal area. Plant productivity is determined by plant height and leaf length as well as by basal area.

A problem with the technique is that it is influenced by plant size and plant numbers in different ways. The method is biased towards higher frequencies if plants have small basal area (Hutchings and Holmgren 1959; Smith 1962; Francis et al. 1972). Measurements are also affected by the shape of plants and the pattern of their distribution, such that there is positive bias towards plants with noncircular shapes (Hutchings and Holmgren 1959). Even with constant basal area then, changes in plant size and shape influence Parker frequencies. Thus, any changes in plant form because of grazing or climate could confound interpretation. If plants were larger in an exclosure for example, the measured grazing effect would be diminished because the method is biased towards smaller plants.

Insufficient sample size may be the most serious limitation of the method. Each half of a cluster pair in YNP is comprised of one to three transects or 100–300 hits on an exclosed/nonexclosed treatment at a site. The number of 100-ft transects required to measure dominant grasses at 95% confidence within 10% of the mean can vary from 2 to 68 (Johnston 1957). Smith (1962) concluded that 200–3,400 hits (loops) are required to establish 95% confidence intervals that are within 10% of the mean, depending on plant abundance. Everson et al. (1990) reached a similar conclusion for plant frequency hits. They estimated that 1,200 hits of a Tidmarsh wheel (Everson et al. 1990) were required to detect changes of plant species comprising 5% or more of the community within 90% confidence intervals that are +20% of the mean. Pooling of species improves accuracy statistically (Smith 1962). Because of limited sample sizes, Barmore (1980) and Houston (1982) were forced to pool plant species frequencies for YNP to conduct statistical tests. Unfortunately, pooling of plant species represents a loss of information.

Plant frequencies measured with the Parker transect method in Yellowstone had high variances. This problem is partly because of small numbers of transects, but also from landscape heterogeneity. Stratification of samples on the landscape could reduce variance. The organization of transects into clusters that have similar soils and plant communities is a form of stratification; but statistical tests cannot be conducted with 1–2 samples per strata. Here, we were forced to treat clusters as samples because the transects are nonindependent and the number of transects per cluster was too small to assess within-cluster variance. Despite the heterogeneity that was covered by the transects, the transects were located primarily on upland sites (Beetle 1974; Houston 1982). No transects were located in swales or valley bottoms, probably because upland sites seemed to be most intensively grazed (Coughenour and Singer 1991).

Despite these limitations, the method does provide important information. The method was sensitive enough to detect changes that have occurred over the 30-year period, which suggests that it would also be sensitive enough to detect significant changes of comparable magnitude that would result from grazing. Whereas it is difficult to determine what the Parker transect data are measuring in an absolute sense, the data contain information about relative differences in plant abundance over time and as affected by exclosure from grazing.

A promising set of procedures for converting old Parker data to equivalent basal area has been developed (Cook et al. 1992). This technique accounts for the various effects of plot size, plant size, shape, and density on loop frequency. Once old data are converted they can be compared to data from future studies that use better sampling methods (although it is unclear how the method might account for changes in plant size and shape within a species over time). We concur with Cook et al. (1992) in recommending that old Parker data be converted to basal area, and that future monitoring programs not include the Parker method.

The Parker transects have provided data over a long period utilizing a consistent methodology. Nevertheless, the value of this longevity is reduced because the data are difficult to interpret, biologically and statistically. We therefore recommend that YNP institute a program that includes more extensive sampling of other plant–soil associations. It should be designed to reduce variance through stratification, with adequate random sampling within strata. More frequent sampling, at least annually, is recommended to enable clearer interpretation of responses to annual and seasonal climatic variation. The attribute or attributes to be measured (frequency versus cover versus biomass) need to be carefully considered. Biomass has the most direct effect on ungulate forage abundance and it is the most direct and incontestable measure of plant abundance; it measures the amount of energy, carbon and mineral elements that are incorporated by the plant. Unfortunately, it is very laborious and costly to obtain biomass data at the species level. Plant community composition may be best sampled with a quadrat-based cover technique. If Parker transects are continued, we recommend their sample sizes be increased severalfold.

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Appendix

Table A1. Frequencies for plants at each cluster of the high winter range sites.[a] There were 2 transects per cluster except at J-62-2 where *n* = 1 and B-57-1 and B-62-1 where *n* = 3. Each value is mean over the transects in a cluster; units are hits per transect.

In/ Out	Year	Cluster[b]	Rep	Grass	Forb	Dwsh[c]	Total	Agsp[c]	Feid[c]	Kocr[c]	Posp[c]	Posa[c]
						Inside						
1	58	B-57-1	4	8.2	5.3	0.8	14.3	4.8	0.3	4.8	[d]	
1	58	B-57-2	5	36	1	1	38	6	12	2		
1	58	L-57-1	8	32	10	0	42	9.5	0	9.5		
1	62	J-62-11	13.5	14.5	0	28	2	2	1.8			
1	62	J-62-22	22.5	8.50	31	4	4	2				
1	62	B-57-14	10.5	12.3	2.5	25.3	1.7	1.3	5.5			
1	62	B-57-25	202	1	23	1	7	0				
1	62	B-62-16	18.7	8.70	27.4	5.8	0	11				
1	62	B-62-27	29.2	7.71	37.95	10.8	1					
1	62	L-57-1	8	22.5	16.5	1	40	11	1	2		
1	62	L-62-1	9	20	8	0	28	8.5	0	4		
1	67	J-62-11	15.2	26.8	0.5	42.5	0.75	8	1.5			
1	67	J-62-2	2	14.5	16.5	0	31	0	8.5	0		
1	67	B-57-1	4	8	20	0.3	28.3	1.2	2	3.2		
1	67	B-57-2	5	17	1	1	19	0	13	0		
1	67	B-62-1	6	18	8	0	21	3.5	0.5	6		
1	67	B-62-2	7	18	7	1	26	0.5	11.5	0.5		
1	67	L-57-1	8	25	6	1	32	15.5	7.5	0		
1	67	L-62-1	9	23	8	0	31	13.5	3.5	2		
1	74	J-62-1	1	35.5	31.8	0.5	67.8	1.5	25	0.75	5	0
1	74	J-62-2	2	40.5	23	0	63.5	0	32.5	2	1.5	0
1	74	J-62-3	3	25.8	27.7	2.2	55.7	4.5	11.2	3.5	2	2
1	74	B-57-1	4	29.5	19.3	0.8	49.6	6.7	9.2	5.3	5.6	2.5
1	74	B-57-2	5	37.5	15.5	0	53	3.8	27.2	0.5	5	0
1	74	B-62-1	6	28.8	18	5.1	51.9	12.2	1.7	0.5	5.2	0
1	74	B-62-2	7	43.8	17.2	0.5	61.5	3.5	27.8	3	1	0
1	74	L-57-1	8	36	15	0	51	7	17	6.8	2.8	0
1	74	L-62-1	9	27.5	11.5	0.5	39.5	6.5	10.2	3.5	4.2	0
1	74	M-57-1	10	36.2	15.2	0	51.4	4.2	24	1.2	4.2	0
1	81	J-62-1	1	34	28.5	0	62.5	0	28.7	4.7	0	0
1	81	J-62-2	2	57.5	10.5	0	68	0	51	4.5	0	0
1	81	J-62-3	3	25.2	27.2	0.5	52.9	2.5	12.5	7.2	0	0
1	81	B-57-1	4	29.7	22.2	0.3	52.2	7.7	15.2	6.3	0.5	0
1	81	B-57-2	5	45.7	13.8	0	59.5	3.7	38.2	3.2	0	0
1	81	B-62-1	6	29.3	13.3	3.3	45.9	10	1	17.7	0	0
1	81	B-62-2	7	61.7	13.2	0	74.9	0	52	1.5	0.25	0
1	81	L-57-1	8	44	12	0	56	6.2	26.5	8.7	2.5	0
1	81	L-62-1	9	32.8	8	0.5	41.3	9.2	9.8	10.5	3	0
1	81	M-57-1	10	55.5	15.5	0	71	2.25	50.7	2.5	0	0
1	86	J-62-1	1	28.8	12.8	0	41.6	0.5	25.8	2.5	0	0
1	86	J-62-2	2	35	4	0	39	0	34	0	0	0
1	86	J-62-3	3	17	7	0	24	2.5	9.5	4.5	0	0
1	86	B-57-1	4	18.8	10.5	0	29.3	1.7	13.7	3.5	0	0
1	86	B-57-2	5	37.2	8.2	0	45.4	2	35.2	2	0	0
1	86	B-62-1	6	24.6	15.3	0.2	40.1	12.8	3.5	7.5	0.3	0.3
1	86	B-62-2	7	43	11.2	0	54.2	3	24.5	0.25	0.5	0
1	86	L-57-1	8	38.5	11.2	0	49.7	11	22.5	4	1	0
1	86	L-62-1	9	24	5	0	29	6	11	7	0	0
1	86	M-57-1	10	42	3	0	45	2.5	38	0	0	0

Table A1. *Continued.*

In/ Out	Year	Cluster[b]	Rep	Grass	Forb	Dwsh[c]	**Total**	Agsp[c]	Feid[c]	Kocr[c]	Posp[c]	Posa[c]
1	89	J-62-1	1	22.2	21.5	0	43.7	1	16.7	1	0	0
1	89	J-62-2	2	32.5	13.5	1	47	1.5	30	1	0	0
1	89	J-62-3	3	22	21.5	0	43.5	4.2	8.2	5	0	0
1	89	B-57-1	4	22	11	0	33	8.5	8.1	2.7	0	0
1	89	B-57-2	5	6	10.7	0	16.7	0.5	1	0	1	0
1	89	B-62-1	6	22.2	10.8	1.1	34.1	12.7	3.7	5.8	0	0
1	89	B-62-2	7	24	6	0	30	2.5	7.8	0.5	1.5	0
1	89	L-57-1	8	29.5	13.5	0.5	43.5	4.2	12.5	2.5	4	0
1	89	L-62-1	9	22.5	10.5	0	33	8.5	7	3.5	0	0
1	89	M-57-1	10	34.5	13	0	47.5	5	25.8	1.5	0	0
						Outside						
2	58	B-57-1	4	11.8	8.8	0	20.6	4.2	1	4	[d]	
2	58	B-57-2	5	28	2.5	0.5	31	2.5	10	2.5		
2	58	L-57-1	6	33.0	6	0	39	3.3	4.2	5		
2	62	J-62-1	1	16.5	13	0	29.5	1.5	6.5	3		
2	62	J-62-2	2	18.5	15.5	0	34	3	4	6		
2	62	B-57-1	4	13.5	10.5	0	24	2.8	0.5	8.2		
2	62	B-57-2	5	29.7	4.8	0	34.5	0	14.5	2		
2	62	L-57-1	6	34	6	0	40	1.8	3.5	3.2		
2	67	J-57-1	1	19.2	19.7	0	38.9	1.5	12	3		
2	67	J-57-2	2	17	17	1	35	1	11	2		
2	67	B-57-1	4	9.5	7.50	17	1	1	6			
2	67	B-57-2	5	24.5	1.81	27.3	0.5	17	2			
2	67	L-57-1	6	38	8.5	0	46.5	1	12	3.2		
2	74	J-62-1	1	35.7	19	0.7	55.4	3	19.2	5.8	3	0
2	74	J-62-2	2	34	21.5	0	55.5	1.5	22	4	5.5	0
2	74	J-62-3	3	30.7	19	0	49.7	1.5	16.8	6.2	5	0
2	74	B-57-1	4	32.8	15.8	0.3	48.9	5	13.7	9.7	3.8	0
2	74	B-57-2	5	49.5	9.2	0	58.7	1.5	33	3	3.5	0
2	74	L-57-1	6	49.7	111.2	0	160.9	4.5	21	5.2	10.85	0
2	74	M-57-1	7	56.7	17.2	0.5	74.4	5.5	31.5	7.8	10	1.5
2	81	J-62-1	1	56.7	15	0.8	72.5	5	28.5	18.5	0	0
2	81	J-62-2	2	56.5	16.5	0.5	73.5	2	29.5	24	0	0
2	81	J-62-3	3	37.2	16.8	1	55	2.5	18.5	14.5	0	0
2	81	B-57-1	4	29.8	18.3	3.3	51.4	7.3	15.7	6.8	0	0
2	81	B-57-2	5	49.8	4.2	0	54	3.2	38.5	1.7	0	0
2	81	L-57-1	6	43.8	11.2	1.8	56.8	7.7	15	4.2	0	0
2	81	M-57-1	7	50.2	10.2	0	60.4	6	31.5	12.8	0	0
2	86	J-62-1	1	38.1	9.5	0	47.6	4.8	24.5	6.8	0	0
2	86	J-62-2	2	27.5	11.5	0	39	1	20.56	6	0	0
2	86	J-62-3	3	29.5	14.5	0.5	44.5	2.5	18.5	8.5	0	0
2	86	B-57-1	4	25.8	6.2	0.3	32.3	7.3	15.5	3	0	0
2	86	B-57-2	5	48.8	5.2	0	54	10.2	33.5	0	0	0
2	86	L-57-1	6	37.7	12.7	0.5	50.9	7.5	16.8	10.2	0	0
2	86	M-57-1	7	38.2	6.2	0	44.4	3.8	27.2	7.2	0	0
2	89	J-62-1	1	26.7	13.7	0	40.4	4.8	9.8	4.8	2	0
2	89	J-62-2	2	30.5	16.5	0	47	2	8.5	4	15	0
2	89	J-62-3	3	20	13.5	0	33.5	4.5	7	3	3.2	0
2	89	B-57-1	4	22.5	10.8	1.7	35	8.2	9.2	2.8	1.7	0
2	89	B-57-2	5	24.7	3.7	0	28.4	1.5	12.3	2.2	0	0
2	89	L-57-1	6	32.2	17.5	0	49.7	2	12	3	2.5	0
2	89	M-57-1	7	39	14	1.2	54.2	2	18.2	11	7.8	0

[a] J = Junction Butte; B = Blacktail; L = Lamar.

[b] Year number in the cluster code refers to the year of establishment.

[c] Dwsh = dwarf shrub; Agsp = *Agropyron spicatum*; Feid = *Festuca idahoensis*; Kocr = *Koeleria macrantha*; Posp = *Poa* spp.; Posa = *Poa sandberghii*.

[d] Blanks indicate values not available for this analysis.

Table A2. Frequencies of plants at each cluster at the low elevation site (Gardiner). Mean for each cluster is the mean over two transects; units are hits per transect.

In/ Out	Year	Cluster[a]	Rep	Grass	Forb	Dwsh[b]	**Total**	Agsp[b]	Feid[b]	Kocr[b]	Posp[b]	Posa[b]
						Inside						
1	58	G-57-1	1	4.5	3	0.5	8	0	0	0	[c]	
1	58	G-57-2	2	9	2.5	1.5	13	8	0	1.5		
1	62	G-57-1	1	6	7	4	17	0	0	0		
1	62	G-57-2	2	14.5	2.5	3	20	2.5	0	1.5		
1	62	G-62-1	3	7	2	0.5	9.5	3	0	0	14.5	
1	67	G-57-1	1	3.5	10	5	18.5	0	0	0.5		
1	67	G-57-2	2	6.5	2.5	4.5	13.5	2	0	1.5		
1	67	G-62-1	3	5.5	6	0.5	12	2	0	0		
1	74	G-57-1	1	8	2.5	13.2	23.7	2	0	4.2	1.8	0
1	74	G-57-2	2	29.2	6.2	5	40.4	7	0	3.5	3.2	0
1	74	G-62-1	3	10	4.5	7.2	21.7	0	0	7.3	2.7	0
1	74	G-62-2	4	19.8	0.5	8	28.3	6.2	0	6.2	2.2	0
1	81	G-57-1	1	9	2	10.5	21.5	0	0	7.8	0.5	0
1	81	G-57-2	2	20.8	8.8	7	36.6	8.5	0	8.8	2	0
1	81	G-62-1	3	19	0.75	9.7	29.45	0	0	18	0.5	0
1	81	G-62-2	4	23	2.8	6.8	32.6	9.5	0	9.5	1.2	0
1	86	G-57-1	1	7	0	8151.505.500						
1	86	G-57-2	2	17	1.8	3.8	22.6	6.5	0	10.5	0	0
1	86	G-62-1	3	8	0.5	4	12.5	0	0	7.5	0	0
1	86	G-62-2	4	14.2	0.5	2.2	16.9	6.5	0	7.2	0	0
1	89	G-57-1	1	5.2	1.5	1.8	8.5	1	0	0	1.8	0
1	89	G-57-2	2	11.8	13	1	25.8	6.2	0	2	3.5	0
1	89	G-62-1	3	2.5	5.5	2.5	10.5	0	0	1	0.5	0
1	89	G-62-2	4	4.5	1	0	5.5	2.5	0	1	0.5	0
						Outside						
2	58	G-57-1	1	10.5	2.5	0	13	4.5	0	4.5	[c]	
2	58	G-57-2	2	5	7	0	12	0	0	0		
2	62	G-57-1	1	15.5	5.9	1.1	22.5	6	0	4		
2	62	G-57-2	2	7	5.2	3.8	16	0	0	0		
2	67	G-57-1	1	12.5	6.5	0	19	4.2	0	6		
2	67	G-57-2	2	5.5	7	3	15.5	0	0	0		
2	74	G-57-1	1	8	0.5	22.8	31.3	0	0	1	6	0
2	74	G-57-2	2	19.8	4.2	1	25	4	0	10.2	1.8	0
2	81	G-57-1	1	6	0.75	15.2	21.95	0	0	3.5	0	0
2	81	G-57-2	2	31	2.5	0.5	34	4.5	0	19	1.5	0
2	86	G-57-1	1	8.5	0	11.2	19.7	0	0	7	0	0
2	86	G-57-2	2	12.2	3.2	1	16.4	3.5	0	4	0	0
2	89	G-57-1	1	3.8	5.2	3.5	12.5	0	0	1	1	0
2	89	G-57-2	2	8	11.7	1.5	21.2	1.5	0	1.2	1	0

[a] Year number in the cluster code refers to the year of establishment.

[b] Dwsh = dwarf shrub; Agsp = *Agropyron spicatum*; Feid = *Festuca idahoensis*; Kocr = *Koeleria macrantha*; Posp = *Poa* spp.; Posa = *Poa sandberghii*.

[c] Blanks indicate values not available for this analysis.

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BIOMASS AND NITROGEN RESPONSES TO GRAZING OF UPLAND STEPPE ON YELLOWSTONE'S NORTHERN WINTER RANGE

Michael B. Coughenour

Natural Resource Ecology Laboratory
Colorado State University
Fort Collins, CO 80523 U.S.A.

SUMMARY

(1) The responses of herbaceous vegetation on upland steppe of Yellowstone National Park's northern winter range to winter grazing by elk were investigated during 1987–88 using exclosures erected at four sites in 1958–62.

(2) Elk winter-grazing on plants reduced standing dead material and litter biomass at most but not all sites and dates. Plant productivity was not reduced.

(3) Live above-ground grass biomass was reduced by winter grazing at one of four sites in 1987 and at three sites in 1988. Live grass was more abundant in grazed areas at two sites in 1987.

(4) Live forb biomass was *c.* 33% of grass biomass, and was not affected by grazing in 1987, but increased slightly outside exclosures in 1988, perhaps because of the dry summer.

(5) Root biomass was not affected by grazing at any site.

(6) Nitrogen concentrations of live grass, dead grass, and *Artemisia frigida* were increased by winter grazing. Total N flow to herbivores in 1987 would consequently have been stimulated by herbivory, and in 1988 would have been depressed by herbivory only one-third as much as biomass.

(7) The net effects of winter grazing appeared to be a redirection of biomass flow from decomposers into elk, accompanied by an enhanced rate of N recycling back to elk. The fact that perennial root biomass has persisted best indicated the net consequences of winter grazing for these plants.

INTRODUCTION

For nearly a century there has been concern about large winter concentrations of elk (*Cervus elaphus*) in the low-lying valleys of the Lamar, Yellowstone, and Gardner Rivers of Yellowstone National Park (Houston 1982; Coughenour & Singer 1990); first for sufficiency of forage, then for the effects of the animals on winter range plants and soils. It has long been believed by some that winter concentrations of elk in Yellowstone are the result of disrupted migration between the park and lower elevation wintering grounds outside the park (Pengelly 1963). This belief, coupled with perceptions of overly high elk numbers and drought in the 1920s and 1930s, caused concern for the condition of the range. This led the National Park Service to commission a long series of studies (Rush 1932; Grimm 1935–38, 1939; Gammill 1939–41; Kittams 1948–58). Most of these studies seemed to indicate deterioration of upland steppe (excluding swales and wet meadows), but whether these changes were due to elk or drought, or a combination of these factors, is still unclear (Despain *et al.* 1986, Coughenour & Singer 1990). There is evidence that large numbers of elk did in fact winter on the northern range in early times (Houston 1975, 1982).

Elk were artificially controlled until 1968, when an effort was begun to determine if elk numbers could be naturally regulated in accordance with the mandate to preserve natural processes to the greatest extent possible in National Parks (Cole 1971; Houston 1971). The herd grew six-fold, from 3200 in 1968 (Houston 1982) to over 19 000 in 1988 (Singer 1990), but numbers were reduced in 1989 (Singer 1990). Renewed concerns for elk effects on their habitat led Congress to mandate that a study be started to determine if the range was overgrazed (Congressional Record, Senate, S 12613, 16 September 1986).

As part of the monitoring of the winter range, a series of large animal exclosures were erected in 1958 and 1962. Areas inside and outside the 2-ha exclosures have been sampled with a series of non-destructive techniques including Parker transects, belt transects, photo-plots, and chart quadrats (Barmore 1980; Houston 1982). These techniques have failed to yield any conclusive evidence of range degradation, but the precision of these techniques may be lower than direct biomass measures. Root mass has never been measured.

This study uses estimates of shoot and root standing crops and nitrogen concentrations in these exclosures to assess more precisely the effects of elk grazing on herbaceous plant communities. Although the exclosures are a small sample of the wide range of landscape variability on the northern range, they offer the best available opportunity for determination of long term elk impacts.

Hypothesized responses

The negative consequences of excessive grazing are well known. Often overgrazing reduces allocation to roots, or stops root growth completely (Jameson 1963). Less water may be available for plant growth due to increased run-off and evaporation (Branson *et al.* 1981). Greater temperatures due to decreased standing dead and self-shading may be detrimental to growth (Sauer 1978). The two most abundant grass species on the Yellowstone northern winter range (*Agropyron spicatum* and *Festuca idahoensis*) have been shown to be sensitive to grazing during the growing season (Evanko & Peterson 1955; Pond 1957; Mueggler 1967; Caldwell *et al.* 1981).

Negative responses to grazing might not be expected on the northern range, however. The plants are grazed primarily when they are dormant, and mainly dead tissues are removed. Only limited early spring grazing may occur. Elk usually come onto the range in late October, and leave in early to mid May (Houston 1982). Clipping for 3 years did not reduce shoot production of *F. idahoensis* (Mueggler 1967). Mueggler later found (1975) that while clipped plants produced shorter leaves, their basal areas were greater. Pond (1957) observed little effect of grazing on basal cover of *F. idahoensis.* Both species withstood heavy clipping when competing vegetation was clipped to the same degree (Mueggler 1972). Blaisdell & Pechanec (1949) found that very late or very early clipping (at the end of October or end of April) reduced *A. spica- tum* herbage production only 10–15%. Clipping early in growth or after leaf senescence had minimal effect on *A. spicatum* or *F. idahoensis* (Mueggler 1967, 1975). *A. spicatum* allocates a high and constant fraction of photosynthate to roots (Caldwell *et al.* 1981; Richards 1984), which could be beneficial over the long term. Finally, rates of nutrient recycling could be enhanced by ungulates (Ruess and McNaughton 1987; Jaramillo & Detling 1988).

METHODS

Study area and sites

The northern Yellowstone winter range has been described by Houston (1982). It comprises 100 000 ha, extending about 80 km down the Lamar, Yellowstone, and Gardner river basins. About half of the range is between 1600 m and 2300 m and a third between 2300 and 2600 m. The vegetation of the northern range is mostly a steppe (27%) or shrub steppe (22%) (Houston 1982; D. Despain, unpublished). The upland portion of the steppe includes hilltops and hillsides, but not valley floors and swales.

Upland steppe of the northern range is dominated by perennial grasses: bluebunch wheatgrass, *Agropyron spicatum;* Idaho fescue, *Festuca idahoensis*; junegrass, *Koeleria cristata*. The shrub layer is dominated by big sagebrush, *Artemisia tridentata.*

The climate of the northern range is generally warmer and drier than the rest of the park. Mean annual precipitation varies from 279 mm at Gardiner (at 1616 m) to 398 mm at Mammoth (1899 m) and 406 mm at Tower Falls (1912 m). Mean monthly precipitation is highest in spring and early summer on the northern range .

This study was done in 1987 and 1988. These years were below average in precipitation (87% and 74% of normal) and above average in temperature. At Mammoth, 190 mm of precipitation was recorded during November 1986–June 1987 (64% of normal). Another 130 mm fell in July and August 1987 (174% of normal). During November 1987–June 1988, 218 mm fell, but in July and August only 40 mm was recorded.

Soils in the area are primarily derived from andesitic rock and limestone brought into the area by glaciers. Deep loams are common in valley bottoms, while thinner, rocky loams are prevalent on ridgetops. The Stevens Creek site is located on ancient mudflows which are higher in clay and lower in fertility.

Sampling design and methods

Sampling was designed to maximize precision in estimating grazing impacts. Of the eight 2-ha exclosures built between 1957 and 1962, four were sampled. The exclosures, in order of increasing elevation are at: Stevens Creek exclosure, on mudflow soils with generally north-easterly aspects; Blacktail, on a ridgetop with general southerly aspect; Junction Butte, on an area of gentle hills interspersed with granite boulders with no prevailing aspect; and Lamar, on a south-west facing hillside and ridgetop.

Landscapes within and surrounding exclosures were stratified to control topographic and soil variance. Only upland sites were sampled because concerns for grazing impacts on the northern range have always been focused there. Uplands at each exclosure site were stratified, based upon slope and aspect, to ensure that comparisons inside and outside exclosures were among similar topographic, soil and microclimatic conditions. Deliberate interspersion of the grazing treatment among small-scale landscape variation is preferred over pure randomization in small experiments to insure that biases are not introduced by inadvertent clumping of samples on different portions of a confounding environmental gradient (Hurlbert 1984). It is doubtful that random sampling in and out of each exclosure would have resulted in comparable distributions of topo-edaphic positions, even with very large sample sizes.

Strata included slopes of 0–30% at Blacktail and Stevens Creek, and 10–30% at Junction Butte and Lamar. Aspects were: NE, N, and NW at Stevens Creek; NW, NE, and SE at Junction Butte; S and NE at Blacktail; SW at Lamar. Within each of four slope/aspect strata, a pair of 5 m × 5 m study plots were randomly chosen, 1 inside and 1 outside the exclosure. These study plots were sampled above and below ground on each of two dates in 1987. A new set of study plots was randomly chosen in the same four slope/aspect strata in 1988, and these were sampled once for above-ground biomass and twice for roots.

On each sample date, four 0.25 m^2 circular clip plots were randomly located within paired study plots, harvested to ground level and separated into grasses, forbs and dwarf shrubs. In 1988, *Artemesia frigida* was separated from other dwarf shrubs, and lichen biomass was sampled. Non-humic litter on the soil surface of each clip-plot was gathered manually. Above-ground plant materials were oven dried at 40° C for 48 hours. Live and dead tissues of grasses, forbs and shrubs were sorted and weighed.

Subsamples were taken at random from herbage materials harvested in each of the clip plots, these were bulked, ground, and a random subsample was taken for tissue nitrogen analysis.

Above-ground biomass was sampled in August and September 1987. Summer 1988 was so dry that growth after the July sampling was highly unlikely. Distinguishing current from last year's dead biomass was attempted in 1987, but little confidence could be attached to visual classification, particularly inside exclosures where much standing dead material had accumulated. In 1987, three of the four clip plots within study plots were randomly selected, and a root core 6.35 cm in diameter was taken at the centre of the clip plot to a depth of 20 cm. In 1988, all four of the clip-plots were sampled for roots in this manner. Roots were sampled in August and September 1987 and July and September 1988. Root cores were stored in freezers until they were washed free of soil, oven dried and weighed. In 1988, root samples were subsampled for ash determination.

Soil water was gravimetrically determined in late July and early August 1987. Ten soil cores were taken inside and outside exclosures in the 5 × 5 m study plots at 0–10 and 10–20 cm depths.

Statistical testing for grazing effects was accomplished primarily through *t*-tests. Tests for skewness and kurtosis, and the Kolmogorov-Smirnov tests indicated distributions were normal, including tests on the populations of all clip-plots at a site. Means of exclosed versus non-exclosed treatments were compared within exclosure sites on each sample date. Means across all sites were also compared within sample dates. Variances were non-equal in a few cases, and the approximate t'-statistic was used (Sokal and Rolf 1981).

RESULTS

Comparisons of the means over all sites of exclosed and unexclosed biomass samples provided a broad view of grazing effects. At all dates there was significantly more dead grass in the exclosures (Fig. 1a). Live grass was more abundant and live forbs (Fig. 1b) were less abundant in exclosures in July 1988, while in 1987 grazing had no effect. There were no grazing effects on dead forbs or live dwarf shrubs (Fig. 1c) at any date. Dead dwarf shrubs were higher inside exclosures in July 1988. Root biomass was not affected by grazing on any date (Fig. 2a). Litter was significantly greater in exclosures on all dates, (Fig. 2b).

Comparisons of standing crops in August 1987 with those in 1988 indicated generally more production in 1988. Live and dead grass were both greater in exclosures in 1988 ($P < 0.05$), but outside exclosures live grass was equally abundant in both years, and dead grass was less abundant in 1988. Dead forbs were more abundant in 1988, but only outside exclosures ($P = 0.01$). Live shrubs were more abundant in 1988, but only inside exclosures ($P < 0.01$).

There were many site-specific exceptions to the generalities stated above (Table 1). Grazing failed to reduce dead grass at Stevens Creek in September 1987 and July 1988. Litter was not affected by grazing at Junction Butte or Stevens Creek in August 1987 or July 1988, nor at Blacktail on July 1988. There was less live grass inside the Lamar exclosure and more inside the Junction Butte exclosure in August 1987, and there was more in the Junction Butte exclosure in September 1987. In July 1988, grazing had no effect on live grass at Stevens Creek. Live forbs were not significantly affected by grazing at any individual site and date. Dead forbs were only affected by grazing at Lamar in September 1987, where they were greater in the exclosure. Live or dead dwarf shrubs were not affected by grazing at any individual site and date. Root mass was greater inside the Junction Butte exclosure in July 1988, but by September there was no difference (Table 2).

Artemeisia frigida biomass was separated in 1988. This species was more abundant inside (11.3 ±

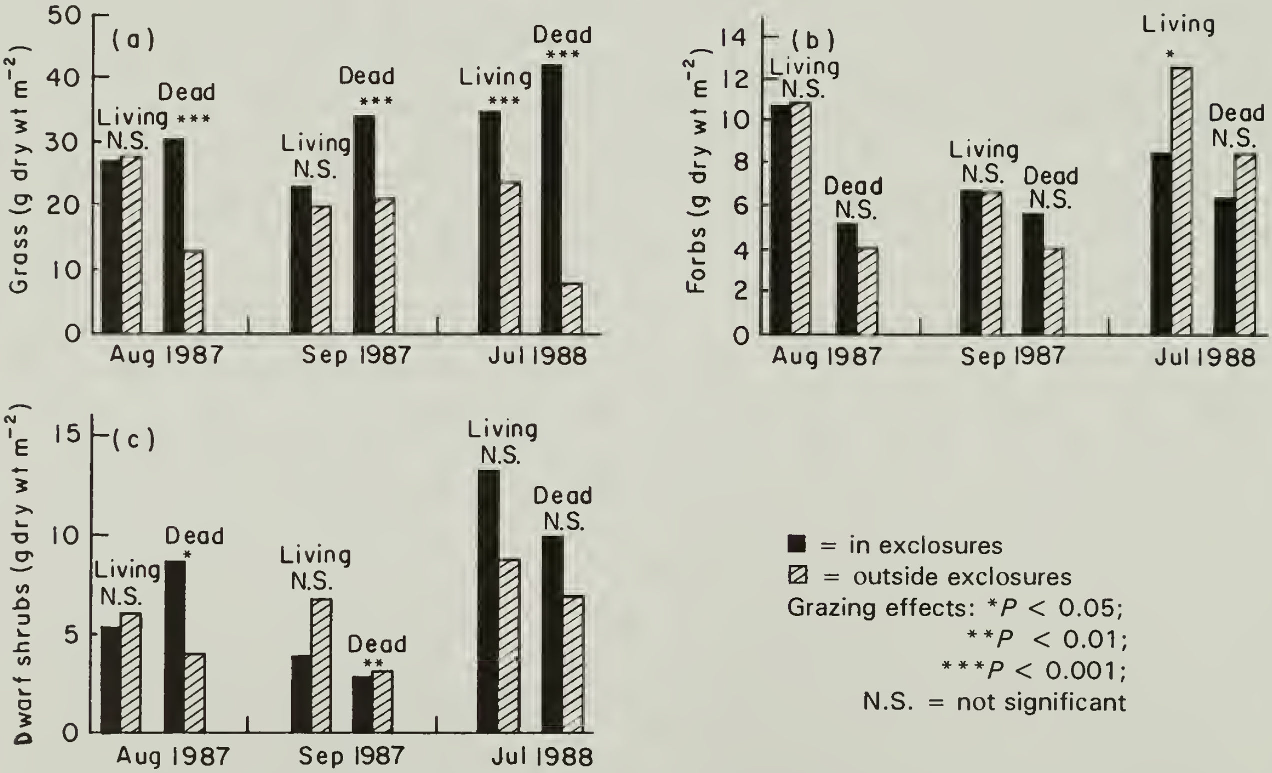

FIG. 1. Grazing effects on (a) grass live and dead standing crops on three dates averaged over the four study sites (b) forb live and dead standing crops, and (c) dwarf shrub live and dead standing crops. ■, in exclosures; ▨, outside exclosures. Grazing effects: $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$; N.S. not significant.

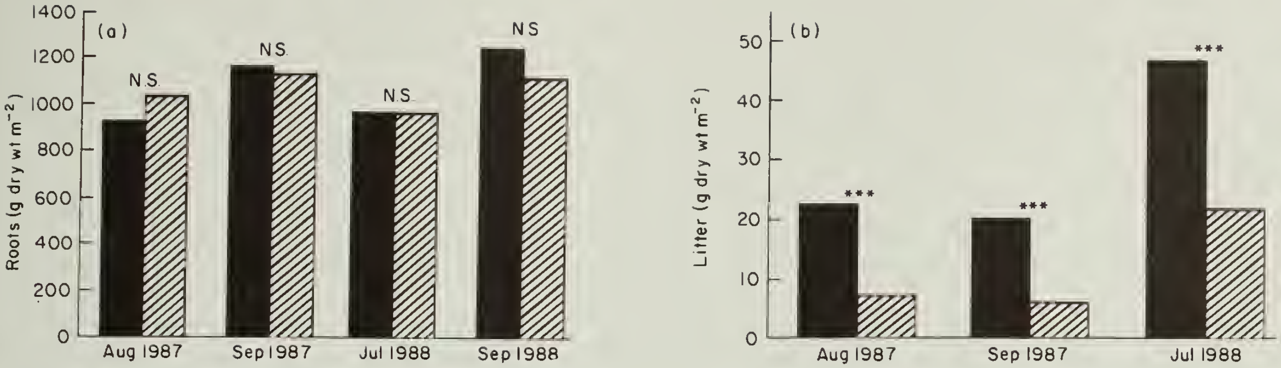

FIG. 2. Grazing effects on (a) root biomass observed on four sampling dates and (b) litter biomass observed on three dates. Key as in Fig. 1.

11.0 live and 3.4 ± 3.6 g m^{-2} dead) than outside (5.5 ± 6.0 and 1.8 ± 3.6 g m^{-2} dead) the Stevens Creek exclosure, and less abundant inside (0.6 ± 1.4 live and 0.4 ± 1.6 g m^{-2} dead) than outside (2.3 ± 3.4 live and 0.8 ± 1.2 g m^{-2} dead) the Lamar exclosure. At Junction Butte (0.52 ± 2.2 g m^{-2} live and 0.64 ± 3.2 g m^{-2} dead) and at Blacktail (1.4 ± 3.0 g m^{-2} live and 0.7 ± 1.3 g m^{-2} dead) there were no effects of grazing.

Nitrogen concentrations were significantly higher in live grass, dead grass, live and dead *A. frigida* tissues sampled from outside exclosures (Fig. 3). There were no grazing effects on forb or root nitrogen concentrations. There were no significant differences among sites or sampling dates.

Lichens, sampled only in 1988, were most abundant at Stevens Creek, where there was significantly ($P < 0.001$) more (27.1 ± 24.9 g m^{-2}) inside than outside (14.6 ± 10.3 g m^{-2}) the exclosure. At Junction Butte there was also significantly ($P = 0.02$) more lichen inside (2.9 ± 2.9 g m^{-2}) than outside (1.0 ± 0.7 g m^{-2}). At Blacktail significantly ($P < 0.001$) less was inside (0.3 ± 0.4 g m^{-2}) than outside (2.1 ± 1.9 g m^{-2}).

Soil moisture sampling in 1987 revealed no significant differences between exclosed and unexclosed areas at any site (Table 3). Soil moisture at 0–10 cm was significantly higher at Lamar than other sites. Water in the 10–20 cm layer was higher at Lamar and Stevens Creek than at other sites.

DISCUSSION

Grazing effects on dead grass and litter

The most pronounced effects of grazing were reductions of dead grass and litter. Reductions of dead grass would be expected given that most grazing occurs during the winter. The exception to this occurred at Stevens Creek. Less standing dead had accumulated at this site than at other sites, probably because productivity was lower there.

Grazing reduction of standing dead material and litter affects microclimate and nutrient cycling. The possibility that removal of standing dead material reduces rainfall interception (Knapp and Seasteadt 1986) was not determined; however, no exclosure effect on soil moisture was observed in 1987.

Litter was only greater inside an exclosure at one site (Lamar) in 1988. Decomposition rates are generally greatest when temperatures are warmest and when soil is moist. Generally higher litter values in 1988 than in 1987 suggest that decomposition rates may have been lower in 1988, due to the lack of rainfall during the warmest months. A very large amount of litter had accumulated in the Lamar exclosure by 1988, partly the result of high productivity. However, accumulation of standing dead material and resultant cooler soil temperatures could also have reduced decomposition rate.

Grazing effects on live above-ground grass biomass

Winter grazing reduced live grass biomass at only one site in 1987, but inhibited grass growth at three of the four sites in 1988. It is possible that the lower values of live grass biomass outside the exclosures in 1988 were a consequence of forage removal in early spring in 1988. However, there were no differences in weather among years that would explain greater early spring grazing in 1988; in fact, the 1987–88 winter was mild. Furthermore, dominant grass species have been shown to tolerate early spring grazing well (Blaisdell & Pechanec 1949; Pond 1957; Wilson, Harris & Gates 1966; Mueggler 1967, 1975).

It is more likely that climatic differences between years significantly altered grazing responses.

TABLE 1. Above-ground biomass (means (n = 16) and S.D.s in parentheses)(g dry wt. m^{-2}) for each exclosure site, date and grazing treatment.

	August 1987		September 1987		July 1988	
Site	Exclosed	Unfenced	Exclosed	Unfenced	Exclosed	Unfenced
Lamar						
Live						
grasses	17.3 (14.8)*	30.3 (18.0)*	16.4 (12.0)	15.5 (7.2)	40.4 (21.6)**	17.9 (5.1)**
forbs	9.3 (8.4)	14.6 (10.4)	10.5 (6.4)	9.6 (6.0)	15.5 (10.8)	18.9 (6.2)
dwarf shrubs	5.3 (10.4)	1.2 (2.2)	3.2 (3.6)	5.0 (16.8)	19.3 (24.8)	8.1 (11.0)
Dead						
grasses	27.2 (25.6)*	12.1 (10.0)*	37.6 (21.6)**	14.4 (8.8)**	35.5 (23.6)*	3.6 (2.2)*
forbs	12.9 (19.6)	8.1 (6.8)	12.1 (8.4)	5.9 (4.4)	4.7 (5.0)	4.6 (4.3)
dwarf shrubs	16.7 (29.2)	2.9 (9.6)	6.5 (10.8)	2.7 (3.7)	13.1 (22.8)	3.7 (5.6)
Litter	32.1 (25.2)***	5.2 (4.5)***	26.3 (17.2)***	6.7 (4.6)***	95.3 (51.2)***	9.7 (8.4)***
Junction Butte						
Live						
grasses	44.4 (18.4)***	23.1 (13.4)	41.7 (13.3)***	21.4 (6.6)***	40.7 (12.5)**	28.9 (8.8)**
forbs	13.3 (13.4)	12.1 (11.0)	7.1 (6.1)	10.5 (6.2)	11.3 (8.5)	20.1 (19.3)
dwarf shrubs	3.7 (3.8)	5.2 (6.8)	2.4 (3.8)	3.5 (3.1)	2.5 (4.4)	5.6 (6.5)
Dead						
grasses	41.7 (28.0)**	18.9 (12.0)**	44.1 (25.2)*	28.7 (11.2)*	58.3 (26.7)***	8.7 (3.6)***
forbs	4.7 (5.6)	3.4 (4.4)	6.3 (7.0)	4.6 (5.8)	11.7 (13.1)	18.6 (18.0)
dwarf shrubs	3.9 (2.2)	9.3 (1.4)	0 (0)	0 (0)	6.8 (7.5)	7.0 (7.0)
Litter	22.4 (22.4)	16.0 (11.6)	23.9 (20.0)*	10.1 (10.0)*	36.6 (16.3)	37.7 (34.8)
BLacktail						
Live						
grasses	29.2 (14.4)	33.8 (14.4)	20.6 (9.2)	23.2 (9.6)	42.1 (20.5)*	29.4 (6.9)*
forbs	13.6 (12.8)	9.9 (8.8)	7.9 (5.7)	4.8 (3.8)	6.8 (7.0)	10.9 (8.6)
dwarf shrubs	4.7 (4.5)	8.3 (8.0)	2.2 (2.5)	6.1 (5.7)	6.3 (7.9)	10.2 (16.4)
Dead						
grasses	36.5 (12.8)***	14.8 (7.8)***	35.6 (19.6)	27.3 (8.8)	57.8 (30.0)***	9.2 (3.8)***
forbs	3.6 (4.8)	1.8 (1.4)	4.2 (3.7)	4.1 (4.6)	9.5 (11.8)	10.6 (14.7)
dwarf shrubs	7.6 (9.1)	6.3 (8.0)	3.5 (5.5)	6.6 (6.4)	9.8 (9.3)	7.3 (15.3)
Litter	28.8 (15.5)***	3.7 (4.2)***	20.0 (9.8)***	6.9 (5.4)***	39.4 (23.4)	29.1 (38.8)
Stevens Creek						
Live						
grasses	15.2 (9.4)	21.4 (10.0)	11.6 (5.5)	18.0 (14.4)	14.7 (12.7)	16.3 (11.6)
forbs	6.4 (6.8)	6.8 (5.4)	1.7 (3.6)	2.0 (4.2)	0.5 (0.9)	0.2 (0.4)
dwarf shrubs	7.8 (5.8)	9.5 (8.9)	8.3 (8.8)	12.4 (12.6)	24.6 (30.9)	11.1 (7.2)
Dead						
grasses	14.7 (10.5)**	4.2 (2.9)**	17.0 (9.2)1	3.2 (8.8)	16.1 (15.2)	9.0 (6.7)
forbs	0.9 (2.7)	2.9 (3.2)	0 (0)	1.6 (4.0)	0.1 (0.4)	0.1 (0.2)
dwarf shrubs	9.0 (9.1)	6.4 (8.0)	1.4 (2.3)	3.2 (3.9)	10.2 (11.0)	9.5 (7.8)
Litter	7.2 (8.0)	3.2 (2.9)	10.5 (13.0)*	1.6 (2.0)*	16.2 (15.2)	10.9 (6.2)

Differences between means inside and outside exclosures: $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$.

April–June rainfall was higher in 1988 (390 mm) than in 1987 (334 mm). These are critical months for growth of these cool-season species which have the C_3 photosynthetic pathway. Consequently, while an additional 335 mm rainfall fell in July and August 1987 (174% of normal), live grass actually decreased and dead grass increased. However, the unexclosed grasses did not respond to greater spring rainfall in 1988. An explanation may be that unexclosed grasses were less buffered from the drought that began in late May 1988 (June received only 24% of normal rainfall). The lack of accumulated standing dead grass outside exclosures could have accelerated soil evaporation and increased temperatures (Whitman 1974; Branson *et al.* 1981) above those optimal for photosynthesis. Sauer (1978) similarly found that removal of standing dead in winter decreased growth of *A. spicatum*.

The fact that the negative grazing response occurred in a very unusual weather year is important

TABLE 2. Root biomass means and S.D.s ($n = 12$ in 1987, $n = 16$ in 1988), 0–20 cm depth (g ash-free dry wt m^{-2})

	1987		1988	
Site and date	Exclosed	Unexclosed	Exclosed	Unexclosed
Lamar				
July/August	953 (627)	1185 (906)	1265 (539)	1588 (1005)
September	976 (687)	999 (7)	1581 (395)	1246 (733)
Junction Butte				
July/August	1325 (2)	1441 (535)	1300 (609)	858 (343)
September	1650 (813)	1534 (7)	2011 (704)	1823 (912)
Blacktail				
July/August	1139 (465)	1139 (418)	987 (598)	1168 (482)
September	1743 (558)	1720 (1046)	957 (632)	918 (393)
Stevens Creek				
July/August	418 (256)	535 (535)	618 (595)	422 (304)
September	488 (325)	488 (302)	562 (271)	614 (422)

Only one significant exclosure effect was found, at Junction Butte in July 1988 ($P = 0.017$).

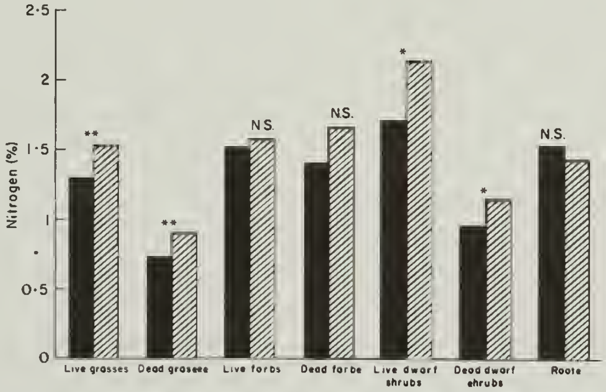

FIG. 3. Grazing effects on nitrogen concentrations of grass, forbs, dwarf shrubs, *A. frigida* (Arfr), and roots. Key and probabilities of significant exclosure effects as in Figs. 1 and 2.

for interpreting longer-term grazing impacts. The results suggest that June rainfall may be especially important for grazing response. The effects of standing dead on microclimate may be especially important when June is very dry. July and August rainfall may be less important because higher temperatures are less favourable for photosynthesis. Assessment of long-term grazing impacts would then depend on careful analysis of seasonal precipitation patterns.

Effects on roots

Grazing had no effect on root biomass. The continuity of root biomass is an important measure of the fitness of long-lived perennial grass genets. Root/shoot ratios ranged from 7 to 10 among exclosed sites in July 1988 and 9–26 in unexclosed sites (based on live plus dead shoot mass and ashed root weight). These ratios are quite comparable to values observed

TABLE 3. Relative water contents (%) (S.D.s in parentheses $n = 10$) sampled in mid-summer 1987 at two depths inside and outside exclosures

Site and depth	Exclosed	Unexclosed
Lamar		
0–10 cm	18.1 (5.3)	18.1 (4.4)
10–20 cm	18.2 (4.2)	13.6 (5.5)
Junction Butte		
0–10 cm	9.1 (1.8)	10.0 (3.8)
10–20 cm	8.9 (1.9)	10.2 (4.3)
Blacktail		
0–10 cm	8.3 (2.6)	8.8 (4.2)
10–20 cm	10.7 (5.1)	9.8 (1.8)
Stevens Creek		
0–10 cm	12.0 (5.7)	10.8 (5.2)
10–20 cm	15.8 (5.2)	19.3 (5.2)

No significant exclosure effects were found.

in other north temperate grasslands (Sims, Singh, & Lauenroth 1978).

A. spicatum is sensitive to defoliation during the growing season (e.g. Pond 1957; Mueggler 1967), largely because it continues to allocate a high proportion of carbon to roots even when defoliation has reduced shoot biomass (Caldwell *et al.* 1981, Richards 1984). However, substantial root allocation may be beneficial under a winter and early spring grazing regime. Greater root investment could enhance resistance of plants to spring grazing or other disturbances. Jaramillo & Detling (1988) found that morphotypes of blue grama growing in areas subject to prairie dog grazing invested more resources in roots than plants in less grazed areas. Nitrogen is retranslocated during senescence and stored in roots. Large proportions of root biomass would increase the likelihood that nutrients are recycled via plant uptake, and that water is taken up effectively. A larger quantity of root biomass that is in place early in the growing season should also increase competitive ability with annual species.

Effects on plant nitrogen

Grazing increased shoot nitrogen concentrations in grasses and in *A. frigida.* Greater shoot nitrogen concentrations due to grazing have been previously observed (Coppock *et al.* 1983, Jaramillo & Detling 1988). Where shoot production was not reduced by grazing, a greater total quantity of protein would be available to grazers. The net annual increase in grass N available to winter grazers can be calculated as the product of peak live grass biomass multiplied by % N of dead grass tissue. This was 0.19 g N m^{-2} inside and 0.25 g N m^{-2} outside exclosures in 1987, and 0.24 g N m^{-2} inside and 0.21 g N m^{-2} outside exclosures in 1988. Total available N in 1988 was reduced half as much by herbivory as was biomass.

Increased shoot nitrogen levels may have resulted from removal of older leaf tissues and replacement by younger tissues. However, it seems unlikely that either of these effects was important here because grazing is confined to the very early growing season. Another explanation of higher shoot nitrogen is that grazing accelerates nutrient recycling rates (Ruess & McNaughton 1987; Detling 1988). Grazers increase nutrient turnover rates by returning mineral N to the soil in a more readily decomposable form, thereby bypassing slower litter decomposition. As noted above, removal of standing dead and litter would also elevate soil temperatures, and this could accelerate decomposition and mineralization in the spring.

Effects on species composition

There was no clear evidence of a marked shift towards ruderals at the expense of long-lived perennials in this study. Irrespective of grazing, the dominant long-lived perennial grasses seemed to maintain a relatively closed community, in accordance with other findings (Evanko & Peterson 1955). Annual grass species were rare among the total grass biomass sampled. There was little evidence of a shift to greater forb abundance except for a small increase in 1988. It is unclear what role the 1988 dry summer played in that response. While lichens were less abundant outside two exclosures, significant amounts had persisted. Root biomass was high and was not reduced by grazing. It is likely that the vast majority of this root mass was that of perennial plant (mostly grass) species because annuals were a small part of aboveground biomass, and root:shoot ratios of annual plants are typically much smaller than those observed here.

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The Ecology of Plants, Large Mammalian Herbivores, and Drought in Yellowstone National Park[1]

Douglas A. Frank[2] and Samuel J. McNaughton

Biological Research Laboratories
Syracuse University
Syracuse, New York 13244-1220
USA

Abstract. The purpose of this study was to examine the effect of abundant native large herbivores on ecosystem function of a spatially and temporally heterogeneous temperate grassland. Net aboveground primary production (ANPP), large herbivore consumption *(C)*, and dung deposition *(D)*, an index of nutrient flow from herbivores to the soil, were measured in grassland and shrub-grassland habitat on winter, transitional, and summer range used by herds of elk *(Cervus elaphus)* and bison *(Bison bison)* in northern Yellowstone National Park. Temporary exclosures (5–7 per site) were moved every 4 wk during the snow-free season to determine ANPP and *C*. Data were collected during 1988, a year of drought and unusually high elk and bison population levels, and 1989, a climatically near-average year, with dramatically fewer elk and bison.

All three processes, ANPP, *C*, and *D*, varied widely among sites: ANPP range: 16–589 g/m^2, *C* range: 0–306 g/m^2, and *D* range: 0–68 g/m^2. An average of 45% of ANPP was consumed by herbivores. Production and consumption, and consumption and dung deposition were positively correlated across all sites. In addition, sites were grazed when plants were growing.

There was a 19% reduction in ANPP from 1988 to 1989, likely caused by death or injury to plants during the 1988 drought. Drought also appeared to be partially responsible for reductions in elk and bison from 1988 to 1989, which were coincident with declines in *C* and *D*. Results indicate direct effects and suggest indirect effects of a single-season drought on grassland function that will persist for several years after the event.

Key words: bison; consumption; drought; elk; forage quality; grassland function; grasslands; herbivory; landscape ecology; primary production; ungulate migration; ungulates; Yellowstone National Park.

INTRODUCTION

Grasslands supporting abundant herds of large mammalian herbivores sustain the highest chronic rates of herbivory of any terrestrial ecosystem (Detling 1988, McNaughton et al. 1989). The effects of grazers on grasslands are profound and cascade through all trophic levels (McNaughton 1985, Detling 1988, McNaughton et al. 1988). When herbivores are migratory, their effects include additional spatial and temporal components (Senft et al. 1987, McNaughton 1989, 1990). A variety of large herbivores have been shown to exhibit habitat preferences with landscapes, including bison, *Bison bison* (Coppock et al. 1983, Norland et al. 1985), feral horses, *Equus caballus* (Turner and Bratton 1987), eastern gray kangaroos

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[1] Manuscript received 27 February 1991; revised 25 November 1991; accepted 20 January 1992.

[2] Present address: Center for Ecological Research and Education, Campus Box 8007, Idaho State University, Pocatello, Idaho 83209-8007 USA

(Macropus giganteus), wallaroos *(M. robustus robustus)* (Taylor 1984), and both resident (McNaughton 1988) and migratory (McNaughton 1990) African ungulates. As a result, large herbivores can play an important role in determining landscape patterns of energy and nutrient fluxes. Furthermore, since the composite effects of herbivores are partially dependent on other trophic processes (McNaughton 1985) that vary temporally (e.g., soil processes; Birch 1958, Burke 1989, Burke et al. 1989), the timing of herbivore use is an important determinant of the impact of grazers on ecosystem processes.

In precolonial times as much as 25% of the terrestrial habitats were grasslands (Shantz 1954), with fauna in most areas dominated by large mammalian herbivores representing Artiodactyla, Perissodactyla, Proboscidea, or Macropodidae (McNaughton 1989). The conversion of grassland to cropland, and the replacement of native grazers with domesticated grazers has severely reduced the extent of these areas (Risser 1988).

Although much is known about the functional properties of grasslands in general (Coupland 1979, French 1979, Huntley and Walker 1982), and about the impact of native grazers on grasslands in particular (e.g., Coppock et al. 1983, Collins and Barber 1985, Krueger 1986, Polley and Wallace 1986, Day and Detling 1990), little is known about the properties of large grassland ecosystems with large herds of Pleistocene mammalian herbivore fauna. The tropical savanna habitat of east Africa, until now, has been our only point of reference (Lock 1972, Sinclair 1975, Edroma 1981, McNaughton 1983, 1985). Here we present a second example from the grasslands and shrub-grasslands of Yellowstone National Park, a North temperate mountainous reserve, with one of the highest concentrations of native ungulates in North America.

An important question facing ecologists today is how ecosystem processes vary both spatially and temporally in terrestrial habitats (Turner 1989). In this paper we examine the effect of large herds of native ungulates on the functional organization of temperate grasslands. We ask: (1) how do plant aboveground production, ungulate consumption, and amounts of dung deposited at sites vary across a temperate grassland landscape, and (2) how are these processes spatially and temporally linked. Our measurements span two disparate years: (1) 1988, a year of drought and landscape-scale wildfires, when elk and bison populations were at their highest levels in recent decades, and (2) 1989, a near-average year in terms of temperature and precipitation, with lower elk and bison populations. Consequently, we also address how functional properties of this temperate grassland dominated by native herbivores responded to a severe, one-year drought.

METHODS

Study area

Yellowstone National Park occupies 8995 km^2 between 44°08′ and 45°07′ N and 111°10′ and 110° W in the northwest corner of Wyoming, USA (Fig. 1). Elevations in the Park range from 1500 m to over 3000 m, through much of the area is a gently rolling plateau between 1200 and 2600 m (Meagher 1973, Houston 1982). The Park is covered mostly by tertiary and quarternary volcanic deposits that have been glaciated several times since their deposition (Keefer 1987). The climate of the Park features long, cold winters and short, dry summers. Eight ungulate species occur in Yellowstone: elk *(Cervus elaphus),* bison *(Bison bison),* mule deer *(Odocoileus hemionus),*

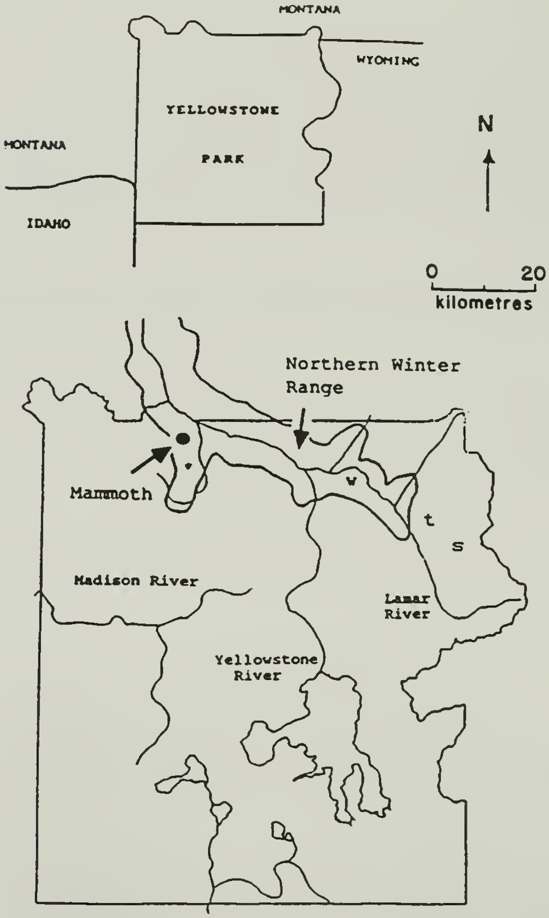

Fig. 1. Map of study region, indicating delineation of the northern winter range and the winter (w), transitional (t), and summer (s) range study site locations. Adapted from Houston (1982).

white-tailed deer *(O. virginianus)*, pronghorn *(Antilocapra americana)*, bighorn sheep *(Ovis canadensis)*, moose *(Alces alces)*, and mountain goats *(Oreamnos americanus)*.

The focus of this study was nonforested habitat in the northeastern portion of Yellowstone used primarily by northern range elk and bison. Herds of northern elk and bison migrate between low-elevation northern winter range and high-elevation summer range. The northern winter range is ≈1000 km^2 in area, comprised of the lower stretches of the Yellowstone River and Lamar River drainages and their tributaries (Fig. 1, Houston 1982). Summer range for northern bison includes ridges and plateaus in the Lamar drainage (Meagher 1973). Northern elk summer range includes high elevations throughout all but extreme southern portions of Yellowstone, and some ridges and plateaus north of the Park (Houston 1982).

Vegetation of the northern winter range is grassland and shrub-grassland with isolated stands of trees. Summer range is dominated by lodgepole pine *(Pinus contorta)* forest. Grassland and shrub-grassland on the summer range can be spatially extensive on ridge lines and in perched drainages on plateaus (e.g., on Mirror Plateau). Most elk and bison summer grazing is concentrated in grassland and shrub-grassland habitat (Cole 1969, Meagher 1973). Nonforested vegetation throughout the study area was markedly heterogeneous due to steep soil and moisture gradients created by uneven topography.

Ungulate management

Management of northern range elk and bison herds has varied considerably, reflecting the evolution of national park policy. Meagher (1973) and Houston (1982) provide thorough histories of bison and elk management in the Park. After 1969, when population reductions (culling) ceased, elk and bison levels were allowed to fluctuate without human interference within the Park (Cole 1971, Meagher 1973, Houston 1982). Northern range elk increased from about 4000–5000 in 1968 to 12 000–16 000 individuals by the late 1970s (Houston 1982). In 1988, after several consecutive years of wet summers and mild winters, northern elk numbered 22 500 (Singer et al. 1989). Meanwhile, northern bison increased from ≈200 in the late 1960s (Meagher 1973) to 577 in 1988 (M. M. Meagher, *personal communication*).

It is impossible to know how current elk and bison population levels compare to those prior to the arrival of white trappers and settlers in the northern Rockies. However, numerous accounts indicate that both elk (Russell 1965, see Houston 1982) and bison (Roe 1951, Meagher 1973, Dary 1974) were abundant in Yellowstone at the time of the Park's establishment in 1872.

Study sites

Study sites were selected to represent a spectrum of topographic positions, primary productivities, and

Table 1. Topographic position, elevation, and vegetation of study sites in the northeast portion of Yellowstone National Park (Wyoming, USA).

Site	Topographic position	Elevation (m)	Vegetation	Herbaceous dominants
Winter range				
w1	Bench	1909	Grassland	*Festuda idahoensis, Lupinus sericeus*
w2	River terrace	1998	Grassland	*Phleum pratense, Poa pratensis*
w3	Valley bottom	1999	Grassland	*Bromus inermis*
w4	River terrace	1888	Sedge meadow	*Carex rostrata*
Transitional range				
t1	Ridgetop	2342	Grassland	*Koelaria cristata, Astragulus miser*
t2	Slope	2318	Grassland	*Phleum pratense, Juncus hallii*
t3	Slope	2294	Shrub–grassland	*Phleum pratense, Acropyron caninum*
Summer range				
s1	Ridgetop	2575	Grassland	*Danthonia unispicata, Poa scabrella*
s2	Slope	2450	Scrub–grassland	*Stipa occidentalis, Bromus carinatus*
s3	Bench	2355	Grassland	*Phleum pratense, Carex* sp.[*]
s4	Bench	2428	Grassland	*Poa* sp.[**], *Stipa occidentalis*
s5	Bench	2428	Forest	*Calamagrostis rubescens*

[*] Includes *C. xerantica* and *C. raynoldsii.*

[**] Includes *Poa nevadensis* and others.

plant community species compositions of nonforested habitat in winter, transitional, and summer range areas (Fig. 1, Table 1). In addition, we studied one summer range forest understory (s5, Table 1). Winter range sites were located in the upper northern winter range, near Crystal Creek (w 1), in the Lamar Valley (w2, w3), and along Slough Creek (w4). Transitional (t1–3) and summer range (s1–5) sites were on the same ridge, between Cache and Calfee Creeks, i.e., Cache–Calfee Ridge. All transitional range communities were within 0.5 km of each other, and summer range sites were separated by no more than 1 km.

Sampling period

Measurements were concentrated during the snow-free periods of two climatically different years: (1) in 1988, a drought year with large landscape-scale wildfires (Romme and Despain 1989), when northern range elk and bison populations were at their highest levels in recent decades, and (2) in 1989, a near-average year in terms of precipitation, when northern range elk were ≈40% (Singer et al. 1989) and bison ≈50% (M. M. Meagher, *personal communication*) of their 1988 levels. The 1988 drought began in early June after above-average moisture in April and May (Singer et al. 1989). Precipitation at Mammoth in the northwest corner of the Park (Fig. 1) was 24% of the 53-mm June (30-year) average, 76% of the 31-mm July average, and 9% of the 38-mm August average (NOAA 1988), resulting in the summer of 1988 being the driest on record (Schullery 1989). In contrast, precipitation at Mammoth for June, July, and August of 1989 was 100%, 99%, and 83% of average, respectively (NOAA 1989). Additionally, in 1988 ≈400 000 ha (45%) of the Yellowstone National Park burned (Schullery 1989). Although no study site burned, fire occurred within 1 km of each site.

Sampling methods, derived variables, and data analysis

Net aboveground primary production (ANPP) and large-herbivore consumption were measured at each site. Aboveground biomass was estimated with the canopy intercept method (Frank and McNaughton 1990), except at a wet sedge meadow (w4) where vegetation was too high for canopy intercept and therefore was clipped instead. The canopy intercept method relates standing crop to the number of hits a pin makes when passed at an angle through vegetation. The technique is affected strongly by plant growth form. Slopes of the regressions of standing crop (g/m^2) on the mean number of contacts for five functional groups encountered in this study ranged from 0.175 to 0.853, and r^2 of the relationships ranged from 0.83 to 0.96.

Temporary exclosures (1.5 × 1.5 m, $n = 5–7$ per site) were used to determine ANPP under grazing and large-herbivore consumption (McNaughton 1985). Exclosures were established at snowmelt and moved at random approximately every 28 d until snow accumulation. During relocation, standing crop was estimated in 0.5-m^2 quadrats in the center of each exclosure and quadrats randomly located in grazed vegetation. Production at each site was calculated as the sum of significant ($P < .05$, one-way ANOVA) increments of standing crop inside exclosures. Consumption was defined as a significant difference ($P < .05$) in standing crop inside vs. outside the exclosures. Consumption for a period greater than one sampling interval at a site was calculated as the sum of the differences during that interval. Variances of production and consumption for periods greater than one sampling interval were calculated by summing interval variances, since variance is additive.

The 28-d sampling interval was a compromise between limiting fencing effects (intensive sampling) and the desire to embrace system diversity (extensive sampling). Notable exceptions to the nominal sampling regimen were 34–36 d intervals for the five summer range sites during July–August 1988, due to restricted back-country access during wildfires. Since most of the vegetation had senesced and no detectable plant growth occurred during these periods, fencing effects were likely negligible. ANPP of *Artemisia tridentata,* a shrub, was taken as peak biomass, since it was not grazed at the two study sites, t3 and s2, where it occurred (Cole 1969, D. A. Frank, *personal observation*). Aboveground biomass of *A. tridentata* was determined with clipped quadrats (0.5 m^2, $n = 10$), because bushes were too tall to be sampled with the canopy intercept method.

Canopy height of herbaceous vegetation was estimated in 1989 as the resting height of a styrofoam sheet (5.0 g, 26 × 21 cm, $n = 10$) when laid gently on the vegetation (McNaughton 1976, 1984). Canopy height and standing-crop estimates were made simultaneously at each site throughout the snow-free season. The concentration of green biomass (GBC, in milligrams per cubic centimetre) was calculated as the quotient of green standing crop (converted to milligrams per square centimetre) divided by canopy height (in centimetres; McNaughton 1976, 1984).

Table 2. Measured vegetation state variables and derived variables.

State variables	
g	Green standing crop
ht	Vegetation canopy height
pg	Standing crop inside movable exclosures
Derived variables	
ANPP	Net aboveground primary production = sum of pg increments
dANPP	Rate of production per day during a sampling interval = (pg increment)/(no. of days in the sampling interval)
C	Consumption during the snow-free season = sum of differences between g and pg
gC	Growing season consumption = sum of differences between g and pg during the growing season[*]
lC	Late-season consumption = sum of differences between g and pg during the late-season[†]
dC	Rate of consumption per day during a sampling interval = (consumption)/(no. of days in the sampling interval)
GBC	Green biomass concentration (mg/cm^3) = g/ht
D	Dung deposited at sites during the snow-free period (Eq. 1)

[*] That period when green biomass was at least 20% of total standing crop.
[†] The period between the end of the growing season and snowfall.

Dung deposition during the snow-free season was calculated as

$$D = \left(\sum_{i=1}^{m} \sum_{j=1}^{10} p_{ij} b_i\right) / 200 \qquad (1)$$

where D (in grams per square metre) is dung deposited during the snow-free period at a site, and p_{ij} and b_i are the number of fecal piles in a 10 × 2 m transect and the mean dry mass of a fecal pile, respectively, for the ith of m ungulate species (e.g., elk, bison) and the jth of 10 transects.

Measured vegetation state variables were standing crop inside movable exclosures *(pg)*, standing crop of grazed vegetation *(g)*, and vegetation height *(ht)*. A list of the derived variables is included in Table 2.

Nitrogen concentrations were determined on aboveground biomass of select grass forages with a Carlo Erba CNS Analyzer using standard protocol. Harvested samples were oven-dried at Yellowstone Park, then shipped to Syracuse where they were rinsed with distilled water, re-oven-dried, and ground to pass a 500 µm mesh screen using a Wiley Mill. Samples were mixed thoroughly before single subsamples were collected from each for analysis.

All the relationships between processes (ANPP, C, gC, lC, dC, dANPP, D) are least-square fits. Between-year differences in processes were examined with paired t tests. Proportions were always arcsine-transformed to satisfy parametric test requirements, except forage nitrogen data, which met assumptions. Nonparametric analyses were used only when satisfying these requirements was impossible. Plant species diversity was indexed with H' (Pielou 1966).

RESULTS

Soils within the major rooting zone (0–10 cm) at the sites were loams, silt loams, and sandy loams (Table 3). Soil pH values were all slightly acidic, ranging from 5.14 in a summer range lodgepole pine forest (the only forest sampled) to 6.75 at the summer range ridgetop site. Bulk density, field capacity, organic matter, and soil nitrogen (N) ranged between 0.83 and 1.32 g/cm^3, 16.0–65.2%, 5.2–25.5%, and 0.1–0.9%, respectively. There was a tendency for pH and bulk density to increase, and field capacity, percentage of organic matter, and percentage of soil N to decline from the base to the top of slopes. A wet sedge meadow in the winter range (w4, Table 1) was notable as having the lowest bulk density and the highest field capacity, percentage of organic matter, and percentage of soil N.

Rates of ecosystem processes

Net aboveground primary production.—An initial objective of the study was to select sites representive of the spectrum of herbaceous aboveground primary productivities (ANPP) encountered by elk and bison. Ranges for ANPP were 27–539 g/m^2 in 1988 and 16–589 g/m^2 in 1989 (Table 4). The least productive community in both years was a summer range ridgetop site (s1, Table 4); the most productive community was a winter range wet sedge meadow (w4, Table 4). Herbaceous production declined from 1988 to 1989 at 6 of 11 sites (Table 4). Moreover, mean ANPP of sites where ANPP was measured during both years declined from 278 g/m^2 in 1988 to 226 g/m^2 in 1989 ($t_{10} = 3.3$, $P <$ .08, paired t test), a decrease of 19%. This indicates that the decline in herbaceous production was a

Table 3. Soil properties at study sites in Yellowstone National Park.

Site	pH	Bulk density (g/cm^3)	Field capacity (% H_2O)	OM* (%)	N (%)	USDA texture categories (%) Sand	Silt	Clay	Soil classification
Winter range									
w1	6.30	1.31	16.0	5.4	0.2	69.7	26.5	3.8	Sandy loam
w2	6.66	1.16	23.6	6.1	0.2	32.2	61.7	6.1	Silt loam
w3	5.84	0.91	34.3	14.2	0.5	38.1	49.4	12.6	Loam
w4	5.67	0.64	65.2	25.5	0.9	23.6	64.1	12.2	Silt loam
Transitional range									
t1	6.14	0.95	35.2	13.8	0.7	43.4	49.9	6.7	Silt loam
t2	5.62	0.90	37.1	18.8	0.7	40.1	52.1	7.9	Silt loam
t3	5.61	0.91	39.6	14.7	0.7	40.1	55.2	4.8	Silt loam
Summer range									
s1	6.75	1.32	19.8	5.2	0.1	59.4	30.1	10.4	Sandy loam
s2	5.89	1.02	30.6	11.3	0.5	48.4	43.1	8.5	Loam
s3	5.57	0.83	46.6	16.6	0.8	42.6	48.2	9.1	Loam
s4	5.45	0.90	35.0	14.5	0.6	37.6	54.1	8.2	Silt loam
s5	5.14	1.06	24.8	7.7	0.2	29.5	52.3	18.2	Silt loam

*Percentage of organic matter from loss on ignition.

landscape phenomenon. Production of *Artemisia tridentata* at two shrub-grassland sites did not differ between years and averaged 55 ± 12 g/m^2 (mean 1 SE, $n = 20$) and 77 ± 14 g/m^2 ($n = 20$) at t3 and s2, respectively.

Table 4. Herbaceous net aboveground primary production (ANPP, means ± 1 SE) and probabilities that 1988 and 1989 values are from the same sample populations. NS denotes nonsignificance ($P > .05$).

Site	ANPP (g/m^2) 1988	1989	*P*
Winter range			
w1	a*	85 ± 7	...†
w2	513 ± 27	380 ± 21	<.001
w3	232 ± 19	204 ± 19	NS
w4	539 ± 31	589 ± 31	NS
Transitional range			
t1	145 ± 23	60 ± 5	<.001
t2	343 ± 19	297 ± 15	NS
t3	241 ± 38	163 ± 37	NS
Summer range			
s1	27 ± 3	16 ± 1	<.01
s2	112 ± 11	84 ± 12	<.01
s3	278 ± 33	248 ± 18	NS
s4	238 ± 22	136 ± 5	<.001
s5	247 ± 18	198 ± 17	<.05

* a = data not available
† Not applicable

Production was associated with several soil properties in both years. For example, Spearman rank correlations showed 1989 ANPP was negatively correlated with bulk density ($P = .05$, $n = 12$, $r_s = -0.56$) and percentage of sand ($P = .03$, $n = 12$, $r_s =$

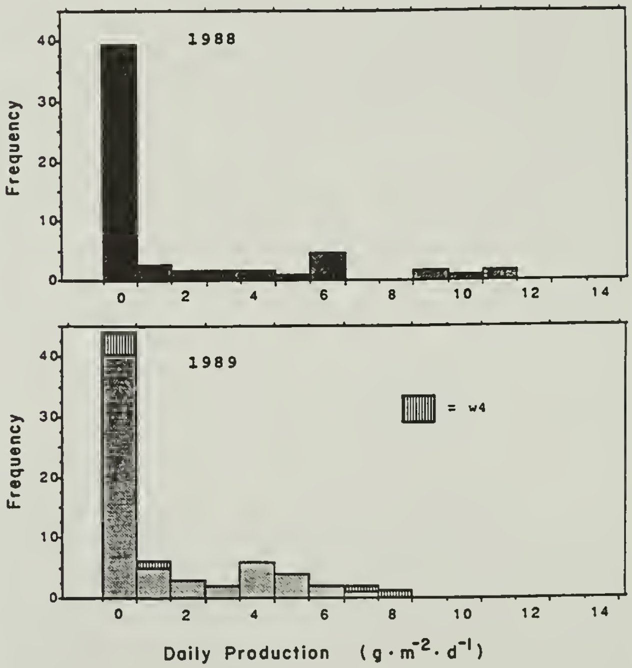

Fig. 2. Frequency histograms of daily aboveground net primary production (*d*ANPP) in 1988 and 1989 at Yellowstone National Park study area. Gray bars represent samples from sites where measurements were made both years.

–0.67), and weakly positively related to percentage of silt ($P = .06$, $n = 12$, $r_s = 0.57$).

The frequency distributions of daily production (*d*ANPP) for both years were distinguished by the large number of zero growth intervals (Fig. 2). For sites sampled in both years (paired sites) no significant growth occurred during 66% and 63% of the intervals in 1988 and 1989, respectively. Daily productivity at paired sites ranged from 0.4–16.7 $g{\cdot}m^{-2}{\cdot}d^{-1}$ in 1988 and 0.36.8 $g{\cdot}m^{-2}{\cdot}\delta^{-1}$ in 1989. The highest *d*ANPP measured during 1989 occurred at a wet sedge meadow (w4) not sampled in 1988. Mean detectable *d*ANPP at paired sites was 5.7 $g{\cdot}\mu^{-2}{\cdot}\delta^{-1}$ in 1988 and 3.2 $g{\cdot}\mu^{-2}{\cdot}\delta^{-1}$ in 1989 ($F_{1,42} = 2.83$, $P = .11$). Maximum *d*ANPP at each of the sites sampled during both years was greater in 1988 than 1989 ($t_8 = 5.09$, $P < .001$, paired *t* test).

Plant growth in Yellowstone occurs locally as a brief, strong pulse, and regionally as a landscape-level wave. Production at the sites began after snowmelt and lasted for 1–2 mo, except in mesic-wet valley-bottoms (w2 and w4) where growth was measured for up to 4 mo (Frank 1990). As in other temperate mountainous regions, the spatial shift of aboveground production in Yellowstone follows the pattern of snowmelt, progressing up elevational gradients, influenced locally by topography, with the advancing season. Plant growth normally begins in March on the lower winter range and sweeps upslope to the upper summer range, lasting in most years into August (D. Despain, *personal communication*).

Nitrogen content of dominant grasses harvested at the same time as biomass estimates declined through the growing season. During the first harvests, ≈28 d after snowmelt, plant nitrogen concentration ranged from 2.5 to 3.7% and was significantly greater than harvests later in the year ($F_{1,31} = 53.3$, $P < .0001$), which ranged from 1.1 to 2.4% (Fig. 3). The percentage of nitrogen (%N) was related to the number of days after snowmelt (d_{as}) ($r^2 = 0.66$, df = 30) by

$$\log \%N = -0.46(\log d_{as}) + 1.15.$$

Implicit in this relationship is a nitrogen wave that is tied to the spatiotemporal pattern of plant growth presented above.

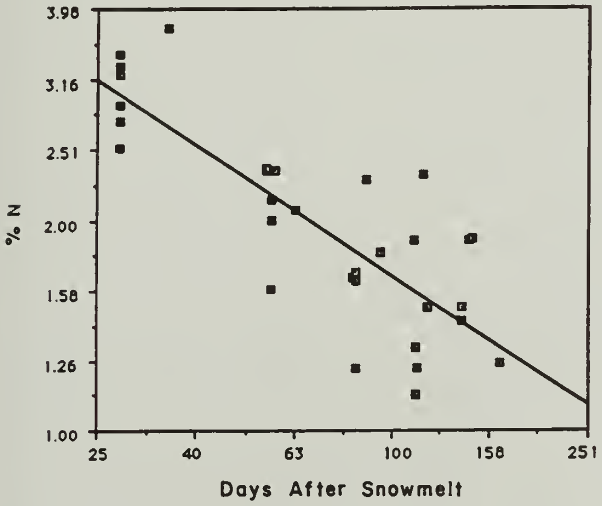

Fig. 3. Relationship of the percentage of nitrogen (%N) of dominant grasses at seven sites in Yellowstone National Park study area and number of days after snowmelt. Note that both axes are log-scaled.

Green biomass concentrations (GBC, in grams per cubic centimetre) and the number of days after snowmelt (d_{as} were negatively related ($r^2 = 0.470$, df = 56, $P < .001$) by

$$GBC = 106.3 - 0.640\ (d_{as})$$

(Fig. 4). Highest values for GBC occurred during the first sample, ≈28 d after snowmelt, at all sites except two, a summer-range ridgetop (s1) and a summer range forest (s5). Restricting analysis to the earliest samples at each site, 32.9% of the variation in GBC was explained by ANPP ($F_{1,9} = 4.41$, $P = .065$), in contrast to ANPP explaining only 4% of the variance ($F_{1,55} = 3.3$, $P = .075$) when both d_{as} and ANPP were included as variables in a multiple regression over the entire snow-free season. From Fig. 4 it is clear that ANPP explains little variation in GBC during the snow-free season, because of a homogenization among sites, e.g., an across-site reduction in GBC, as the season progresses.

Correlation analyses of the relationship between d_{as} and the two components of GBC, green biomass and canopy height (Table 2), showed the decline in

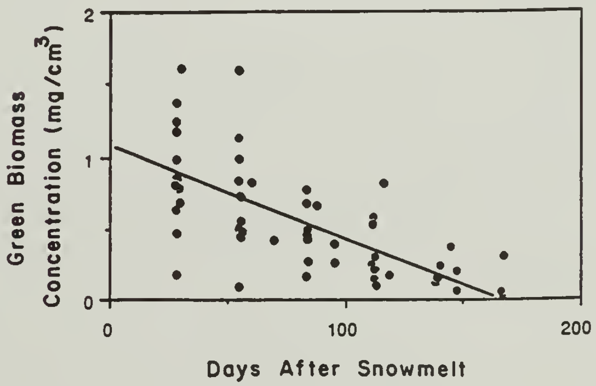

Fig. 4. Relationship between green biomass concentration (GBC) and number of days after snowmelt (d_{as}) at Yellowstone National Park study area.

GBC with length of season was due to a contemporaneous decline in standing green biomass and an increase in canopy height. Days after snowmelt was negatively related to green biomass ($P = .02$, $r = -0.31$, df = 56) and positively related to canopy height ($P = .002$, $r = 0.41$, df = 56).

Herbivore consumption (C).—Whether a herbivore grazes live or dead tissue has important implications for both the herbivore and the plant that is grazed. Therefore, in addition to presenting consumption data for the entire snow-free period, we report offtake during the growing season, arbitrarily defined as that portion of the season when green biomass comprised at least 20% of the standing crop, and the late season, that period after the growing season until snowfall.

Consumption varied widely and was affected strongly by northern-range herd size. Growing-season consumption *(gC)* at sites sampled in both years and grazed in at least one year ranged between 32 and 249 g/m^2 in 1988 and 20–137 g/m^2 in 1989 (Table 5). At wl, where only 1989 data exist, offtake was 20 g/m^2, the lowest of any site sampled that year. Mean *gC* for grazed sites measured in both years declined from 111 g/m^2 in 1988 to 63 g/m^2 in 1989 (t_7, = 2.5, P .04, paired t test), a decrease of 43%. Reductions in *gC* occurred at six of eight sites (Table 5). Most notable was a 65% decline at w2, which in 1988 had the highest rate of *gC*.

At t3 and s2, shrub-grassland sites where *A. tridentata* occurred, herbaceous vegetation between and under shrubs was sampled separately. At no time did significant consumption occur under *A. tridentata*, or did we find evidence of browsing on *A. tridentata* (D. A. Frank, *personal observation*). This suggests a negative relationship between sagebrush abundance and herbivory across the landscape.

The percentage of ANPP consumed during the growing season at grazed sites ranged between 22 and 58 % in 1988 and 23–51 % in 1989. Mean percentage of herbivory for sites grazed in either year declined somewhat from 39.2% in 1988 to 29.0% in 1989 ($t_7 =$ 2.17, $P = .07$, paired t test), and the number of sites that were not grazed increased from three in 1988 to five in 1989.

Offtake late in the season *(lC)* differed markedly between years. In 1988, detectable *lC* occurred in five communities, ranging between 24 and 107 g/m^2, and averaging 60 g/m^2 (Table 5). In contrast, no grazing occurred during the late season at any site during 1989.

Consumption during the entire snow-free season *(C)* at grazed sites ranged between 32 and 306 g/m^2 in 1988 and 20–137 g/m^2 in 1989 (Table 5). Herbivory declined from 1988 to 1989 at six of eight sites (Table 5). Mean *C* for sites grazed during at least one of the years declined from 149 g/m^2 in 1988 to 63 g/m^2 in 1989 ($t_7 = 3.9$, $P < .006$, paired t test), a reduction. Note that since no late-season consumption occurred during 1989, *gC* equalled *C* during that year.

Daily consumption *(dC)* was calculated as the amount consumed during an interval divided by the number of days of the interval. Frequency histograms of *dC* at grazed sites for 1988 and 1989 (Fig. 5) are similar to those for *d*ANPP (Fig. 2). In both years no

Table 5. Consumption during the growing season *(gC)*, late-season consumption *(lC)* and consumption during the snow-free season *(C)* during 1988 and 1989, all as means ± 1 SE. Probabilities and units as in Table 4.

	g			*lC*			*C*		
Site	1988	1989	*P*	1988	1989	*P*	1988	1989	*P*
Winter range									
w1	a[*]	20 ± 6	...[†]	a	0	...	a	20 ± 6	...
w2	249 ± 49	86 ± 25	.01	0	0	NS	249 ± 49	86 ± 25	.01
w3	50 ± 11	0	...	56 21	0	...	106 ± 16	0	...
w4	0	0	...	0	0	...	0	0	...
Transitional range									
t1	47 ± 13	0	...	63 ± 6	0	...	111 ± 46	0	...
t2	199 ± 19	137 ± 15	.05	10 7± 14	0	...	306 ± 15	137 ± 15	.001
t3	90 ± 28	53 ± 15	NS	0	0	NS	90 ± 28	53 ± 15	NS
Summer range									
s1	0	0	...	0	0	...	0	0	...
s2	32 ± 3	20 ± 2	.01	0	0	NS	32 3	20 2	.01
s3	97 ± 24	127 ± 15	NS	51 ± 8	0	...	148 15	127 15	NS
s4	124 ± 15	77 ± 5	.01	24 ± 8	0	...	149 23	77 13	.001
s5	0	0	...	0	0	NS	0	0	...

[*] a = data not available

[†] Not applicable.

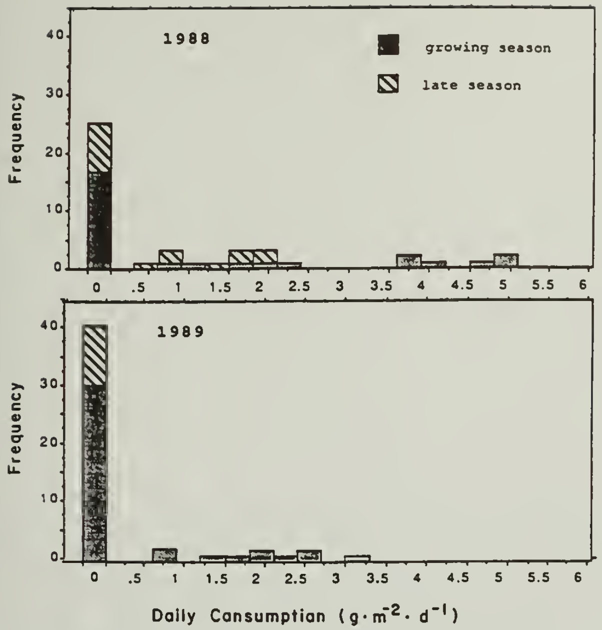

Fig. 5. Frequency histograms of daily consumption *(dC)* by large herbivores in Yellowstone National Park study area in 1988 and 1989.

Table 6. Dung deposited during 1988 and 1989. Probabilities and units as in Table 4.

	Dung deposited, *D* (means ± 1 SE)		
Site	1988	1989	*P*
Winter range			
w1	22 ± 6	7 ± 3	<.04
w2	28 ± 8	12 ± 3	NS
w3	15 ± 5	12 ± 4	NS
w4	0	0	...†
Transitional range			
t1	22 ± 4	2 ± 2	<.001
t2	41 ± 7	20 ± 5	<.03
t3	4 ± 2	8 ± 3	NS
Summer range			
s1	2 ± 1	0	...
s2	18 ± 5	6 ± 1	<.03
s3	68 ± 9*	21 ± 6	<.001
s4	14 ± 3	45 ± 9*	<.001
s5	4 ± 2	1± 1	NS

*Site used as elk bedding area.
†Not applicable

significant offtake occurred during the majority of the sampling intervals: for 61 % and 76% of the growing season samples, and 57% and 76% of all samples in 1988 and 1989, respectively. The range of *dC* in 1988 was 0.5–5.0 g·m^{-2}·d^{-1} and in 1989 was 0.7–3.1 g·m^{-2}·d^{-1}. Mean detectable *dC* during the growing season declined from 3.1 g·m^{-2}·d^{-1} in 1988 to 1.9 g·m^{-2}·d^{-1} in 1989 ($F_{1,19} = 4.80$, $P = .04$). In 1988, mean detectable *dC* was lower in the late season, 1.7 g·μ^{-2}·δ_{-1}, than during the growing season ($F_{1,17} = 8.92$, $P = .008$). This indicates the offtake rate in 1988 among the sites was greater during the growing season than after it.

Flux of dung from ungulates to the soil.—Oven-dry masses of elk, bison, and pronghorn fecal piles randomly collected near the study sites were 92 ± 10.6 g (mean 1 SE, $n = 38$), 294 ± 25.6 g ($n = 36$), and 37 ± 4.2 g ($n = 10$), respectively. Maximum values of *D* during the snow-free periods of both years occurred at sites that, in addition to receiving inputs while animals were grazing, were used as bedding areas by elk: s3 received 68 g/m^2 in 1988 and s4 received 45 g/m^2 in 1989 (Table 6). For the remaining communities, fecal return ranged between 2 and 41 g/m^2 in 1988 and 0–21 g/m^2 in 1989 (Table 6). Mean D at those sites declined from 15 g/m^2 in 1988 to 8 g/m^2 in 1989 ($P <$ .02, $F_8 = 3.1$, paired *t* test), a decrease of 48%. This indicates that the reduction of herbivores from 1988 to 1989 dramatically depressed the flux of dung from grazers to the soil across the Yellowstone landscape.

During the snow-free season, D did not differ between seasonal-use areas ($F_{2,217} = 0.26$). However, over the entire year it is likely that *D* varied substantially at this spatial scale, since herbivores concentrate in the winter range for at least 5 mo (November to March). During the winter of 1988–1989, dung deposited at winter range sites wl, w2, w3, and w4 equalled 35.5 ± 8.0, 48.2 ± 4.5, 57.7 ± 7.1, and 166.1 ± 14.1 g/m^2, respectively (means ± 1 SE). These amounts were 160%, 170%, 380%, and 791% of the quantities deposited at the same sites during the snow-free season. Site w4, a wet sedge meadow, was grazed intensely by elk and bison during the winter. The dung deposited at w4 appeared to be as concentrated as at any site we observed in the northern range.

Relationships between processes

Net aboveground primary production and herbivory.—In an effort to understand fully the link between plants and herbivores, consumption was related to vegetation in several ways. Consumption during the growing season *(gC)* was associated with ANPP and community species diversity (*H′*) in 1988 ($r^2 = 0.63$, $P = .0002$, df = 8) by

$$gC = -108.9 + 0.33(\text{ANPP}) + 68.8(H'),$$

and in 1989 ($r^2 = 0.53$, $P = .006$, df = 10) by

$$gC = -68.3 + 0.16(\text{ANPP}) + 47.9(H'),$$

with ANPP and H' explaining 36.7% and 26.6% of the variation in 1988, and 19.7% and 33.6% of the variation in 1989, respectively.

The contribution of H' in predicting gC is almost solely due to a summer-range forest, s5, and a winter-range wet sedge meadow, w4. If these sites are omitted in the analysis, H' no longer is significant and gC becomes linearly and positively associated with ANPP among sites where the variables were measured during both years, in 1988 ($r^2 = 0.90$, $P = .0001$, df = 7) by

$$gC = -30.8 + 0.55(\text{ANPP})$$

and in 1989 ($r^2 = 0.53$, $P = .025$, df = 7) by

$$gC = -4.0 + 0.34(\text{ANPP})$$

(Fig. 6A). Slopes of the relationship could not be discriminated from one another ($F^{1,14} = 2.47$, $P = .14$) and intercepts were indistinguishable from zero ($t_7 = -1.61$ for 1988; $t_7 = -0.16$ for 1989). A winter range grassland sampled only in 1989 (w1) lies well within 95% confidence limits calculated from other samples that year.

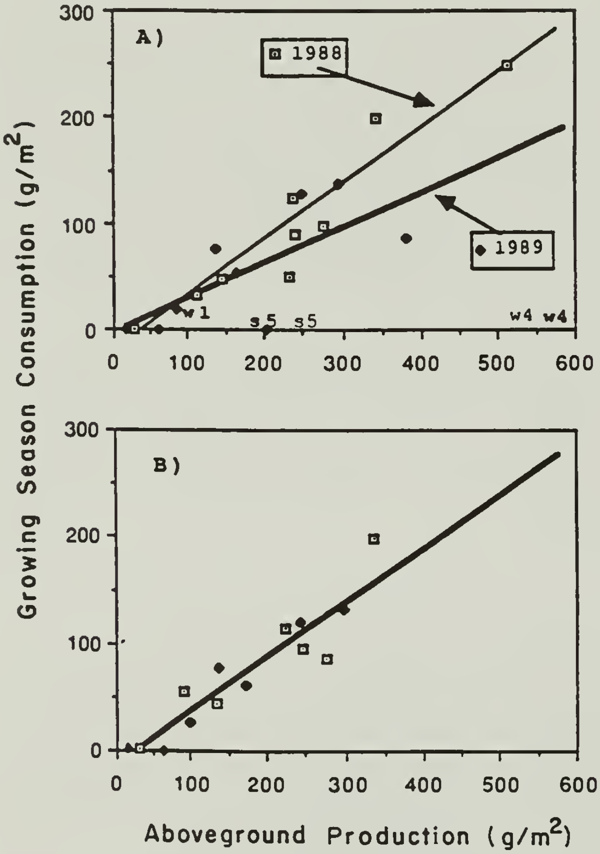

Fig. 6. Relationship of growing-season consumption (*gC*) on aboveground net primary production (ANPP) during 1988 and 1989 at Yellowstone National Park study area for (A) all sites, and (B) transitional and summer range sites only. Alphanumerically coded samples were not used to calculate regression equations. For w4 and s5, 1989 samples are in bold lettering.

It is clear from Fig. 6A that w4 and s5 were not grazed, despite exhibiting high productivities. Both sites were dominated by single graminoid species that represented 90% of the total standing crop: *Carex rostrata* at site w4, and *Calamagrostis rubescens* at site s5. Furthermore, w2, a relatively productive winter range grassland (two-year mean ANPP equalled 218 g/m^2) was not grazed in 1989 and had one grass, *Bromus inermis,* contributing >90% of the aboveground biomass. The nearly monospecific composition of these communities was profoundly different from that of other communities. This is reflected in the low H' values for the three sites, ranging from 0.37 to 0.71, compared with values from 1.41 to 2.74 for other sites. These results suggest there are two different types of plant communities in Yellowstone, distinguished by both their structure and function: one of low species diversity avoided by large herbivores during the snow-free season, and a second possessing higher species diversity and grazed by large herbivores during the snow-free year. Although only 3 of 12 sites studied here exhibited near-monospecific compositions, sites dominated by single species in this fashion are common in lodgepole pine forests throughout Yellowstone Park, and therefore, constitute an important structural and functional component of Yellowstone at the ecosystem level.

For sites that were grazed during the study, in 1989 there was a weakly significant lower slope for the relationship between gC and ANPP for winter-range sites compared to the slope calculated from higher elevation sites ($F_{1,6} = 5.20$, $P < .06$). In contrast, during 1988 there was no difference between winter and other seasonal ranges ($F_{1,5} = 0.76$, $P < .42$).

To examine rates of herbivory at sites off the winter range, the relationship between gC and ANPP was reevaluated for transitional and summer range sites only. Because we were just interested in grazed vegetation, the ungrazed forest summer range site, s5, and ungrazed areas beneath *A. tridentata* were omitted. There was a positive relationship between gC and ANPP in 1988 ($r^2 = 0.86$, $P = .003$, df = 5) with

$$gC = -14.8 + 0.53(\text{ANPP})$$

and in 1989 ($r^2 = 0.94$, $P = .0003$, df = 5) with

$$gC = -17.4 + 0.54(\text{ANPP})$$

(Fig. 6B). Two points should be noted. First, ANPI was a precise predictor of *gC*, explaining 86% and 94% of the variation in *gC* in 1988 and 1989, respectively. Second, the regression lines are so similar that they cannot be visually distinguished in Fig. 6B. This indicates that, despite the great differences in climate and ungulate numbers between years, the rate of grazing per unit of production was the same in transitional and summer range areas.

Consumption during the snow-free season *(C)* and site production (ANPP) in 1988 were positively relate ($r^2 = 0.74$, $P = .003$, df = 7) by

$$C = -8.50 + 0.60(\text{ANPP})$$

(Fig. 7). The relationship between *C* and ANPP in 1989 was the same as that for *gC* and ANPP. The difference in late-season consumption between years, high in 1988 vs. none in 1989, was not enough to differentiate slopes, of *C* on ANPP for the two years ($F_{1,14} = 2.02$, $P = .18$). In addition, intercepts could not be discriminated from zero ($t_7 = -0.24$ for 1988; $t_7 = 0.16$ for 1989).

To explore temporal interactions between herbivores and vegetation, daily consumption *(dC)* was related to a variety of seasonally fluctuating plant variables. Correlation analyses performed on 1989 data revealed no association between daily consumption *(dC)* and either green standing crop ($P = .40$) or total standing crop ($P = .44$). Instead, *dC* was positively associated with both daily production, (*d*ANPP, $r = 0.54$, $P < .0001$) and green biomass concentration (GBC, $r = 0.45$, $P = .003$). A stepwise regression with *dC* as the response variable and *d*ANPP and GBC as independent variables loaded *d*ANPP only, indicating that GBC did not explain any further variance in *dC*. Among grazed sites that were sampled in both years, daily consumption *(dC)* during the growing season and daily production were positively related in 1988 ($r^2 = 0.50$, $P = .0001$, df = 26) with

$$\text{dC} = 0.25 + 0.34(d\text{ANPP})$$

and in 1989 ($r^2 = 0.30$, P .0003, df = 39) with

$$\text{dC} = 0.13 + 0.23(d\text{ANPP})$$

(Fig. 8A). Much of the dispersion of the samples around the regression lines was due to animals leaving the winter range early in the growing season when plants were growing. When the relationship was reevaluated for transitional and summer ranges only, *dC* was related to *d*ANPP in 1988 ($r^2 = 0.92$, $P < .0001$, df = 16) by

$$dC = 0.082 + 0.42(d\text{ANPP})$$

and in 1989 ($r^2 = 0.79$, $P < .0001$, df = 28) by

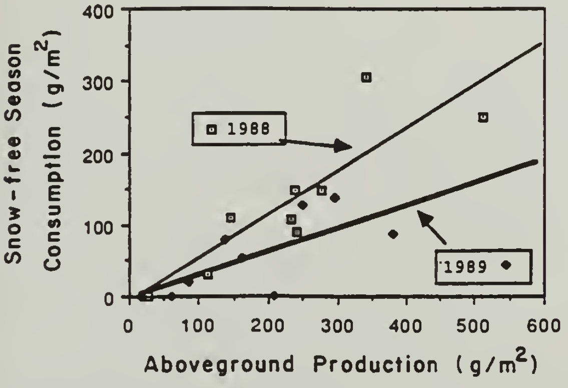

Fig. 7. Relationship of consumption during the snow-free season *(C)* to aboveground net primary production (ANPP) for 1988 and 1989 at the Yellowstone National Park study area.

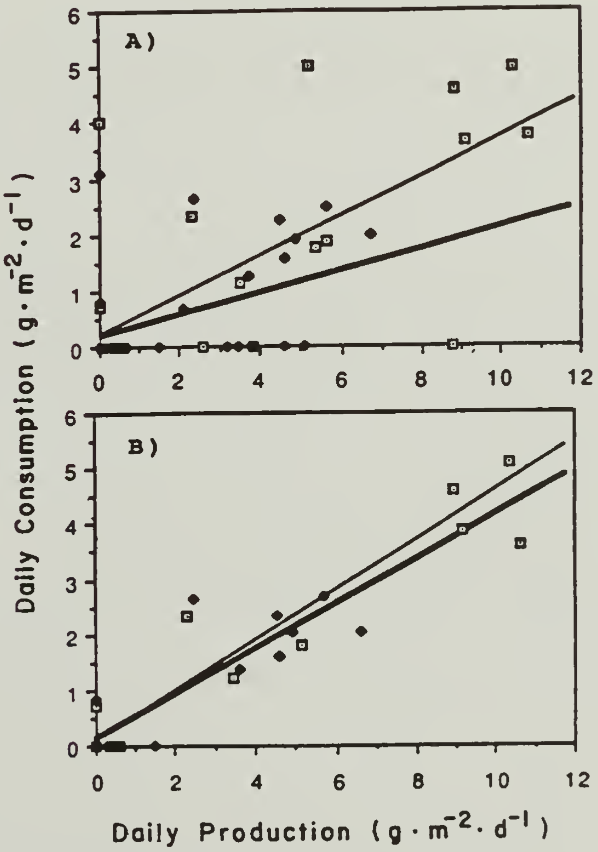

Fig. 8. Relationship of growing season daily consumption *(dC)* to daily aboveground net primary production (*d*ANPP) at the Yellowstone National Park study area for (A) all grazed sites and (B) transitional and summer range grazed sites only. Symbols and lines as in Fig. 6.

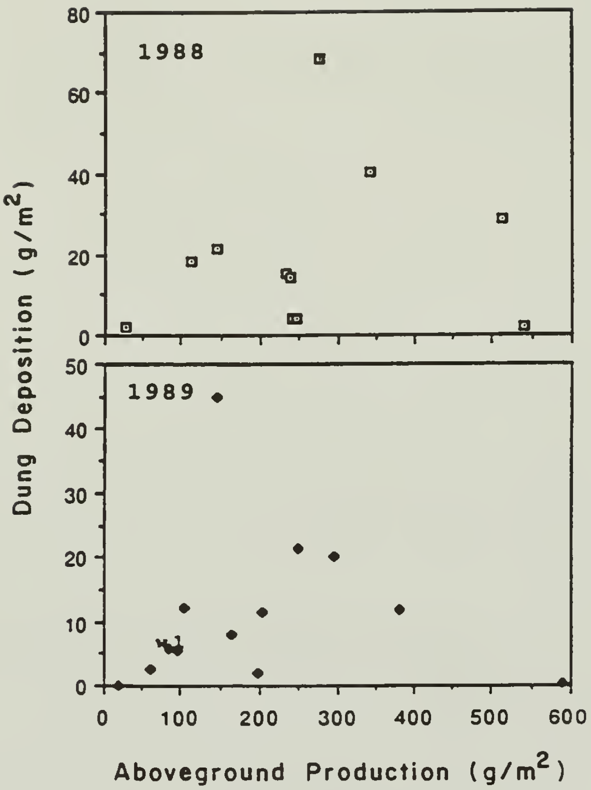

Fig. 9. Scattergram of dung deposition *(D)* relative to aboveground production (ANPP) for 1988 and 1989 at the Yellowstone National Park study area. Symbols are sites sampled in both years.

$$dC = 0.048 + 0.385(d\text{ANPP})$$

(Fig. 8B). Slopes for the two years were the same ($F_{1,34} = 0.59$) and intercepts could not be discriminated from zero ($t_{16} = 0.53$ for 1988; $t_{28} = 0.55$ for 1989).

Dung deposition, herbivory, and aboveground net primary production.—There was no first- or second-order polynomial relationship between D and ANPP (Fig. 9). However, D and consumption during the snow-free season *(C)*, omitting elk bedding areas that were statistical outliers (outside the 95% prediction limits of the regressions), were positively related in 1988 ($r^2 = 0.79$, $P < .0001$, df = 8) by

$$D = 3.99 + 0.11(C),$$

and in 1989 ($r^2 = 0.81$, $P = .0004$, df = 8) by

$$D = 2.94 + 0.12(C)$$

(Fig. 10). Slopes could not be discriminated between years ($F_{1,16} = 0.20$, $P = .66$), and intercepts for both years were indistinguishable from zero (t = 1.44 for 1988; t = 1.09 for 1989).

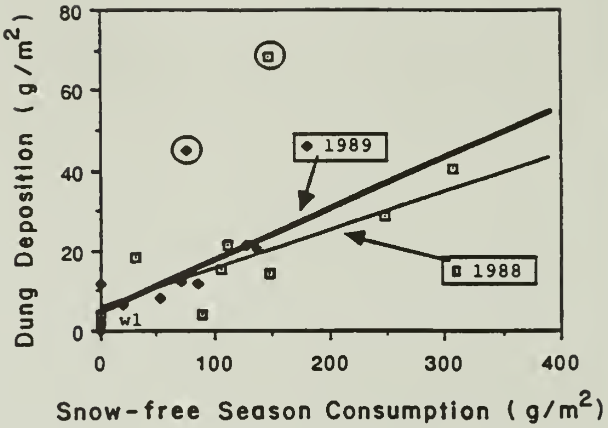

Fig. 10. Relationship of dung deposition *(D)* to consumption during the snow-free season *(C)* for 1988 and 1989 at the Yellowstone National Park study area. Circled samples were elk-bedding areas and were not included in calculations.

If the relationship between D and ANPP is considered only for sites that were grazed and where elk did not bed, D was positively related to ANPP for pooled 1988 and 1989 data ($r^2 = 0.47$, $P = .003$, df = 14) by

$$D = 2.84 + 0.05(\text{ANPP}).$$

The intercept could not be differentiated from zero ($t = 0.75$). Therefore, in areas that they graze, large herbivores return nutrients to the system at a constant rate per unit ANPP.

DISCUSSION

Temporal association between processes: plant growth and ungulate grazing

Aboveground net primary production (ANPP) in Yellowstone occurs as a brief pulse locally and regionally as a nitrogen-rich wave that follows the elevational gradient. ANPP begins in the low winter range in the early spring and ends in the high summer range in late summer. There is a link between the timing of plant growth and the timing of consumption. Since forage nitrogen content (%N) and green biomass concentration (GBC) are highest during plant growth, ungulates increase forage quality and the yield of high-quality forage per bite by grazing young vegetation. Yellowstone may be able to support large herds of herbivores because of its size, the elevation gradient that makes this young, nutritious, and concentrated forage available for up to 6 mo/yr, and the migratory behavior of the most abundant grazers.

In the Serengeti ecosystem, ungulate migration is also associated with animals following a seasonal wave of green vegetation (McNaughton 1979). However, in contrast to the predictable pattern of plant growth along an elevational gradient in Yellowstone, production in the Serengeti is distributed stochastically in space according to rainfall events. The high level of concordance between Yellowstone and the Serengeti with reference to grazer migration suggests that the spatial and temporal dynamics of primary production is a fundamental factor in the functional organization of grassland ecosystems with abundant large herbivore populations.

There was evidence for functional dissimilarity between the winter range and other seasonal ranges. During 1989 the rates of herbivory (slope of the relationship between consumption during the growing season, *gC*, and ANPP) were lower at winter range sites than at transitional and summer range sites. There was no difference between seasonal ranges in 1989, suggesting that grazing intensity during the growing season may be lower on the winter range than other areas of the Park during years of moderate elk and bison population levels (1989), and the same when populations are large (1988). Seasonal segregation of grazing leading to forage conservation during the food-limiting period of the year, e.g., winter in temperate grasslands and the dry season in tropical grasslands, is a feature common to ecosystems supporting large herds of migratory herbivores (Sinclair and Norton-Griffiths 1979, Morgantini and Hudson 1988). These results indicate a potential interaction between herbivore population size and winter forage quantity in Yellowstone.

Spatial associations of ecosystem processes

The nonforested landscape of Yellowstone's northern range is functionally heterogeneous. All three processes measured in this study, aboveground net primary production (ANPP), ungulate consumption *(C)*, and dung deposition *(D)* ranged widely among study sites. Aboveground productivity varied by ≈20-fold in 1988 and by >35-fold in 1989. Consumption ranged from 0 to 306 g/m^2 in 1988 and 0 to 137 g/m^2 in 1989. Fecal deposition at study sites ranged from 2 to 68 g/m^2 in 1988 and 0 to 45 g/m^2 in 1989.

The spatial pattern of ecosystem processes in semiarid habitats is tied to soil properties, which are influenced by topography (Schimel et al. 1985, Burke 1989, Burke et al. 1989). In Yellowstone, aboveground production was associated with several soil characteristics. However, since large herbivores have profound direct and indirect effects on ecosystem processes (Detling 1988, McNaughton et al. 1988, Pastor et al. 1988), grazers may alter the spatial pattern of energy and nutrient fluxes by their pattern of landscape utilization. In this study, consumption was positively and linearly associated with site aboveground production. This indicates that as production of a landscape patch increases, so too does consumption at a constant rate per unit of productivity. In addition, the fecal return by ungulates was positively and linearly linked to both production and consumption, except in elk-bedding areas. Ungulates excrete >90% of the phosphorous they ingest, ≈99% of which is fecal, and 65-95% of their ingested nitrogen, ≈85% of which is urinary (Ruess 1987). Excretal phosphorous and nitrogen are in forms readily available to plants and soil microbes (Wilkinson and Lowery 1973, Floate 1981). If dung deposited at the sites is used as an index of nutrient return from ungulates to the soil, the positive association between dung deposition and both aboveground grassland production and grazing suggests that production and grazing are coupled to herbivore-facilitated nutrient cycling in Yellowstone.

It is notable that a winter range wet sedge meadow (w4) and a summer range forest (s5) exhibited dramatically different relationships between ANPP and consumption than other sites. Although both sites were productive, neither was grazed. In addition, a productive winter range grassland site, w3, was avoided in 1989. All three communities were quasi-monocultures, with a single species contributing >90% of the standing crop. Ungulates grazed areas adjacent to each site, suggesting the communities were avoided because of their low forage quality or palatibility. The environmental factors promoting both exceptionally high species dominance in the vegetation and low herbivore utilization is not clear.

Consumption in Yellowstone's northern range compared to other ecosystems

Rates of primary production and herbivore consumption are fundamental properties of ecosystem food-web structure. Although aboveground production and herbivory have been examined in most habitats, these measurements are rare for areas, such as Yellowstone, that support large populations of native large herbivores.

Here we compare herbivory in Yellowstone with other ecosystems using a previously reported data set (McNaughton et al. 1989) of coupled aboveground production and herbivore consumption (by both insects and large herbivores) for a variety of terrestrial habitats. Herbivore consumption *(C)* and net foliar

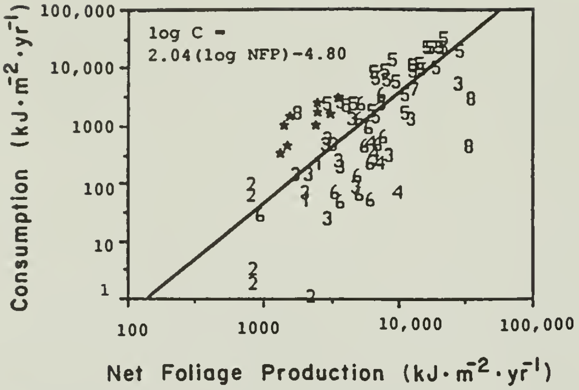

Fig. 11. Relationship of herbivore consumption, *C*, to net foliage production, NFP, for terrestrial ecosystems. Codes are: 1 = desert; 2 = tundra; 3 = temperate grassland, 4 = temperate successional old field; 5 = unmanaged tropical grassland; 6 = temperate forest; 7 = tropical forest; 8 = salt marsh; 9 = agricultural tropical grassland; and * = Yellowstone grassland. Adapted from McNaughton et al. 1989, 1990.

production (NFP) were strongly and positively related in that data set. Foliar production equalled ANPP for all habitats except forests, where it did not include wood production, which is considered largely unavailable to herbivores. The relationship was heavily influenced by samples from East African parks and game reserves (Sinclair 1975, McNaughton 1985) that had greater proportions of their primary production grazed than all other ecosystems. Superimposing samples of grazed sites in Yellowstone, representing single-year measurements or, when available, two-year averages (Fig. 11), it is clear that rates of herbivory at Yellowstone lie consistently above the best-fit line determined by McNaughton et al. (1989) for terrestrial ecosystems in general. A Waller-Duncan Bayes LSD range test, adjusted for unequal sample sizes (Kramer 1956), on arcsine-transformed proportion-consumed data, grouped African and Yellowstone samples together, which verifies statistically what is visually apparent from Fig. 11: the percentage of NFP consumed in these two ecosystems is similar and higher than in other terrestrial ecosystems. Yellowstone was also grouped with the salt marsh, indicating offtake in salt marshes can also be high. Consumption averaged 62% at African game reserve sites and 45% at grazed northern-range Yellowstone sites. Herbivory was over six times as high in Yellowstone as in other temperate grassland sites (consumption = 7.9%), which were small reserves with, likely, small populations of large herbivores.

These results suggest that grassland ecosystems with abundant large herbivores are functionally similar to aquatic systems that support high chronic levels of herbivory (Carpenter and Kitchell 1984, Berquist and Carpenter 1986, Detling 1988), and an understanding of these terrestrial grazing ecosystems can come only from their direct study and not by extrapolation from other ecosystems. Furthermore, these findings suggest that high rates of herbivory and concomitant structural and functional food-web properties may have been typical for grassland ecosystems that, prior to the spread of European influence, supported large herds of ungulates throughout all of Africa (Ford 1971), North America (Roe 1951, Dary 1974), and Eurasia (Bannikov et al. 1961), and Macropods in Australia (Newsome 1971, 1975).

The effect of drought on ecosystem processes

Climate is the principal driving variable of ecosystem processes. We documented dramatic reductions in aboveground primary production, consumption, and the flux of nutrients from ungulates to the soil, one year after a major drought in the Yellowstone grasslands.

The frequently reported relationship between grassland production and climatic estimates of water balance using temperature and precipitation (Lieth 1973, Sims and Singh 1978, Lauenroth 1979, Stephenson 1990), and the demonstrated stimulation of grassland production by irrigation (Dodd and Lauenroth 1979), implicates moisture as an important limiting factor of grassland productivity. We thus were surprised that production in Yellowstone was higher in 1988, a year of drought, than in 1989, a year of near-average precipitation. A likely principal contributing factor in the decline was the death or injury of plants during the 1988 drought, which reduced the productivity potential at the sites in 1989. Grasses that possess belowground perennating structures are considered protected from drought (Coughenour 1985). The near disappearance of some dominant grass species from 1988 to 1989, e.g., peak biomass decline of *Danthonia unispicata* from 16.7 g/m^2 to 0.7 g/m^2 at an ungrazed summer range site, s1 (Frank 1990), is testimony to the severity of the 1988 drought in some parts of the northern range.

The 1988 drought affected herbivores by reducing the duration of nutritious forage late in the season (Frank 1990), which likely led to ungulates entering the ensuing winter in relatively poor condition. Furthermore, drought-induced wildfire burned portions of the northern winter range and limited winter forage. These direct (reduced late-season forage quality) and indirect (reduced winter range) drought effects interacted with a severe 1988-1989 winter that produced: (1) a large number of winter-killed elk and (2) a larger-than-normal winter migration out of the Park where many elk and bison were shot (Singer et al. 1989). The result was dramatic declines in northern-range elk and bison populations, and, consequently, reductions in average growing season consumption by 43%, and dung deposition by 47%. Because large herbivores have effects on ecosystems that pervade all trophic levels (McNaughton et al. 1988), factors that determine the numbers of grazers have important indirect effects on ecosystem function. The reduction in nutrient fluxes through herbivores may have reduced rates of nutrient cycling across the landscape in 1989.

A second potential type of functional response to drought is its effect on the relationship between processes. Although results must be interpreted cautiously since data are limited, there were between-year consistencies in the relationships of three pairs of processes: (1) growing season consumption *(gC)* and aboveground production (ANPP), particularly on transitional and summer ranges, (2) daily aboveground production (*d*ANPP) and daily consumption *(dC)*, and (3) dung deposition *(D)* and consumption during the snow-free season *(C)*. These results suggest grassland functional integrity through time in reference to the relationships between trophic levels. However, information from years of high ungulate numbers and low plant production, or vice versa, are needed to thoroughly explore this phenomenon. In contrast, there was a marked difference in grazing during the late season between years. During 1988 five sites were grazed at an average rate of 60 g/m^2, while in 1989 no site was grazed. An explanation for this stark between-year distinction stems from the 1988 fires that concentrated ungulates on unburned areas in late summer and fall 1988, and in 1989 may have drawn grazers away from the study sites into burned valleys that provided high-quality forage (Knight and Wallace 1989). Wildfire did not appear to affect ungulate foraging patterns during the growing season of either year (Frank 1990).

Synthesis

Large mammalian herbivores are mobile and functionally integrated components of the semiarid habitats that they dominate. By tracking young vegetation in Yellowstone, herbivores prolong a nutritionally rich diet while simultaneously maintaining high foraging efficiency. Topographically determined edaphic patterns are important determinants of energy- and nutrient-flux patterns in most semiarid habitats. Because of the direct and indirect effects large herbivores impart on semiarid landscapes, their pattern of landscape use can bear substantially on patterns of ecosystem processes. Processes measured in this study (ANPP, *C, D*) varied widely among sites in Yellowstone. Furthermore, there were positive spatial associations between (1) aboveground production and consumption, and (2) consumption and nutrient return to sites from herbivores. These results suggest native herbivores may steepen gradients of energy and nutrient fluxes in landscapes, beyond those gradients induced by topography alone.

Drought had a severe effect on grassland and shrub–grassland ecosystem function. Results indicate large direct and indirect effects of drought on net energy and nutrient flux in Yellowstone. Direct drought-induced death and injury of plants reduced the base of the food web, and, thus, the energy- and nutrient-capturing capacity of the ecosystem. Direct effects on ungulate condition and indirect effects through wildfire were likely involved in the decline in elk and bison numbers, which in turn meant reductions in both consumption and nutrient flux through grazers (indexed with dung deposited at sites). The decline in grazers probably had indirect cascading effects on trophic processes that should be expected to reverberate in this grazing-dominated ecosystem until herbivore populations recover. These results show how dramatically a severe drought of one-year duration can alter ecosystem function.

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Evidence for the Promotion of Aboveground Grassland Production by Native Large Herbivores in Yellowstone National Park

Douglas A. Frank, Samuel J. McNaughton

Biological Research Laboratories
Syracuse University
Syracuse, NY 13244-1220 USA

Abstract. We examined the effect of native large herbivores on aboveground primary production of nonforested habitat in Yellowstone National Park, Wyoming. Productivity of vegetation grazed by elk *(Cervus elaphus)* and bison *(Bison bison)* was compared with that of ungrazed (permanently fenced) vegetation at four sites. Two methods were used that, we believed, would provide the most accurate measurements under the different grazing regimes encountered in the study. Production of ungrazed vegetation in permanent exclosures (10 × 10 m or 15 × 15 m, 3 per site) and that of vegetation that was grazed only in the winter was taken as peak standing crop. Production of vegetation grazed during the growing season was the sum of significant increments ($P < 0.05$) in standing crop inside temporary exclosures (1.5 × 1.5 m, 6 per site) moved every four weeks to account for herbivory.

Aboveground productivity of grazed vegetation was 47% higher than that of ungrazed vegetation across sites ($P < 0.0003$). This result could be explained by either a methodological or grazer effect. We believe it was the latter. Results from a computer simulation showed that sequential sampling with temporary exclosures resulted in a slight underestimation of production, suggesting that the reported differences between treatments were conservative. We suggest that stimulation of aboveground production by ungulates may be, in part, due to the migratory behavior of native ungulates that track young, high quality forage as it shifts spatially across the Yellowstone ecosystem.

Key words: Herbivory – Grasslands – Primary production – Yellowstone National Park

Field evidence for large herbivores facilitating aboveground grassland production is limited to tropical ecosystems. Native migratory grazers in Africa (McNaughton 1979a, 1979b; Tomlinson 1986) and free-ranging domesticated cattle in India (Pandey and Singh 1992) have been shown to stimulate aboveground production as a result of a positive feedback loop produced by indirect herbivore effects on other trophic levels (McNaughton et al. 1988; Holland et al. 1992). Although recent computer simulations suggest herbivores can stimulate productivity of North American shortgrass steppe (Holland et al. 1992), presently, no field study has documented such a response by temperate grasslands to grazers (Detling 1988).

Yellowstone National Park, part of a large temperate mountainous ecosystem, supports among the highest concentrations of native migratory ungulates in North America, with rates of grassland herbivory similar to those of African ecosystems

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(Frank and McNaughton 1992). In this paper we provide evidence that grazers, primarily elk *(Cervus elaphus)* and bison *(Bison bison),* stimulate grassland aboveground production. Furthermore, we discuss the potential role that the spatiotemporal pattern of grazing by native herbivores plays in regulating grassland function.

Study sites and methods

Yellowstone National Park is a 9000 km^2 mountainous reserve located in the northwest corner of Wyoming, USA. Meagher (1973) and Houston (1982) provide detailed descriptions of the Park. We compared aboveground production of grazed vegetation to that of permanently fenced, ungrazed vegetation at four nonforested sites in northeastern Yellowstone National Park, part of the northern range (Meagher 1973; Houston 1982) and home for large herds of elk and bison. Northern range elk and bison herds migrate between low elevation winter range and high elevation summer range. Two study sites were located on winter range (w1, w4), one on transitional range (t2), and one on summer range (s4). Sites were grasslands, except w4 which was a wet sedge meadow. Details of soil properties and vegetation at the sites are provided elsewhere (Frank and McNaughton 1992).

The study spanned two disparate years: (1) 1988. a regional drought, and (2) 1989, a climatically near-average year. The onset of the 1988 drought was early-June, leading to the driest summer on record in the Park (Schullery 1989). The drought was preceded by a wetter than average spring; precipitation during April and May. 1988, was 168% of normal (Singer et al. 1989). In 1989 precipitation during June through August was 97% of normal (Frank 1990). We measured production of grazed and permanently fenced vegetation during both years at t2 and s4, and only during 1989 at w1 and w4.

We used two methods to determine aboveground production, which, we believed, would provide the best measurements under the grazing regimes encountered in this study. We discuss a bias in the techniques below that indicates our results may be conservative.

Production of ungrazed vegetation was taken as peak aboveground biomass in three permanent exclosures established in 1987 (w1, t2 and s4) or 1988 (w4) at each of the sites. Lauenroth et al. (1986) recommended using peak standing crop, versus multiple sampling, for estimating aboveground productivity of ungrazed vegetation. Standing crop for each permanent exclosure, representing one replication, was the average of 3–4 randomly located 0.5 m^2 quadrats. Dimensions of permanent exclosures were 10 × 10 m at sites w4, t2, and s4, and 15 × 15 m at site w1. At site w4, where grazing did not occur during the growing season, but was intense during the winter months, production of unfenced vegetation was estimated as the peak biomass outside permanent exclosures. Therefore, the same method was used to measure grazed and ungrazed vegetation at this site.

Measuring aboveground production of vegetation where grazing occurred during the growing season required that we sequentially sample using temporary exclosures (1.5 × 1.5 m, 6 per site) to account for consumption by ungulates (Frank and McNaughton 1992). Temporary exclosures were moved randomly throughout each community every four weeks. Production at a site was calculated by summing statistically significant increases in standing crop ($P < 0.05$, Oneway ANOVA; growth) inside temporary exclosures (McNaughton 1985). Biomass loss due to decomposition prior to peak standing crop likely was negligible for both grazed and ungrazed vegetation because of the brief periods of plant growth at grassland sites, and the preponderance of live, green tissue at peak biomass (for grazed, 93%, SE = 1; for ungrazed 90%, SE = 3).

Standing crop was measured with canopy intercept, except at w4 where vegetation was too tall and, therefore, was clipped. Canopy intercept is an indirect method that relates biomass to the number of contacts a pin makes when passed at a fixed angle through vegetation. Its use during this study already has been described (Frank and McNaughton 1990). The r^2 values for relationships of the five functional plant growth forms encountered in the study ranged from 0.83 to 0.96.

Statistical analyses and sampling bias

We examined the effect of elk and bison on aboveground production across all sites with the paired *t*-test. Data were normalized with common log-transformation.

To determine if we biased our results by using two different methods to measure production at w1, t2, and s4, one for grazed and the other for ungrazed vegetation, we simulated each method following procedures similar to other workers who have examined methodological effects on production estimates (Singh et al. 1984; Lauenroth et al. 1986; Sala et al. 1988; Biondini et al. 1991). We drew randomly from normal distributions representing simulated samples of standing crop in a plant community. Mean production of grazed and ungrazed vegetation was assigned the same value, 127 g/m^2; but determined in different ways to reflect the two methods used in this study. The standard deviations (sd) for simulated distributions of grazed and ungrazed standing crop were calculated from the average coefficient of variation (cv) of standing crop at the four sites during the study; cv for grazed areas, using quadrats as the sampling unit, equalled 0.28, and that for ungrazed areas, using permanent fences as the sampling unit equalled 0.09. Sample sizes in the simulations reflected those used in the field.

To simulate measuring production of permanently fenced vegetation, we drew three samples from a distribution with a mean (μ) of 127 and sd of 11. This was done three times per community, once for each permanent exclosure. Aboveground productivity of ungrazed vegetation equalled the average.

To stimulate measuring production of grazed vegetation, we assumed plant growth over two sampling periods: the average duration of growth at w1, t2, and s4. The mean standing crop inside temporary exclosures after one month was arbitrarily given a value of 100 g/m^2, and that of simulated standing crop outside the temporary exclosures, in the grazed vegetation, was set at 56 g/m^2. Standing crop of grazed vegetation was calculated by using the average proportional difference between plant biomass inside and outside temporary exclosures after one month. Mean standing crop inside the temporary exclosures after the second sample period was set at 83 g/m^2, reflecting the original standing crop (56 g/m^2) plus growth, calculated by using the average relative growth (gram growth/gram initial biomass) during the second month at sites w1, t2, and s4. Therefore, grazed productivity equalled 127 g/m^2, the growth during the first month (100 g/m^2) plus that during the second month (27 g/m^2). Grazed and ungrazed productivity was simulated 20 times each.

Results

Results of the simulations are provided in Fig. 1. Grazed production averaged 123 g/m^2 (SE = 4.3), and ranged from 90 to 146 g/m^2. Simulated ungrazed production averaged 128 g/m^2 (SE = 1.2), and ranged from 117 to 137 g/m^2. On average, grazed measurements were slightly underestimated because for 7 of the 20 simulations there was no statistically significant increment in standing crop inside temporary exclosures during the second sampling period. This resulted in a negatively skewed distribution and indicates that the sampling method we used for grazed vegetation at w1, t2, and s4 on average slightly underestimated production. Thus, our comparisons of grazed versus ungrazed productivity at these sites were biased against finding higher production in grazed areas compared to ungrazed areas (i.e., ungulate stimulation of production).

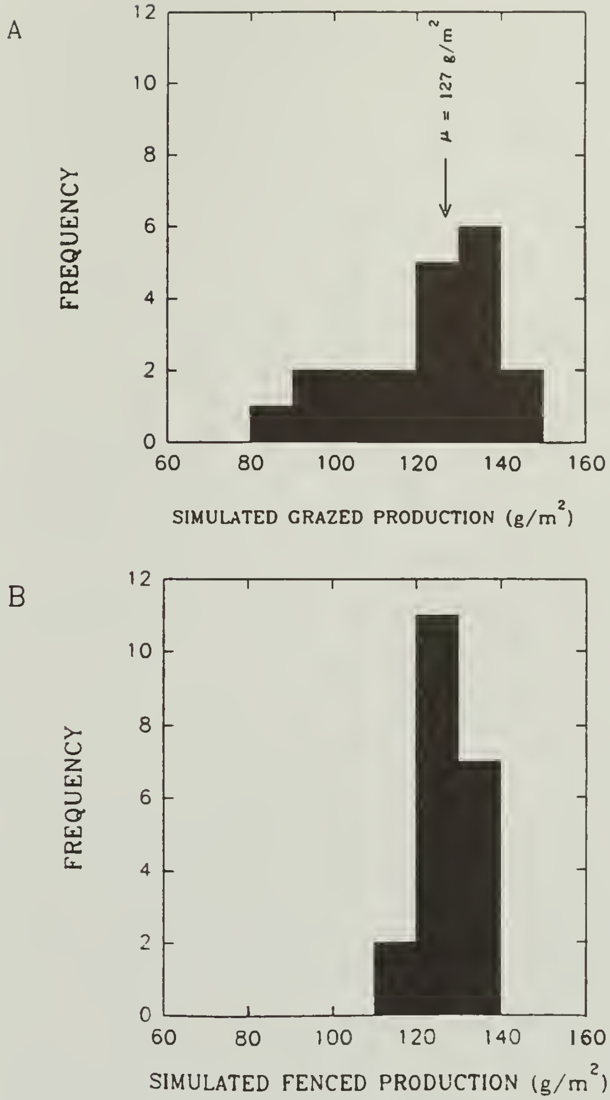

Fig. 1. Simulated aboveground production estimates by two methods: (A) multiple measurements within temporary exclosures for grazed vegetation, and (B) single measurements in permanent exclosures for ungrazed vegetation. Production (μ) was 127 g/m^2 in both cases.

Our field results indicated that production of grazed vegetation was greater ($t = 9.0$, $df = 5$, $P < 0.0003$) than that of ungrazed vegetation among a wide range of sites (Fig. 2); by an average of 48% across sites and ranging from 11% at s4 in 1989 to 85% at t2 in 1988. The decline in productivity of grazed and ungrazed vegetation at s4 from 1988 to 1989 was likely a result of the extreme drought conditions that high elevation sites experienced in 1988 (Frank 1990).

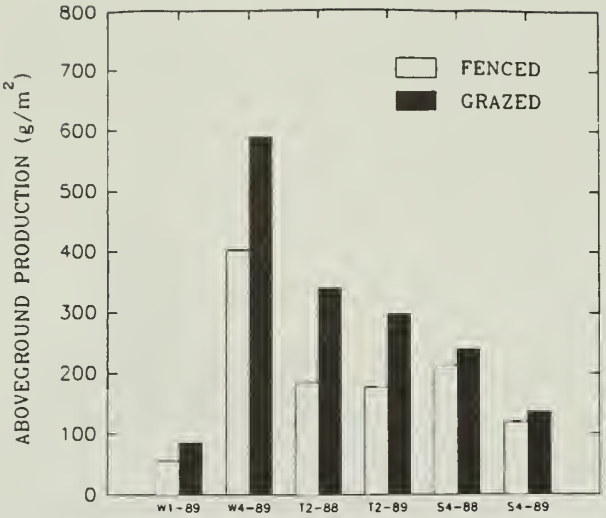

Fig. 2. Net aboveground production of grazed and ungrazed vegetation at four sites on winter (*w1, w4*), transitional (*t4*), and summer ranges (*s4*) of elk and bison in Yellowstone National Park. Sites *t2* and *s4* were sampled in 1988 and 1989, and sites *w1* and *w4* were only sampled in 1989.

Discussion

General findings

The lower aboveground production of permanently fenced areas may be explained by two alternative hypotheses: (1) the method used for grazed vegetation systematically overestimated production relative to that used for ungrazed vegetation, or (2) ungulates stimulated aboveground production. We believe the second explanation. We showed by computer simulation that there indeed existed a bias in the sampling regimes: however, instead of indicating that the measurements for production of grazed vegetation overestimated production, the simulations showed that grazed productivity in this study likely was underestimated. This suggests that the differences between the production of grazed and ungrazed vegetation reported in this paper are conservative. Moreover, at w4, where we used the same methods (clipping at peak biomass) inside and outside permanent fences, the response to grazing was consistent with that measured at the other sites using the two different methods. These results suggest that native large herbivores promote aboveground grassland production in Yellowstone National Park and play a central role in the functional organization of this ecosystem.

Possible mechanisms

Large mammalian herbivores have many indirect effects on nutrient and energy fluxes in grassland habitats that go well beyond the direct impacts of the removal of plant tissue (McNaughton 1985; McNaughton et al. 1988; Detling 1988; Naiman 1988). Defoliation opens the canopy allowing greater light penetration (Laude 1972; Monsi et al. 1973), while causing plants to allocate a greater proportion of photosynthate to aerial parts (Gifford and Marshall 1973; Detling et al. 1979, 1980; Oesterheld and McNaughton 1988). Allocation to aboveground structures in response to grazing has been shown to reduce root growth in some cases (Davidson and Milthorpe 1966; Evans 1973a, 1973b; Hodgkinson and Bass Becking 1977), and have no effect on root growth in other studies (Dyer et al. 1991; van der Maarel and Titlyanova 1989; Coughenhour 1991). Reduced root growth caused by herbivory may depress carbon: nitrogen ratios of soil organic material and increase net mineralization rates (Holland and Detling 1990; Holland et al. 1992). Regrowth after defoliation has higher photosynthetic rates (Parsons and Penning 1988; Gold and Caldwell 1989; Wallace 1990), which can lead to higher relative growth rates for grazed plants compared to ungrazed plants (Oesterheld and McNaughton 1988, 1991; Polley and Detling 1990). Removal of transpiring surface area may result in soil moisture conservation (McNaughton 1985; Wraith et al. 1987), and higher water use efficiency (McNaughton 1985). By limiting the accumulation of standing dead and litter, herbivores indirectly increase soil irradiation and warming and, likely, decomposition (Knapp and Seastedt 1986; Ruess 1987; McNaughton et al. 1988). Finally, herbivores remove (graze) nutrient poor material and add (excrete) material that is rich in nutrients and readily available to plants and soil microbes (McNaughton 1985; Ruess 1987).

In a previous paper (Frank and McNaughton 1992) we showed that during their spring and summer migration, elk and bison tracked young and nutritious vegetation as it progressed up an elevational gradient through the growing season. At sites w1, t2, and s4, grazing occurred during the first 1–2 months following snowmelt, then the ungulates migrated on; a pattern that was observed for Yellowstone northern range grasslands in general (Frank and McNaughton 1992). Because w1, t2, and s4 were grazed early in the growing season when, presumably, soil moisture was high and nutrients were readily available to plants (Burke 1989; Burke et al. 1989), grazed plants may have been provided with both the resources to regrow and time to recover. In the Serengeti, where ungulates also have been shown to stimulate aboveground production, large herbivores graze young vegetation by following spatially stochastic rainfall events

(McNaughton 1976, 1979a). The similarity between these two latitudinally and climatically disparate ecosystems in (1) the migratory behavior of the dominant herbivores in relation to the phenological stage of their forage and (2) the response of vegetation to ungulates further suggests that the spatiotemporal pattern of grazing by native free-roaming ungulates may be an important factor contributing to their positive feedback on forage in grasslands.

However, this explanation for herbivore stimulation of productivity is only relevant for sites w1, t2, and s4 where grazing occurred during the growing season. Herbivores also enhanced production at w4, even though grazing occurred at this site only in the winter when plants were dominant. Consequently, herbivores must have stimulated productivity at w4 by mechanisms other than plant regrowth after defoliation, e.g., fertilization or standing dead removal (Knapp and Seastedt 1986). This bolsters the contention that a thorough understanding of mechanisms underpinning the facilitation of production by grazers cannot be achieved by examining singular responses alone, e.g., clipping, but must be sought in an integrated approach that takes into account the many effects herbivores have on a plant's physiology and growing environment.

Native large herbivores are inextricably enmeshed in a complex web of grassland energy and nutrient flows (McNaughton et al. 1988). These results suggest that elk and bison have substantial indirect effects on energy and nutrient flows in Yellowstone grassland, in addition to their direct consumption of plant tissue, and that positive feedback from herbivores to their forage is not a feature unique to tropical grasslands and savannas. Furthermore, these findings suggest the importance of considering the spatiotemporal pattern of herbivore use of landscapes when predicting the effect of grazers on the functional properties of grasslands.

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Characterization of Soils From Grazing Exclosures and Adjacent Areas in Northern Yellowstone National Park

John R. Lane[1]

Geographic Information Systems
P.O. Box 168
Yellowstone National Park, Wyoming 82190

Cliff Montagne

Department of Plant, Soil and Environmental Sciences
Montana State University
Bozeman, Montana 59717

Abstract. Paired plots in Yellowstone National Park's northern winter range were studied in 1986 and 1987 to determine if differences in soil chemical and physical properties occurred between areas inside and outside of eight ungulate grazing exclosure sites. Sampling for soil surface bulk density, double ring infiltration, and nutrient analysis was conducted inside and outside of all exclosures. Simulated rainfall was applied inside and outside of five exclosures under three separate treatments: vegetation undisturbed, vegetation clipped, and clipped vegetation and litter removed. Some differences ($P = 0.10$) were identified in soil chemical properties, but no consistency was identified between inside and outside of exclosures. Soil surface (0–5 cm) fine earth bulk density was significantly higher outside of exclosures at four of eight sites. One site had significantly higher infiltration inside the exclosure. For the simulated rainfall study, no differences in runoff were significant for treatment 1 (vegetation undisturbed). Runoff was higher outside at three sites for treatment 2 (vegetation clipped), and at two sites for treatment 3 (vegetation and litter removed). Two sites had significantly higher sediment yield outside the exclosure for treatment 3 (vegetation and litter removed). Because baseline soils data were not collected when the exclosures were established, no conclusions can be made concerning changes over time due to grazing or protection from grazing.

Key words: Bulk density, erosion, grazing exclosures, infiltration, runoff, sediment yield, soil characterization, Yellowstone National Park.

A concern about overgrazing on the northern winter range by wild ungulates had been raised by range scientists (Tyers 1981) and others, especially because elk numbers increased between 1967–70 and 1986–88 (Singer and Norland 1994). In response, this study and others were initiated on the northern winter range inside Yellowstone National Park.

Many studies of the effects of grazing on soil bulk density, infiltration, runoff and sediment yield exist, most of which evaluate summer grazing by domestic livestock, mainly cattle and sheep. Little information is available on the effects of grazing by free ranging ungulates during the winter and early spring when soils may be covered by snow or are undergoing freeze–thaw cycles. Some authors report higher bulk density and lower infiltration with prolonged grazing; others report the opposite. Some authors believe that the variability in the findings is related to the influence of weather conditions during the time of year the study takes place. Lodge (1954), Knoll and Hopkins (1959), and Orr (1960) found higher bulk density on grazed areas compared to ungrazed areas at some locations, but there were no differences at other areas. Laycock and Conrad (1967) found similar soil bulk densities in grazed plots and exclosures in both early and late summer. Bulk density

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[1] Present address: 1535 South 12th West, Missoula, Montana 59801.

increased over the summer for both the grazed and ungrazed areas. Packer (1963) and Reed and Peterson (1961) found consistently higher bulk densities in grazed areas. These conflicting results probably reflect variations in soil, soil moisture, or other conditions (Laycock and Conrad 1967; Orr 1975).

Gamougoun et al. (1984) found that pastures ungrazed for 27 years had significantly higher infiltration rates than grazed pastures. The ungrazed pastures had the lowest sediment production. Results for sediment production, however, were highly variable; differences were not significant for all treatments for all years.

Many authors (Lowdermilk 1930; Meyer et al. 1975; Gabriels and Moldenhauer 1978) report that raindrop splash causes considerable runoff and erosion by breaking down soil aggregates. The resulting smaller soil particles are transported by drop splash and surface flow or deposited into pore spaces to seal the soil surface (Lowdermilk 1930; Ellison 1950).

Wood and Blackburn (1981), McCalla et al. (1984a, 1984b), Lusby (1965), and Thompson (1968) all reported that standing vegetation, litter, bare ground, total ground cover, bulk density, initial soil moisture content, organic matter content, rock cover and climatic factors had some influence on infiltration, runoff, and sediment yield. Frank et al. (1975) and Johnson and Gordon (1986) determined that most sediment yield from their study watersheds was from snowmelt and from rain on frozen soil. Johnston (1962) studied the effects of various types of cover on water-intake with treatments of 1) check, 2) current growth of vegetation removed to ground level, 3) fresh mulch removed, and 4) all vegetation and mulch removed to ground level. Water absorption and intake rates were significantly higher on undisturbed plots. Soil loss was negligible except with bare soil.

More bare soil was found outside most of the exclosures and litter was 6.2 times higher inside all exclosures (Francis J. Singer, Grazing influences on Yellowstone's northern winter range, Summaries of research studies, Yellowstone National Park, Wyo.). These differences are probably due to ungulate grazing. Coughenour et al. (this volume), however, point out that variation in precipitation between 1958 and 1989 resulted in parallel inside and outside of exclosure increases and decreases in plant frequency.

Our objectives were to determine if soil chemical and physical properties differ inside and outside of ungulate grazing exclosures; and to determine, using simulated rainfall, if there were differences in surface runoff and sediment yield inside and outside the exclosures. We compared paired outside of exclosure grazed and inside of exclosure ungrazed plots at a point in time. No preexclosure baseline data exist for comparison of the possible effects on soils of increasing numbers of elk over time.

Materials and Methods

The study included eight grazing exclosure sites at five areas on the northern winter range of Yellowstone National Park (Fig. 1). The Gardiner, the Blacktail Ponds, and Lamar Valley areas each contain two exclosures; and the Mammoth Hot Springs and the Junction Butte areas each contain one exclosure. The exclosures (approximately 2 ha) were established in 1957 and 1962 on land that is mostly rolling swales and ridges. The vegetation is characterized by bunch grasses and big sagebrush, especially Idaho fescue (*Festuca idahoensis*) and big sagebrush (*Artemesia tridentata*) habitat types. We obtained our data within or adjacent to paired 10 × 10 m plant ecology study plots inside and outside of the exclosures. The locations of the plots were selected by Yellowstone National Park researchers to represent similar topography and soil (Coughenour et al., this volume). It was difficult to select similar plots outside the exclosure.

Many of the soils in the study area are derived from glacial till. The Gardiner site is on landslide

Fig. 1. Location of the Northern Winter Range and the general locations of the study sites (Courtesy of Geographic Information Systems Laboratory, Yellowstone National Park).

material. Soil profiles were described and samples collected within 10 m of the plant ecology study plots to determine soil type. Profiles were described and classified following national standards (Soil Survey Staff 1975). The soils at the Gardiner site are Typic Ustochrepts. The soils at the Blacktail site are Typic Haploborolls. The Lamar Valley sites have Typic Haploborolls at the west exclosure and Typic Calciborolls at the east exclosure. The soils are Typic Argiborolls at the Mammoth site. Soils at the Junction Butte site are Typic Haploborolls.

Soil samples for nutrient analysis were collected from three depth increments, 0–15 cm, 15–30 cm, and 30–45 cm, at nine random locations. At each plot, the nine samples for each depth were combined to form three composite samples. Samples were placed in a cooler for transport and were frozen within 8 hours of collection until processing at the laboratory.

Electrical conductivity and pH were analyzed with glass electrodes in a 1:2 (soil:water) dilution. Samples were analyzed for nitrate nitrogen following the cadmium reduction technique outlined by Sims and Jackson (1971), and ammonia nitrogen by the colorimetric Berthelot reaction on a Technicon Auto Analyzer II. Percent organic matter was determined using the Sims-Haby colorimetric method (Sims and Haby 1971). Available phosphorus was determined using Olsen's sodium bicarbonate extraction technique (Olsen et al. 1954). Available calcium, sodium, magnesium and potassium were determined by ammonium acetate extraction (Bower et al. 1952). The micronutrients copper, iron, zinc, and manganese were determined by the DTPA-TEA extraction method modified from Lindsay and Norvel (1969). Sulfur was analyzed following Bardsley and Lancaster (1965).

Bulk density measurements were obtained by the volumetric displacement method with four replications inside and outside at each exclosure. Infiltration measurements were replicated three times inside and outside the exclosures using double ring infiltrometers. A nearly constant rate of infiltration was reached after approximately 30 min (Lane 1990).

A modified drip-type rainfall simulator (Meeuwig 1971) was used to apply 1.27 cm of rain at an intensity of 2.54 cm/h for 30 min at the two Gardiner sites, the two Blacktail sites, and Lamar Valley east site. Rainfall simulator plots were 66 × 66 cm in size. Paired rainfall simulations were adjacent to the plant ecology study plots at each site. Three treatments were applied to each site each time the simulator was used: (1) undisturbed control, (2) vegetation clipped and left on the surface, and (3) vegetation and litter removed. The first treatment was followed by the second and by the third on the same soil surface—about 15 min elapsed between each treatment. All water and suspended sediment running off the plot were collected for each simulated rainfall event. The sediment was oven-dried, weighed, and converted to kg/ha.

A *t*-test was used to compare the outside and inside of exclosure means of the various soil characteristic measurements at each site. All statistical differences reported are at the 90% confidence level ($P < 0.10$) derived using the SAS (1985) probability value.

Results

Soil Chemical Characteristic

No nutrient difference was evident between inside and outside exclosures for any element across all sites (Lane 1990). Differences for some nutrients at certain sites were identified, but the results were highly variable (Tables 1, 2, and 3). For a particular depth, some sites had higher amounts of one nutrient in the inside exclosure samples while others had higher amounts in the outside exclosure samples (Lane 1990).

Bulk Density

At four of the eight sites, Junction Butte, Mammoth, Gardiner east, and Lamar Valley east, the surface bulk density was higher outside of exclosure (Fig. 2).

Double Ring Infiltration

Higher average double ring infiltration rates occurred inside the exclosure at the Lamar Valley west site (Table 4). Average rates at the Blacktail east and Gardiner west sites were higher in the outside exclosure samples. The Gardiner west site had higher infiltration and soil surface bulk density outside the exclosure. This is contradictory to the expected relation of higher bulk density and lower infiltration, and may be due to the high clay and sodium content of these soils.

Rainfall Simulator Study

Treatment 1 (vegetation undisturbed) had the lowest runoff and sediment yield followed by treatment 2 (vegetation clipped and left on the surface). Treatment 3 (vegetation and litter removed) had the highest runoff and sediment yield. None of the differences for inside versus outside exclosures were significant for treatment 1 (vegetation undisturbed).

Table 1. Average values of organic matter (%) and nutrients (µg/g) in the 0–15 cm depth at eight sites on the Northern Winter Range, Yellowstone National Park.

Exclosure	OM	NO_3	NH_4	P	S	Na	Ca	Mg	K	Fe	Cu	Mn	Zn
Gardiner													
East													
In[a]	1.42	1.67	2.71	16.29	5.53	351.40	4665.73	780.27	216.60	13.10	2.03	9.53	0.50
Out[b]	1.34	1.28	2.10	11.21	38.70	1139.60	4509.67	546.80	298.87	10.03	2.83	7.60	0.60
West													
In	1.33	1.25	3.90[c]*	5.87	23.27	322.20	7140.47*	1446.07*	297.73	8.83	2.60	3.43	0.47
Out	1.96	2.35	2.08	16.36*	8.13	160.27	2893.33	821.33	226.80	14.10*	1.87	14.27*	0.60
Blacktail													
East													
In	3.41	1.93*	6.58	8.75	2.62	32.67	1808.73	181.47	128.73	12.94	2.30	6.62	2.45
Out	3.18	0.44	5.65	6.79	2.13	62.07	2113.33	382.73*	221.13*	14.06	3.85*	10.51*	2.52
West													
In	2.68	1.04	1.82	5.39	18.00	20.53*	1973.20	214.27	247.07	14.40	1.27	13.57	0.73
Out	3.96*	1.24	1.82	6.38	7.15	15.07	2112.87	255.33	407.07*	15.33	1.17	13.57	1.70*
Lamar Valley													
East													
In	3.78*	0.56	6.02	11.02	2.65	19.13	3717.80	1026.40*	351.20*	19.41*	3.19	8.07	1.63
Out	2.69	0.42	4.65	8.21	2.47	20.63	3843.33	951.27	257.53	11.75	2.47	7.12	0.80
West													
In	5.08	3.40	7.18	7.44	3.48	21.73	2796.47	638.73	426.67	30.13*	3.32*	7.81*	2.90*
Out	4.67	1.03	4.74	6.70	4.76	23.80	3187.13	646.33	438.27	15.19	1.17	5.62	0.67
Mammoth													
In	5.08	0.33*	5.71	10.86*	3.94	50.87	2056.87	231.20	442.20	41.29*	3.21	10.36	2.41
Out	4.67	0.20	5.55	8.15	3.72	24.13	2137.93	236.40	438.27	30.80	2.40	8.12	2.76
Junction Butte													
In	3.41	0.22	4.67	8.44	2.18	27.00	1339.40	332.60	293.93	38.84	3.05	7.75	2.33
Out	4.07*	0.33*	5.30	9.73	3.76	31.20	1747.27*	342.20	315.60	38.39	2.65	8.33	2.09

[a] Inside the exclosure.

[b] Outside the exclosure.

[c] Numbers followed by asterisk (*) are significantly higher than their paired counterparts.

For treatment 2 (vegetation clipped and left on the surface), three sites had higher outside of exclosure surface runoff. No significant differences for sediment yield were identified. When the clipped vegetation and litter were removed (treatment 3), surface runoff at two sites and sediment yield at two sites were higher outside the exclosure (Tables 5 and 6).

Discussion

Glacial till and landslide deposits have high variability because of their mode of deposition. The sizes and locations of most exclosures allow for a wide difference in clay percentages and soil texture, both inside and outside. This variability compounds the difficulty in assessing possible effects of grazing versus nongrazing. The differences we identified may result from inherent soil and site variability rather than differences in grazing due to the exclosures.

Our results are similar to other studies in which chemical properties and nutrient levels were not widely affected by grazing versus nongrazing. Bauer et al. (1987) found that differences in soil nutrient levels were not consistently larger in either the grazed or nongrazed system. Rhoades et al. (1964) reported small and insignificant differences in organic matter and soil nitrogen levels between grazing at various stocking rates and a 20-year-old grazing exclosure. On the Texas plains, Wood and Blackburn (1984) found that soil organic matter content differed slightly among six grazing treatments and two exclosures.

The differences in surface bulk density and infiltration indicate effects from either grazing or protection from grazing. For the most part, our bulk density and infiltration findings follow results reported by Lodge (1954), Knoll and Hopkins (1959), Orr (1960), and Wood and Blackburn (1981, 1984) where bulk density was significantly higher and infiltration lower outside of some exclosures and that there were no differences at other exclosures.

Table 2. Average values of organic matter (%) and nutrients (µg/g) in the 15–30 cm depth at eight sites on the Northern Winter Range, Yellowstone National Park.

Exclosure	OM	NO_3	NH_4	P	S	Na	Ca	Mg	K	Fe	Cu	Mn	Zn
Gardiner													
East													
In[a]	1.02	0.84	2.37	8.17	25.77	593.40	5978.07	685.40	91.60	14.50	1.57	4.20	0.33
Out[b]	1.41	1.05	3.16	12.86	8.13	2093.33[c]*	6977.07	588.47	160.27	11.40	1.77	3.23	0.37
West													
In	0.77	0.92	3.71	9.94	483.67	504.87	8331.93*	1312.33	166.00	8.13	2.57	1.97	1.70
Out	1.58*	1.08	3.28	2.11	37.77	708.33	6125.93	1340.93	210.93	12.47*	2.00	5.20	0.40
Blacktail													
East													
In	2.35*	1.16*	6.58	5.80	0 8.32*	51.13	3779.27	249.73	128.73	9.37	2.38	3.00	2.
Out	1.30	0.20	4.31	5.79	1.58	35.87	2717.73	447.07*	137.80*	10.93	3.74*	3.34	2.40
West													
In	1.56	0.80	1.89	3.11	10.73	16.53	2490.80	229.27	120.87	10.53	1.10	7.23	0.10
Out	2.74*	0.86	1.58	6.71*	4.43	16.20	2478.47	312.67*	294.33*	15.93*	1.17	13.70*	0.30*
Lamar Valley													
East													
In	2.24	0.20	5.15	6.07	1.78	22.33	4012.53	1149.07	242.00	16.73*	3.90*	4.82	1.25
Out	2.24	0.13	4.74	5.10	2.62	33.53	4570.40*	1096.13	214.67	11.35	2.22	4.45	0.46
West													
In	3.94	0.20	3.94	5.82	7.31	19.40	4789.00	762.07	240.67	13.38*	1.58	2.94*	0.43
Out	2.93	0.42	3.69	5.65	7.58	75.20*	4897.07	957.53*	208.07	9.16	1.28	1.80	0.32
Mammoth													
In	2.46	0.37	3.89	6.62	3.01	39.40	2071.53	198.60	356.40*	26.78*	3.18*	4.97	1.52
Out	2.79	0.22	6.22	5.32	15.00	38.20	3518.73	186.27	283.60	17.86	2.04	4.47	2.09
Junction Butte													
In	1.22	0.01	1.76	5.81	3.26	35.87	1368.87	413.40	232.87	14.07	1.49	6.35*	0.21
Out	1.38	0.27*	2.55	6.51	4.64	18.53	1916.80*	371.87	218.53	24.55*	2.49*	4.95	0.67

[a] Inside the exclosure.

[b] Outside the exclosure.

[c] Numbers followed by asterisk (*) are significantly higher than their paired counterparts.

Results at the Gardiner west and Blacktail east sites did not follow the bulk density and infiltration trends. Both sites had different surface soil textures inside and outside of exclosures (Lane 1990). The bulk density results for both sites are higher for the soils with less clay, regardless of whether they are inside or outside of exclosure. At Gardiner west, the infiltration is higher outside of exclosure on a soil with less clay. At Blacktail east infiltration is higher outside of exclosure on a soil with more clay.

The results of runoff and sediment yield were as predicted from the site characteristics. The Gardiner sites had the finest textured soils. If raindrops break aggregates, the resultant fines may then clog surface pores, reducing infiltration and increasing runoff and sediment yield. The Gardiner sites had the greatest runoff and sediment yield for all three treatments. The Gardiner east site also had the highest surface bulk density of any of the sites (1.06 g/cm^3), which could limit infiltration.

The higher runoff and sediment yield of outside the exclosure treatments may be related to higher bulk densities and lower amounts of vegetative cover outside the exclosures. The higher bulk density would reduce infiltration and increase runoff. The higher amount of bare soil would be more vulnerable to raindrop splash with subsequently more soil detachment and transport.

Inside of exclosures, runoff was significantly higher at three sites for treatment 2 (clipped vegetation and litter left on the surface) though differences in sediment yield were not significant. The vegetation and litter may have acted as conduits to transmit the simulated rainfall downhill into the collection tray without striking the ground surface.

Packer (1963) indicated that soil surface bulk density must be below 1.04 g/cm^3 and ground cover must be 70% or more to stabilize the soil surface and protect it from accelerated erosion on winter range sites along the Gallatin River. All but one outside-of-exclosure plot (Gardiner east, 1.06 g/cm^3) have bulk

Table 3. Average values of organic matter (%) and nutrients (µg/g) in the 30–45 cm depth at eight sites on the Northern Winter Range, Yellowstone National Park.

Exclosure	OM	NO3	NH4	P	S	Na	Ca	Mg	K	Fe	Cu	Mn	Zn
Gardiner													
East													
In[a]	0.69	0.92	2.18	5.61	29.13	760.53	6540.87	600.53	69.13	15.83	1.83	4.80[b]*	0.83
Out[c]	1.36*	1.00	4.25*	62.41	1238.23	2218.67*	11629.00	598.47	188.47*	14.47	2.43	2.50	0.50
West													
In	0.37	0.72	3.57	10.35	612.63	985.33	18908.93	1355.60	208.73	8.03	2.77	2.37	1.23
Out	1.14*	0.80	3.04	3.37	43.72	719.47	6208.13	1256.33	195.27	12.20*	2.10	3.07	0.43
Blacktail													
East													
In	1.49	0.44	4.61	5.33	14.80*	85.80	5386.17	334.00	62.47	6.25	1.36	2.31	1.22
Out	1.31	0.38	4.15	3.72	8.87	50.00	4116.67	432.27	132.67	7.36	3.46*	2.49	2.49*
West													
In	0.93	0.75	1.27	2.53	11.47	16.20	3466.27	130.07	38.67	6.03	0.87	3.70	0.10
Out	1.84*	0.60	1.24	5.92*	30.30	19.80	2347.07	309.07*	225.67*	12.53*	0.90	9.87*	0.10
Lamar Valley													
East													
In	1.56	0.35	4.14	5.49	2.08	28.53	4177.20	1133.13	176.87	14.81	3.61	4.27	2.16
Out	1.49	0.06	3.86	5.51	4.45	36.73	5074.00*	1142.53	135.27	13.98	2.57	3.70	0.76
West													
In	1.65	0.06	2.94	5.49	10.51*	55.27	5572.80*	865.40	140.47	9.02*	1.40	2.39	0.28
Out	2.04	0.19*	2.90	5.55	7.12	116.87	4801.27	1607.87*	98.87	7.24	1.50	2.18	0.15
Mammoth													
In	1.63*	0.32	3.70*	5.91	22.84	36.73	5442.60	174.73	178.20*	9.97*	2.21	3.46*	1.22
Out	1.28	0.31	3.42	4.34	26.04	42.60	5393.47	154.67	143.00	7.36	1.57	1.82	2.48
Junction Butte													
In	0.76	0.34	2.15	5.05	99.69	50.80	4196.93	462.93	187.33	12.27	2.45	2.44	1.09
Out	1.21*	0.65	3.10	6.62	20.27	28.00	4422.93	449.60	174.33	17.63*	2.30	3.20	0.69

[a] Inside the exclosure.

[b] Numbers followed by asterisk (*) are significantly higher than their paired counterparts.

[c] Outside the exclosure.

densities below Packer's threshold. Almost half of our plots (four of eight inside of exclosure and three outside of exclosure) have greater than Packer's recommended 70% cover. Using Packer's criteria, 1 plot may be susceptible to accelerated erosion because of high bulk density, and 9 of 16 plots may be susceptible due to low percent ground cover.

Dadkhah and Gifford (1980) suggest that 50% ground cover provides adequate protection against erosion. All eight inside-of-exclosure plots and five of eight outside-of-exclosure plots exceed this recommendation.

It seems that fewer than half of the study plots could be susceptible to accelerated erosion because of low-percent ground cover. Sediment could be generated from overland flow and interrill erosion, but would likely be trapped in swales of the glacial till and landslide microtopography characteristic of the exclosure areas. It is doubtful that any sediment generated by a single summertime thunderstorm on

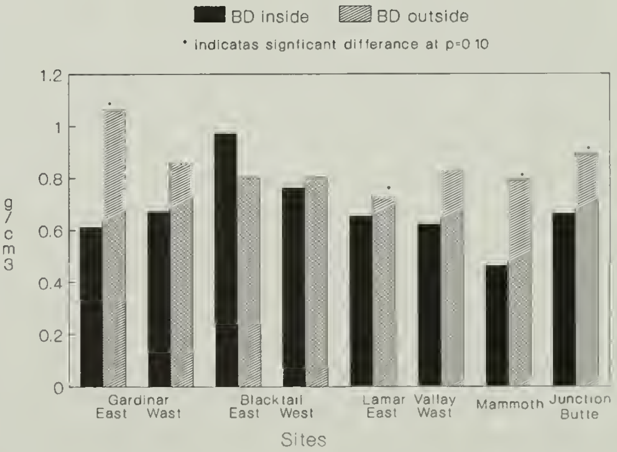

Fig. 2. Bulk density of the surface five cm for the eight exclosures.

upland range sites would reach stream channels of the Yellowstone River.

Table 4. Average equilibrium infiltration rates from the double ring infiltrometers for the eight exclosures.

Exclosure	Treatment[a]	Mean (cm/h)
Gardiner		
East	Out	1.093
	In	5.333
West	Out	15.867
	In	12.800
Blacktail		
East	Out	8.136
	In	7.068
West	Out	14.533
	In	20.400
Lamar Valley		
East	Out	4.667
	In	5.200
West	Out	6.667
	In	13.468*[b]
Mammoth	Out	5.737
	In	8.000
Junction Butte	Out	6.400
	In	11.868

[a] In is inside and out is outside of exclosure.
[b] Asterisk (*) denotes significant difference at $P = 0.10$.

Conclusions

Our study of the effects of grazing versus nongrazing on soil chemical and physical properties was conducted by comparing inside- and outside-of-exclosure samples related to eight grazing exclosures on the northern winter range, Yellowstone National Park. Some significant differences were identified in soil chemical properties inside and outside of the exclosures but no trends occurred across all sites. Some sites had higher inside-of-exclosure levels for some elements but not for others. Four of eight sites had significantly higher bulk densities outside the exclosures. Most sites had higher average double ring infiltration rates inside the exclosures where there was lower average soil bulk density. Infiltration measurements, however, were not significantly different at most sites. Average sediment yield and surface runoff from simulated rain tended to be higher outside of all exclosures for three plant cover-soil treatments, but only a few differences were significant.

Our results display some statistically significant differences and a number of trends. The following

Table 5. Average simulated rainfall sediment yield (kg/ha) of all three plant-cover conditions for the five exclosures.

	Treatment		
Exclosure[a]	1	2	3
Gardiner			
East			
In	63.76	119.76	287.23
Out	57.93	140.10	185.88
West			
In	257.97	342.72	469.13
Out	614.02	919.98	1199.11*[b]
Blacktail			
East			
In	11.07	6.03	0.89
Out	26.14	14.87	11.08*
West			
In	39.16	24.49	26.17
Out	75.31	50.49	72.87
Lamar Valley			
East			
In	16.20	57.57	39.87
Out	19.34	67.30	94.06

[a] In is inside and out is outside of exclosure.
[b] Numbers followed by asterisk (*) are significantly higher than their paired counterparts.

Table 6. Average simulated rainfall surface runoff (milliliters) of all three plant-cover conditions for the five exclosures.

	Treatment		
Exclosure	1	2	3
Gardiner			
East			
In	425.7	1120.0	2929.7
Out	1540.3	3400.7*[a]	3111.7
West			
In	1263.3	2229.3	2982.7
Out	1481.7	2768.7	3488.3
Blacktail			
East			
In	138.7	211.7	88.3
Out	250.3	486.3*	578.0*
West			
In	211.0	420.0	279.3
Out	398.3	1082.0	1166.7*
Lamar Valley			
East			
In	83.3	283.3	280.7
Out	83.3	1748.7*	1483.0

[a] Numbers followed by asterisk (*) are significantly higher than their paired counterparts.

points may assist in interpreting these trends and planning follow-up studies.

1. Seasonal soil moisture changes, like shrinking and swelling, affect soil properties sensitive to grazing and trampling, such as bulk density, infiltration, and runoff.
2. Our somewhat scattered and nonsignificant data may indicate a high degree of natural variability in soils and site factors. A follow-up study with more samples would probably reduce the variance in the data and show significance where current data show only trends.
3. A study contrasting several different levels of grazing may provide a more accurate picture of a continuum of grazing intensities and effects. The exclosures of the current study were all established on land being used as winter range, so there are no truly ungrazed control baseline data. Furthermore, the exclosure conditions of no grazing are not realistic, there will always be some level of grazing on the winter range.
4. No preexclosure soils data exists. Therefore, we do not know if the exclosure soils have changed since the exclosures were erected. The soil differences documented in this study may be due to the current grazing regime, to cessation of ungulate grazing within the exclosures, or a combination of both.
5. Like landslides, significant events of accelerated erosion tend to be threshold events occurring infrequently and only under special combinations of weather, soil, and vegetation conditions. It may be necessary to experimentally *push the system* to determine the threshold conditions of grazing and trampling, precipitation, soil and vegetation which lead to accelerated erosion and sedimentation.

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Responses of bluebunch wheatgrass, Idaho fescue, and nematodes to ungulate grazing in Yellowstone National Park

Evelyn H. Merrill, Nancy L. Stanton, and John C. Hak

Merrill, E. H., Stanton, N. L. and Hak, J. C. 1994. Responses of bluebunch wheatgrass, Idaho fescue, and nematodes to ungulate grazing in Yellowstone National Park. Oikos 69: 231–240.

We sampled above and belowground biomass of Idaho fescue *(Festuca idahoensis)* bluebunch wheatgrass *(Agropyron spicatum)* plants and nematode densities under these species inside and outside a 2-year old exclosure on the northern range of Yellowstone National Park in May through September, 1990. Native ungulates grazed the site primarily in winter and early spring. Grazing during this period removed essentially all the standing dead plant material. In early May, green biomass of plants of both species outside the exclosure was significantly lower than plants in the exclosure but off-take by ungulates accounted for only 18–51% of this initial difference. Indirect effects of grazing, such as the effects of removing standing dead material on microclimatic conditions, likely influenced early growth. By the end of the growing season, both species had similar biomass to ungrazed plants despite an increase in root-feeding nematodes early in the growing season. Lower root biomass, higher densities of bacteria-feeding nematodes (no./g root biomass), and higher concentrations in foliar nitrogen (N) with grazing suggested that root mortality, due to spring grazing, provided a short-term source of carbon for microbial activity and that microbial-feeding nematodes increased the turnover rates of microbial bound N. Densities (no./g root biomass) of root-feeding nematodes increased rather than decreased with grazing. Because N concentration of roots did not differ between grazed and ungrazed plants, we suggest that there was a reduction in secondary chemicals or and increase in root hairs, which are preferred sites for nematode feeding.

E. H. Merrill, N. L. Stanton and J. C. Hak, Dept. of Zoology and Physiology, Univ. of Wyoming, Laramie, WY 82071-3166 USA.

Management of elk (*Cervus elaphus*) on the northern winter range of Yellowstone National Park has remained a controversial subject through most of this century (Singer 1989). Until 1968, elk were artificially controlled because it was thought that ranching outside the park excluded elk from winter ranges and resulted in unnaturally high populations in the Park. In 1968 elk reductions were terminated and by 1971 a policy of "natural regulation" was formulated by Park biologists (Cole 1971, Boyce 1991, Coughenour and Singer 1991). Despite criticism of presumably deteriorated winter range (Beetle 1974), the natural regulation policy has been maintained based on the argument that animals have not greatly altered the range and that the primary purpose of natural areas such as Yellowstone is to "maintain ecological processes" (Houston 1982).

Examination of historical photographs of grasslands in the 1970s supported the natural regulation hypothesis (Cayot et al. 1979, Barmore 1980). However, the first detailed information of grassland plant responses to grazing on the northern winter range came from studies which compared vegetation inside and outside exclosures established

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by the Park in the late 1950s (Coughenour 1991, Singer unpubl.). These studies found that with few exceptions (i.e. *Koeleria cristata* and *Agropyron dasystachyum*) ungulate grazing on winter ranges did not change species composition nor vegetation productivity except in drought years. However, grazing increased aboveground plant nitrogen content and reduced litter accumulation. Frank and McNaughton (1992) also found that ungulate grazing in winter stimulated subsequent plant production in some areas of the northern range of Yellowstone Park. Coughenour (1991) concluded that the "net effect of winter grazing by ungulates appeared to be a redirection of carbon flow from decomposers to ungulates, accompanied by an enhanced rate of N recycling back to elk".

In April 1990, we initiated a study to measure the effects of winter and short-term, spring grazing on above and belowground plant biomass and nitrogen (N) content, plant morphology, and soil nematode densities. Because nematodes are abundant and comprise a number of trophic categories (e.g., herbivores, bactivores, fungivores), they may reflect belowground processes changed either directly or indirectly by grazing. Houston (1982:154) reported that nothing is known about the effects of nematodes on the native grasses of the northern range especially in combination with aboveground grazers.

Furthermore, root-feeding nematodes are major herbivores in other grassland systems where they consume a significant amount of the Net Primary Production (NPP) (Stanton et al. 1981, Stanton 1983, 1988, Ingham and Detling 1984). In shortgrass and mixed grass prairies, phytophagous nematodes can reduce both shoot (Smolik 1974) and root production (Stanton et al. 1981, Stanton 1983).

The response of nematodes to aboveground grazing currently is not well understood. Densities of phytophagous nematodes are lower under heavily grazed (70% aboveground biomass removal) plants than under ungrazed plants due to a reduction in root biomass (Stanton 1983). However, densities tend to be higher under grasses exposed to moderate defoliation than no defoliation (Smolik and Rodgers 1976, Smolik and Dodd 1983, Stanton 1983, Ingham and Detling 1984, Seastedt 1985, Yeates 1987). Seastedt et al. (1988) suggested that rootfeeders exhibit a curvilinear response to aboveground herbivory with maximum densities of soil animals occurring at intermediate levels of grazing. This was experimentally shown by Stanton (1983) for nematodes. Since most evidence indicates a decline in root growth due to foliage removal, Seastedt et al. (1988) hypothesized that changes in root quality counteracted the absolute decline in resource, i.e. roots of grazed plants may have higher nitrogen concentrations than ungrazed plants.

Anderson et al. (1983) suggested that belowground herbivory also may have a substantial effect on nutrient dynamics. Because of the close proximity of belowground herbivores to the decomposer food web, nutrient cycling in the plant-belowground herbivore system may be faster than the plant-aboveground herbivore system. For example, in a pot experiment Stanton (1983) found that the presence of phytophagous nematodes increased the density of bacterial-feeding nematodes. At Wind Cave National Park, mineralization rates and populations of Rhabditida (bacterial-feeders) and Tylenchida (plant parasites) were both higher in mixed grass prairie sites that were grazed by prairie dogs than in ungrazed areas (Ingham and Detling 1984, Holland and Detling 1990). Thus, densities of bacterial- and fungal-feeding nematodes could be indicative of changes in other belowground processes such as decomposition and mineralization.

We hypothesized four general responses of plants and nematodes to defoliation. First, we hypothesized that intensive spring grazing (70% aboveground green biomass removal) would increase root mortality. Second, as a result of root mortality we hypothesized that root-feeding nematodes would be lower and densities of bacterial-feeding nematodes would be higher because of the increased carbon (C) availability for decomposers. Third, as regrowth occurred, grazed plants would recover above and belowground biomass because of low phytophagous nematode densities. Finally, shoot and root N would be higher because of high microbial activity and mineralization by bacterial-feeding nematodes.

We focused our attention on bluebunch wheatgrass *(Agropyron spicatum)* and Idaho fescue *(Festuca idahoensis)* because of their importance as winter range forages and because of the different responses they exhibit to grazing. Both are sensitive to grazing but clipping studies have shown that bluebunch wheatgrass recovers much more slowly than Idaho fescue (Mueggler 1975).

Study area

The northern Yellowstone winter range comprises over 100 000 ha stretching about 80 km along the Lamar, Yellowstone and Gardiner river basins (Houston 1982). Mean annual precipitation at Yellowstone Park, Wyoming (elevation, 1900 m) is 402 mm with the highest precipitation in May. Highest mean daily temperature (18° C) occurs in July. Total precipitation was above normal in September–October 1989 (+12 mm), below normal in January–March 1990 (– 40 mm), above normal in April–May 1990 (+10 mm), and below normal in June–August 1990 (–44 mm).

Our study site was located in the upper portion of the northern winter range near Crystal Creek at an elevation of approximately 1900 m. The site was a flat bench created by glacial deposits. Frank and McNaughton (1992:Table 3) described soils at the site as sandy loam having a bulk density of 1.31 g/cm^3, pH of 6.30, organic matter content of 5.4% and 0.2% nitrogen content. Vegetation is characterized as a xeric grassland dominated by bluebunch wheatgrass, Idaho fescue, junegrass *(Koeleria cristata)*, needle and thread grass *(Stipa comata)*, lupine *(Lupinus sericeus)* and horsebrush *(Tetradymia canescens)* (Wallace, pers. comm.). This study was conducted in the second growing season after the extreme drought and fires of 1988.

Although the northern winter range is grazed year-round by large ungulates, primarily elk, bison *(Bison bison)* and pronghorn *(Antilocapra americana)*, it receives its greatest use by all species in the winter and spring (Houston 1982, Frank and McNaughton 1992, Wallace, pers. comm.). Elk, the most abundant ungulate species in the Park, usually move onto the range in late October, and leave in early to mid-May (Houston 1982). Our study took place in 1990, a year after a major ungulate die-off in the Park (Singer et al. 1989).

Methods

We collected plant–soil cores (4.8 cm diameter, 10 cm depth) centered on 6–10 randomly selected bluebunch wheatgrass and Idaho fescue plants on 11 May, 8 June, 17 July and 8 September inside a large exclosure (15 m × 15 m) and from areas adjacent to the exclosure but open to natural grazing regimes. The exclosure was established in August of 1987 and had not received any ungulate grazing for more than two years (Frank 1990:17). Additionally, we sampled the aboveground biomass of two plant cores inside six (n = 12) small exclosures (1.5 × 1.5 m), which were established on 9 April 1990, before green-up, to provide an index of off-take by ungulates during early spring green-up (April–early May) when grazing was expected to be highest.

Cores were kept coot with ice while transported to the laboratory where they were refrigerated until processing. Vegetative and reproductive tillers per plant core were counted and heights of plants were measured as the average of the tallest three vegetative tillers. Aboveground biomass was clipped at 2 cm and standing dead and green biomass was separated, dried at 40° C for at least 48 h, and weighed.

The soil cores were suspended in cold water and the soil gently washed from the roots. The suspension was sieved first to remove plant tissue (sieve #18) and then to remove nematodes (sieve #325). Crowns, including the aboveground biomass to 2 cm, were cut from the roots. Roots and crowns were dried at 40° C for at least 48 h and weighed. We made no attempt to distinguish between dead and live roots of the two species. We used dry weights in our analysis because dry root weight and ash-free weight is highly correlated (Stanton 1983: r = 0.94). Nitrogen content of aboveground, crown, and root biomass was analyzed using standard macro-kjeldahl techniques.

Eight additional cores (4.8 cm diameter, 10 cm depth) were collected, four within the large exclosure and four in grazed areas at each sampling time to determine soil moisture. Soil moisture was determined gravimetrically after drying at 100° C to a constant weight.

Nematodes were extracted on Baermann funnels for 48 h (Christie and Perry 1951). The number and trophic category of nematodes in each sample was determined by counting the number of individuals present in 2 1-ml subsamples of a 30 ml suspension (Smolik 1974). Numbers of nematodes recovered were corrected for extration efficiencies, which were determined by reextracting 3 of every 20 soil samples at each sampling period. Extraction efficiencies averaged 92% for Rhabditida (saprobes), 91% for Dorylaimida (predators and plant parasites), 86% for fungal-feeders *(Aphelenchus, Neotylenchus)* of the Tylenchida, 93% for plant feeders (Tylenchida), and 73% for Monhysterida. In the trophic grouping, Monhysterida were classified as bacterial-feeders.

Only data on plant height and nitrogen concentration were normally distributed (Lillefors 1967). We used a logarithmic (natural) transformation of biomass data (green, standing dead, crown, and root) and a square root transformation ($x + 0.5$) of count data (tillers and nematodes) before data analysis. A 2-factor ANOVA design tested for differences in plant parameters between treatments (grazed vs ungrazed) and sampling dates. Pairwise comparisons were made using a least significant differences (LSD) test (SYSTAT, Version 5.0).

Results

Plant biomass and nitrogen concentration

Grazing during the winter and early spring essentially removed all previous years growth (standing dead >2 cm) (Fig. 1). The difference in standing dead between grazed and ungrazed plants narrowed during June and July as standing dead plant material from previous years growth on ungrazed plants fragmented, decomposed, or was eaten by small herbivores.

In May, aboveground green biomass of ungrazed plant cores was approximately 3 to 4 times greater than plants grazed in winter and spring (Fig. 2). Data from plants protected from spring but not winter grazing indicated that off-take by ungulates during April and early May accounted for only 18–51% (Fig. 2) of the difference we measured in green biomass between grazed and ungrazed plants in May. Green biomass of Idaho fescue in the large exclosure significantly declined from May to June (Fig. 2). This reflected a significant reduction in the number of vegetative tillers/plant core (Fig. 3) rather than a reduction in plant height (Fig. 4). Ungrazed plants were significantly taller through June (Idaho fescue) and July (bluebunch wheatgrass). In July, the number of flowering culms of ungrazed bluebunch wheatgrass ($\bar{x} = 6.3 \pm 2.0$) was significantly higher than grazed plants ($\bar{x} = 1.7 \pm 0.80$; t-test, $P \leq 0.05$). No flowering stalks were observed on grazed fescue plants and very few ($\bar{x} = 0.11 \pm 0.11$) occurred on ungrazed plants.

Crown biomass was highest in May ranging from 2.29 to 3.14 g/plant core in both species but dropped by 48 and 64% after May in bluebunch wheatgrass and Idaho fescue, respectively. No significant differences existed between grazed and ungrazed plants at any sampling date.

Root biomass of ungrazed plants declined (LSD, $P \leq 0.05$) during the summer with declines occurring earlier in bluebunch wheatgrass than in Idaho fescue (Fig. 5). Root biomass of grazed plants was 60–75% of ungrazed plants in May (both species) and June (Idaho fescue). In July and September, root biomass did not differ significantly between grazed and ungrazed plants for either species. After spring grazing, May

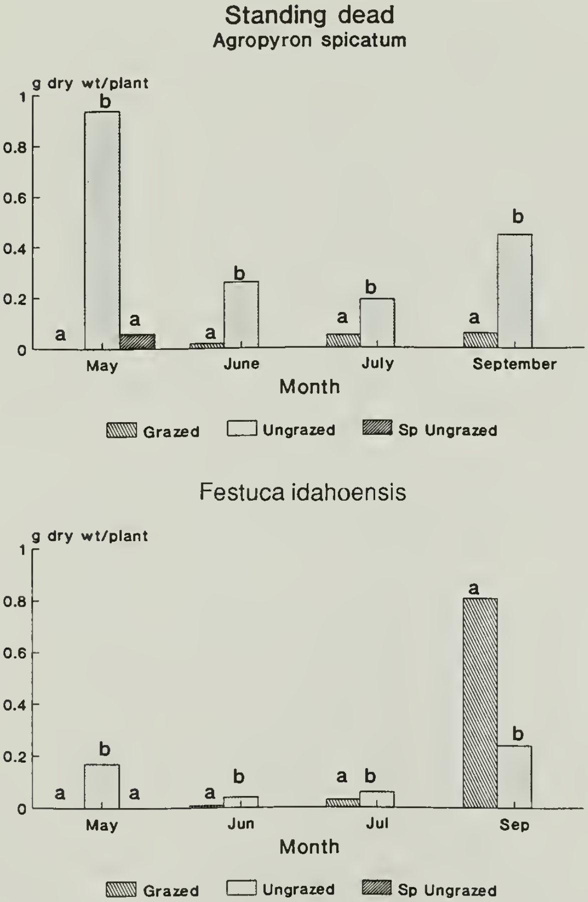

Fig. 1. Standing dead litter (g dry matter/plant core) in plants of *Agropyron spicatum* and *Festuca idahoensis* inside (ungrazed) and outside (grazed) a permanent exclosure in the 1990 growing season on Crystal Bench, Yellowstone National Park. Dissimilar letters indicate significant differences (LSD, $P \leq 0.05$).

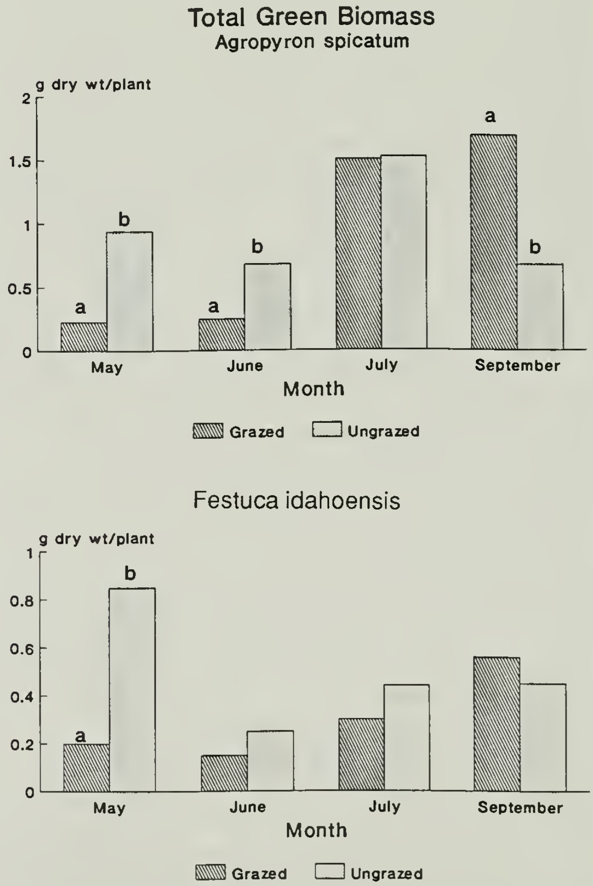

Fig. 2. Total green biomass (g dry matter/plant core) of *A. spicatum* and *F. idahoensis* plants in the 1990 growing season inside (ungrazed) and outside (grazed) a permanent exclosure and inside 6 temporary exclosures established before spring growth (spring) on Crystal Bench, Yellowstone National Park. Dissimilar letters indicate significant differences (LSD, $P \leq 0.05$).

root/shoot ratio of both species was higher in grazed (Idaho fescue: 5.10; bluebunch wheatgrass: 4.26) than in ungrazed (Idaho fescue: 1.62; bluebunch wheatgrass: 1.61) plant cores (Table 1). The high root/shoot ratio of ungrazed Idaho fescue (7.41) plant cores a month later was related to a decrease in aboveground green biomass associated with a decrease in tiller numbers. By July, root/shoot ratios did not differ with treatment in either species.

Nitrogen concentrations

In June and July, nitrogen concentration of aboveground biomass but not root biomass was significantly greater in plants grazed by ungulates than ungrazed (Table 2).

Nematode densities

The orders of nematodes by abundance were the Rhabditida, the Dorylaimida, the Tylenchida (including the genera *Aphelenchus, Tylenchus, Neotylenchus, Tylenchorhynchus and Pratylenchus*) and the Monhysterida (Table 3). The Rhabditida (bacterial-feeders) had densities a magnitude higher than the other three orders. Seasonal abundance of nematodes followed a bimodal distribution with the low occurring in July when soil moisture was at its lowest (2%) (Table 3). Densities (no./m^2) of nematodes did not significantly differ between treatments or between the two grass species despite marked differences in the overall root structure: Idaho fescue had many, fine roots versus bluebunch wheatgrass which had few, coarse roots.

When densities were expressed on the basis of dry root weight (no./g root), plant parasites were significantly higher under grazed plants than ungrazed plants in May (both species) and in June (Idaho fescue) (Fig. 6). Densities of bacterial-feeding nematodes (Rhabditida and Monhysterida) were higher under grazed plants than ungrazed plants of both species in both May and June (Fig. 7).

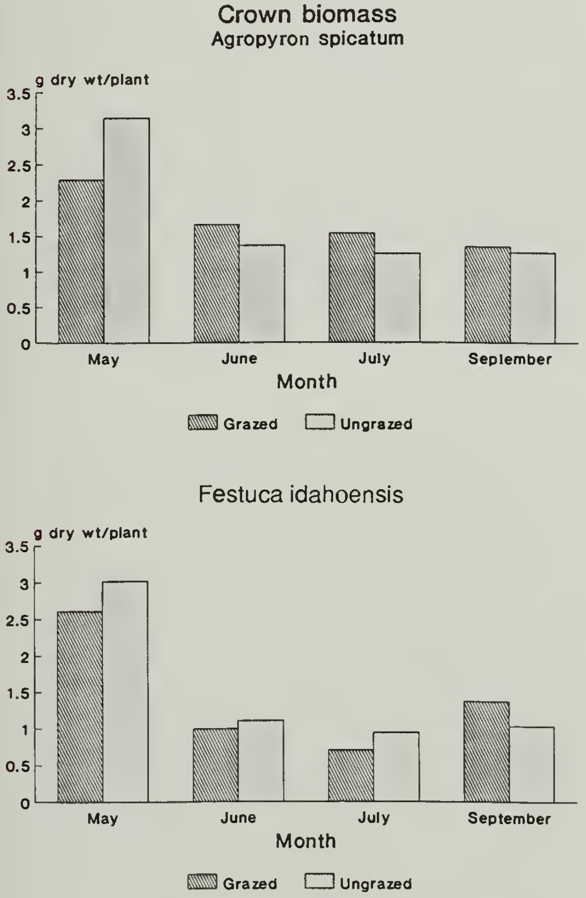

Fig. 3. Tillers (no./plant core) of *A. spicatum* and *F. idahoensis* plants inside (ungrazed) and outside (grazed) a permanent exclosure in the 1990 growing season on Crystal Bench, Yellowstone National Park. Dissimilar letters indicate significant differences (LSD, $P \leq 0.05$). *September samples were damaged.

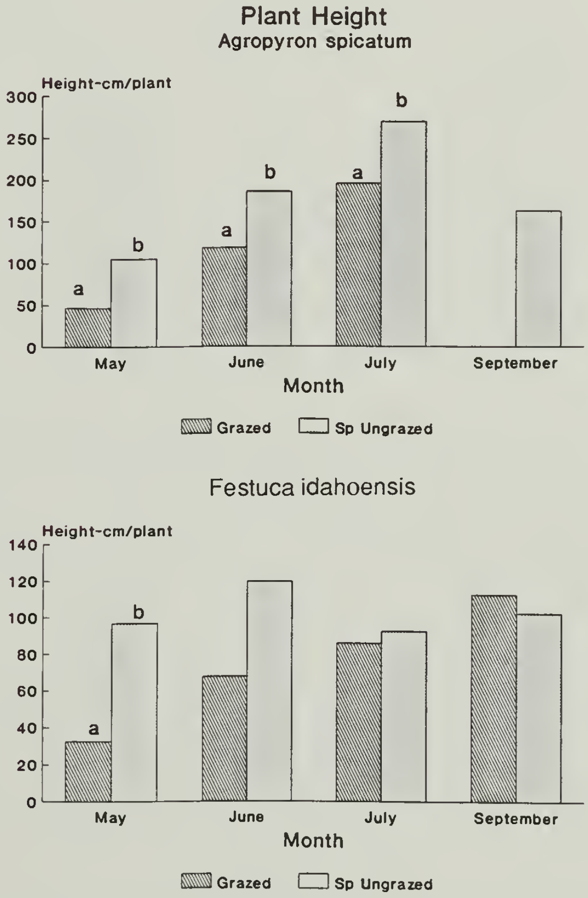

Fig. 4. Plant height (mm) of *A. spicatum* and *F. idahoensis* plants inside (ungrazed) and outside (grazed) a permanent exclosure in the 1990 growing season on Crystal Bench, Yellowstone National Park. Dissimilar letters indicate significant differences (LSD, $P \leq 0.05$).

Plant-feeders included *Tylencholaimus* of the Dorylamida and all Tylenchida except for *Aphelenchus* and *Neotylenchus.* Fungal-feeders *(Aphelenchus* and *Neotylenchus)* tended to be more abundant under grazed Idaho fescue but not under bluebunch wheatgrass (Fig. 8). Dorylamida were most numerous in May but exhibited no response to grazing under either species (Fig. 9).

Discussion

In 1990, grazing by ungulates on Crystal Bench in winter and spring removed essentially all standing dead material in Idaho fescue and bluebunch wheatgrass. The off-take we measured accounted for only about 18–50% of the difference in green biomass between the plants inside and outside the 2-year old exclosure in May. Microclimatic changes, resulting from indirect effects of grazing, may account for the difference. For example, Sauer (1978) found that removal of standing dead from bluebunch wheatgrass resulted in a 28% decrease in culm and leaf weight and a 25% decrease in leaf height in the following growing season. Alternatively, we also observed that plants with standing dead litter served as "snow fences" during the winter. The accumulation of snow around tall plants in the exclosure may have increased soil moisture sufficiently enough to affect plant growth.

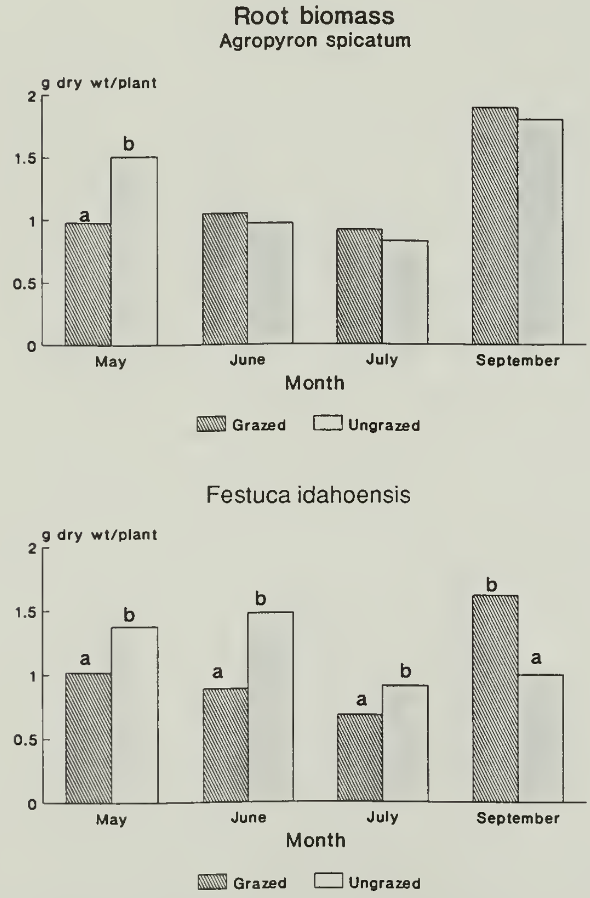

Fig. 5. Root biomass (g dry matter/plant core) in plants of *A. spicatum* and *F. idahoensis* inside (ungrazed) and outside (grazed) a permanent exclosure in the 1990 growing season on Crystal Bench, Yellowstone National Park. Dissimilar letters indicate significant differences (LSD, $P \leq 0.05$).

Despite early-season differences, grazed plants recovered both below and aboveground biomass by the end of the growing season. Recovery after spring grazing has been reported for these species elsewhere (Blaisdell and Pechanec 1949, Pond 1957, Donart and Cook 1970, Mclean and Wikeem 1985) and may be attributed to increased photosynthetic rates of remaining foliage (Caldwell et al. 1981, Nowak and Caldwell 1984), increased light saturation of the lower leaves (Caldwell et al. 1983), removal of transpiring tissue resulting in soil moisture conservation (Wraith et al. 1987), or other belowground processes.

Frank and McNaughton (1992) found that grazing stimulated aboveground primary production by 36% at the Crystal Bench site in 1989, a year of above average (149%) precipitation in May (76 mm), average (108%) precipitation in June (53 mm) and below average (79%) precipitation in July (31 mm). In this study, plants recovered from spring grazing when precipitation was 127% above average in May (66 mm), and 89% (44 mm) and 23% (9 mm) of average in June and July, respectively. However, Coughenour (1991) found that aboveground grass production did not recover after grazing at three of four sites on the northern winter range when, after

Table 1. Root:shoot ratios of *A. spicatum* and *F. idahoensis* plants inside and outside a permanent exclosure in the 1990 growing season on Crystal Bench, Yellowstone National Park. Shoot and root biomass were averaged between treatments before calculating ratios where differences were not significant.

	Inside	Outside
Agropyron spicatum		
May	1.61	4.25
June	1.49	4.03
July	0.58	0.57
September	1.50	1.50
Festuca idahoensis		
May	1.62	5.10
June	7.41	4.44
July	2.15	2.15
September	3.35	3.35

Table 2. Seasonal changes in nitrogen concentrations (% N) of roots and aboveground green biomass of *Agropyron spicatum* and *Festuca idahoensis* inside and outside a permanent exclosure on Crystal Bench in Yellowstone National Park, 1990.

	Roots		Aboveground biomass		
	Inside	Outside	Inside		Outside
Agropyron spicatum					
May	1.22+	0.93	2.81		2.46+
June	1.14	1.39	1.65	*	2.38
Festuca idahoensis					
May	1.01	1.06	1.72	*	2.58
June	1.16	1.16	1.33	*	1.74

+ small n precluded statistical analysis.

* indicates a significant difference $P < 0.05$ between plants inside and outside the exclosure.

above average May precipitation (180%, 92 mm), a drought began and precipitation in June and July was only 25% (12 mm) and 60% (24 mm) of normal, respectively. Thus, precipitation has an important effect on plant responses to spring grazing on the northern winter range.

We did not find that grazing influenced tillering in either species. Spring tillering rarely has been observed in bluebunch wheatgrass (Mueller and Richards 1986) and tillering dynamics of Idaho fescue are not well studied. We found a decline in the number of tillers/plant core from May to June in ungrazed Idaho fescue plants. Tillers of Idaho fescue form a tightly clustered bunchgrass with considerable self-shading. Caldwell et al. (1983) found that older, shaded tillers of compact tussocks of *Agropyron* spp. were light-limited and showed inefficient wateruse. If shaded Idaho fescue tillers did not maintain a positive carbon balance, they would have died. However, we did not see a comparable increase in standing dead and suspect the tillers were defoliated by other herbivores (rodents or grasshoppers). Since we found a reduction in flowering culms of grazed plants, reduced seed production may be an important effect of grazing, if seed abundance is an influential factor in the dynamics of these grasslands.

Defoliation arrests root growth and causes root mortality (Jameson 1963, Hodgkinson and Baas Becking 1977), and likely contributed to lower root biomass of grazed than ungrazed plants in May (both species) and June (Idaho fescue). Studies have shown that bluebunch wheatgrass allocates a high proportion of carbon to roots after defoliation (Caldwell et al. 1981, Richards 1984). High densities of root-feeding nematodes/g root biomass under grazed bluebunch wheatgrass plants may have slowed root growth since there was no increase in root biomass until September.

Our observations of root recovery are consistent with those of Coughenour (1991), who found that total root biomass of herbaceous vegetation inside and outside exclosures erected some 30 years earlier on the northern range was different at only one of four sites and that difference disappeared by September. However, our generalizations about root biomass are based on root biomass only in the top 10 cm of this site because the rocky, shallow soil at Crystal Bench

Table 3. Densities ($1000/m^2$) of nematode taxa under *Festuca idahoensis* and *Agropyron spicatum* plant cores from inside and outside a 2-year old exclosure on Crystal Bench, Yellowstone National Park in 1990.

	Festuca idahoensis								*Agropyron spicatum*							
Nematode	May		June		July		Sept		May		June		July		Sept	
order	In	Out	In	Out	In	Out	In	Out	In	Out	In	Out	In	Out	In	Out
Monhysterida																
$\bar{x}$	11	85	60	98	8	0	8	2	55	45	58	91	4	4	30	3
s.e.	5	55	29	29	8	0	3	2	24	22	23	30	2	4	17	3
Dorylaimida																
$\bar{x}$	464	486	95	87	41	30	158	259	559	378	126	107	65	43	201	61
s.e.	65	88	27	17	14	9	33	26	80	58	24	26	23	13	48	17
Rhabditida																
$\bar{x}$	1127	1110	263	363	140	162	451	1131	1108	862	278	385	177	148	520	438
s.e.	235	114	100	91	38	54	101	448	123	140	76	79	43	37	93	136
Tylenchida																
$\bar{x}$	144	365	102	187	37	36	110	179	228	28	123	136	51	37	99	132
s.e.	20	101	23	33	16	20	28	69	57	81	43	26	17	12	24	57
Total density	1746	2046	520	735	226	228	719	157	119	5015	7058	5719	297	232	850	634

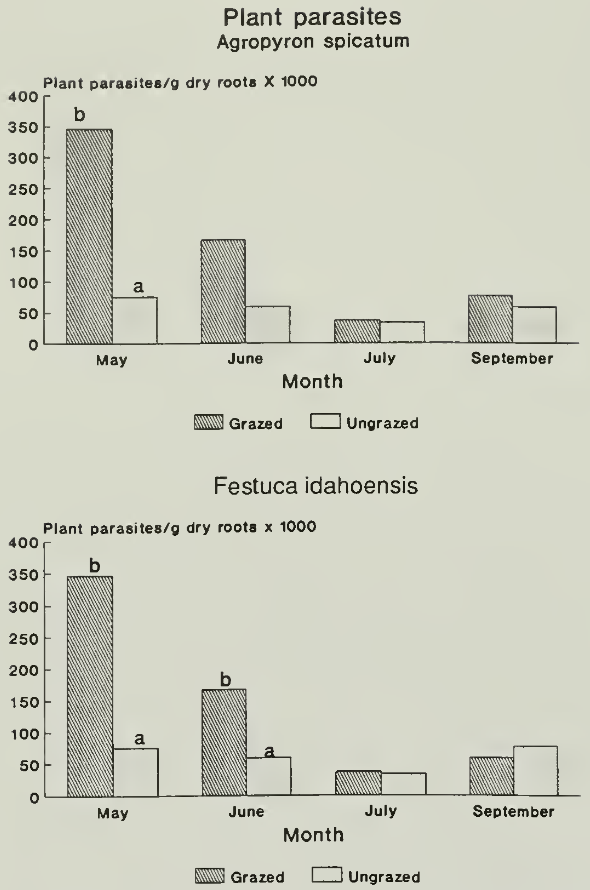

Fig. 6. Plant-parasitic nematodes and bacterial-feeding nematodes (g dry matter × 1000) under plants of *A. spicatum* and *F. idahoensis* inside (ungrazed) and outside (grazed) a permanent exclosure in the 1990 growing season on Crystal Bench, Yellowstone National Park. Dissimilar letters indicate significant differences (LSD, $P \leq 0.05$).

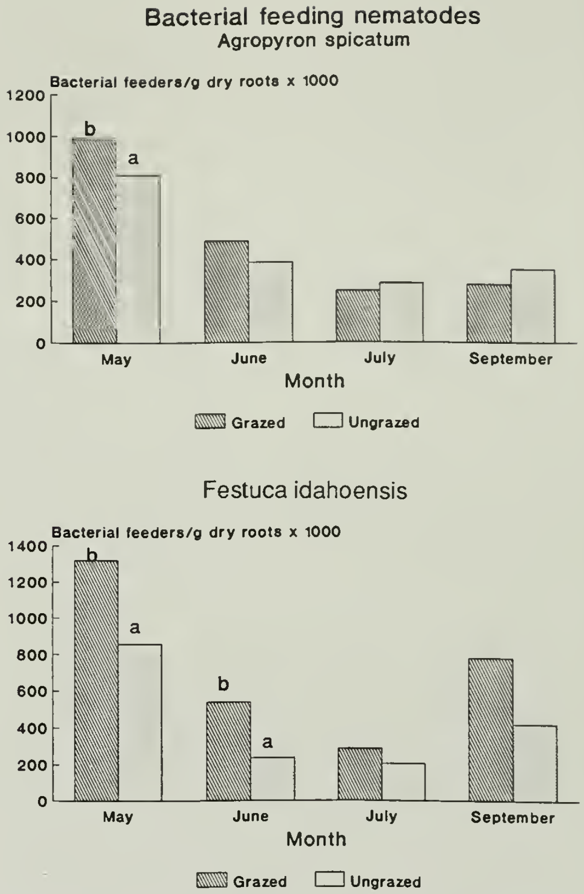

Fig. 7. Fungal-feeding nematodes and Dorylamida (no./g dry wt × 1000) under plants of *A. spicatum* and *F. idahoensis* inside (ungrazed) and outside (grazed) a permanent exclosure in the 1990 growing season on Crystal Bench, Yellowstone National Park. Dissimilar letters indicate significant differences (LSD, $P \leq 0.05$).

precluded our sampling much deeper. Weaver and Smolik (1987), who sampled root biomass in a *F. idahoensis–A. caninum* community in Montana to a depth of 50 cm, found that the top 10 cm contained about 50% of the root biomass.

Nematode densities on both the grazed and ungrazed plants were well within the ranges reported from other arid grasslands (Stanton et al. 1981, 1984, Smolik and Dodd 1983, Ingham and Detling 1990), but were somewhat lower than Weaver and Smolik (1987) reported for a Montana Idaho fescue grassland. They sampled by 10-cm intervals to a depth of 50 cm and found that the highest percentage of biomass occurred in the top 10 cm, but it accounted for only 25% of the total nematode biomass. Because of the shallow nature of the soil at Crystal Bench, our 10-cm-deep cores probably contained more than 25% of the nematode population.

Nematode densities showed a seasonal decline from May to July which is probably a response to changes in soil moisture. Similar declines in nematode populations have been reported in the mixed and shortgrass prairie communities (Smolik 1974, Smolik and Dodd 1983, Ingham and Detling 1984, Stanton et al. 1984). Grazing by ungulates increased some groups of soil nematodes. For example, densities (no./g root biomass) of root-feeding, fungal-feeding, and bacterial-feeding nematodes were higher under grazed plants in May (both species) and June (Idaho fescue). Ingham and Detling (1984) suggested two reasons why they found higher densities of microbial-feeding nematodes on grazed prairie dog towns versus ungrazed areas. First, reduced vegetative cover on the prairie dog towns may have altered the soil moisture and temperatures for more favorable nematode growth. A similar argument can be made for root-feeding nematodes since Smolik (1982) showed an increase in reproductive potential and densities of root-feeding nematodes with higher soil temperatures. Reductions in standing dead material and increases in

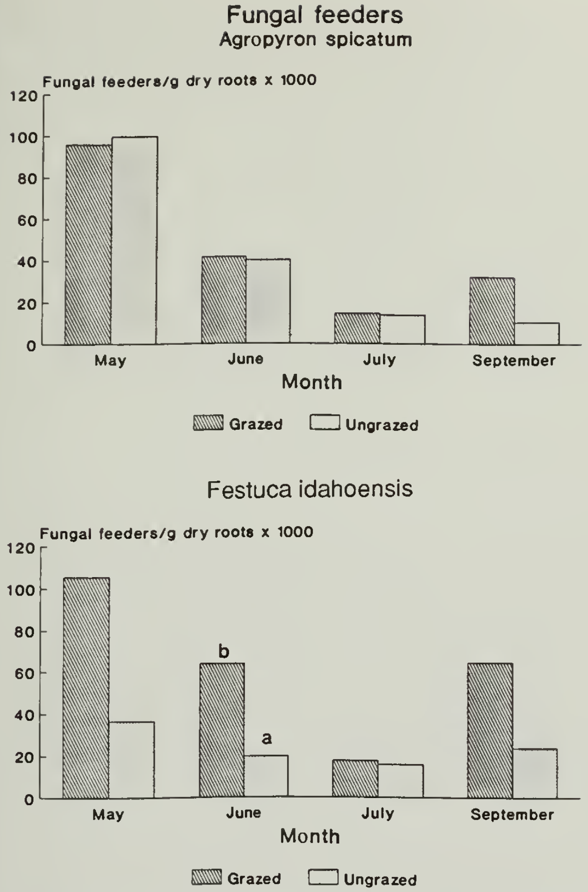

Fig. 8. Fungal feeding nematodes (no. g/dry wt × 1000) under plants of *A. spicatum* and *F. idahoensis* inside and outside a permanent exclosure in the 1990 growing season on Crystal Bench, Yellowstone National Park.

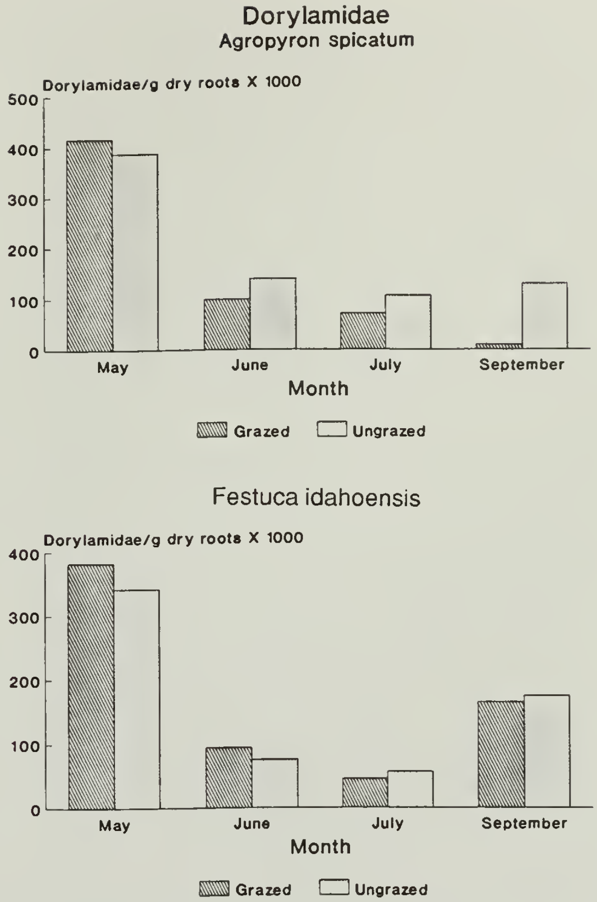

Fig. 9. Dorylamidae (no. g/dry wt × 1000) under plants of *A. spicatum* and *F. idahoensis* inside and outside a permanent exclosure in the 1990 growing season on Crystal Bench, Yellowstone National Park.

bare ground in grazed areas on the northern winter range, relative to ungrazed areas, have been documented (Cough- enour 1991, Singer 1992, this study) and may influence soil conditions. We did not measure soil temperatures but Pierson and Wight (1991) reported that grass crown litter had little influence on soil surface temperatures because heat could easily move into or be lost to the surrounding uninsulated soil, thus controlling the soil temperature beneath the insulated areas.

Second, Ingham and Detling (1984) found that there was significantly more total soil N on the grazed prairie dog colony in Wind Cave National Park than off the towns indicating a reduced C:N ratio. They suggested that the reduced C:N ratio favored a more rapidly growing microbial community, thus supporting a higher standing crop of bacterial-feeding nematodes/g root in May and June. However, because root biomass was lower on grazed areas, Holland and Detling (1990) argued that repeated grazing reduced carbon inputs to microbes via roots which decreased N immobilization, increased net nitrogen mineralization, and increased nitrogen availability to plants. In contrast, neither this study nor that of Coughenour (1991), found lower root biomass at the end of the growing season in grazed areas than ungrazed areas on the northern range.

We suggest that at our study site in Yellowstone root mortality due to spring grazing provided a short-term increase in carbon which favored a rapidly growing microbial community and supported a high standing crop of bacterial-feeding nematodes. High microbial activity increased mineralization rates, while at the same time, bacterial-feeding nematodes increased turnover rates of microbial-bound N, which facilitated regrowth, and resulted in an increase in foliar nitrogen in grazed plants (Ingham et al. 1985, Hunt et al. 1987). The seasonality of ungulate grazing in Yellowstone, as compared to prairie dogs grazing in Wind Cave National Park, in part, may be responsible for different patterns in nutrient dynamics between these areas.

Neither this study, nor that of Coughenour (1991) found that concentration of nitrogen in roots increased as a result of grazing as Seadstadt (1985) hypothesized. Thus, while many studies have demonstrated increased nitrogen concentration in shoots of grazed plants (e.g., Coppock et al. 1983, Ruess et al. 1983, Ruess and McNaughton 1984, Seastedt et al. 1988), only Seastedt et al. (1988), in a pot experiment, demonstrated that the actual concentration of nitrogen increased in roots on clipped plants.

Alternative explanations for increases in root-feeding nematodes with grazing may be that grazed plants experience a reduction in secondary chemicals that deter nematode feeding (Ingham and Detling 1984), or produce more roots hairs (preferred nematode feeding sites). It seems reasonable to assume that plants, subject to chronic belowground herbivory, would evolve mechanisms to maintain a low nitrogen concentration and a high level of secondary substances even when grazed (Seastedt 1985). Since mineralization rates increase with grazing (Holland and Detling 1990), it would be advantageous for plants to produce more roots hairs to take advantage of increased nutrient availability. We could find no data on root hair response to grazing. However, injury to root tips (e.g. nematode feeding) has been reported to stimulate lateral root growth (Bridge and Hague 1974, Torrey 1976). This phenomenon would also explain the increased nitrogen concentration measured in new shoot growth after grazing. These belowground interactions may be confounded by the presence of mycorrhizae; but data on nitrogen absorption mechanisms relative to changes in root hairs or mycorrhizal hyphae as a function of grazing pressure are lacking.

In summary, our data supported all but one of our original hypotheses. Grazed plants did recoup above- (off-take) and belowground (root mortality) biomass losses by the end of growing season under the climatic regimes of our study. Thus, plant responses at Crystal Bench were consistent with plants in other areas on the northern range (Coughenour 1991). Lower root biomass, higher densities of bacterial-feeding nematodes, and higher concentrations in foliar nitrogen with grazing are consistent with our hypothesis that root mortality, due to spring grazing, provided a short-term source of carbon for microbial activity and that microbial-feeding nematodes increased the turn-over rates of microbial bound N. Contrary to our predictions, we found that densities of root-feeding nematodes (no./g root biomass) were higher with grazing. We suggest that grazed plants experienced a reduction in secondary chemicals that deter nematode feeding (Ingham and Detling 1984), or produced more roots hairs (preferred nematode feeding sites). We can not dismiss indirect effects of grazing on soil conditions, such as increased soil temperatures due to increased bare ground (Singer 1992), reduced standing dead (Coughenour 1991; Singer 1992, this study), or increased soil moisture due to removal of transpiring tissue (Wraith et al. 1987). Our findings support the conclusion of Coughenour (1991) that the net effect of aboveground grazing by ungulates on the northern range is a redirection of carbon from decomposers to aboveground grazers and an increase in the rate of N cycling back to aboveground herbivores, but implicate the importance of spring grazing and the role of nematodes in this phenomenon.

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EFFECTS OF BROWSING BY NATIVE UNGULATES ON THE SHRUBS IN BIG SAGEBRUSH COMMUNITIES IN YELLOWSTONE NATIONAL PARK

Francis J. Singer

Division of Research
P.O. Box 168
Mammoth Hot Springs,
Yellowstone National Park, Wyoming 82190

and

Colorado State University
Fort Collins, Colorado 80523

and

Roy R. Renkin

Resources Management Division
Box 168
Yellowstone National Park,
Wyoming 82190

ABSTRACT. The effects of elk (*Cervus elaphus*), pronghorn (*Antilocapra americana*), and mule deer (*Odocoileus hemionus*) browsing on shrubs in big sagebrush (*Artemisia tridentata*) communities were monitored over a 31-year period in Yellowstone National Park. Ungulates were restricting Wyoming big sagebrush (spp. *wyomingensis*) heights, size and recruitment on the lower elevation stratum only, while no such suppression was observed on the high elevation stratum; parallel increases in mountain big sagebrush (spp. *vaseyana*) densities and cover occurred over the study period on both browsed and unbrowsed sites at the higher elevation stratum, although big sagebrush, green rabbitbrush (*Chrysothamnus viscidiflorus*), and horsebrush (*Tetradymia canescens*) were slightly taller and crown sizes were slightly larger on unbrowsed versus browsed sites. Wyoming big sagebrush utilization (percent leader use) was eight times higher $\bar{x} = 87 \pm 7.2\%$ (by pronghorns, mule deer and elk) on the low elevation winter range stratum (the Boundary Line Area portion of the winter range) while mostly mountain big sagebrush with leader use averaged only $11 \pm 4.1\%$ (nearly all by elk) on the high elevation range stratum. in addition, annual aboveground biomass production of big sagebrush did not differ between browsed and unbrowsed study sites on the high elevation stratum of the winter range. Population turnover was higher on browsed big sagebrush at the high elevation plots; seedling germination and survival rates were higher on browsed plots versus unbrowsed plots. No difference was observed in percent dieback of big sagebrush adult plants between browsed and unbrowsed plots at the higher stratum. Browsing did not influence the number of leaves or seedstalks per plant ($P > 0.05$), but leaves averaged 45% longer and seedstalks averaged 42% longer on browsed big sagebrush. Ungulate browsing, however, apparently suppressed production, germination, and survival of Wyoming big sagebrush on the low elevation stratum. Numbers of Wyoming big sagebrush declined 43% and cover declined

6%–35% that of unbrowsed sites, and big sagebrush recruitment was less on browsed sites. Percent leader use of big sagebrush did not differ between the period of ungulate reductions, 1962–69, and the 1980's on the lower stratum ($\bar{x} = 87\%$ leader use), but utilization was less on the higher portions of the winter range during the period of elk reductions ($\bar{x} = 2\%$) than during the 1980's following cessation of elk controls ($\bar{x} = 11\%$).

Key Words: Big sagebrush browsing, northern Yellowstone elk, pronghorn, mule deer, *Cervus elaphus.*

Native populations of elk (*Cervus elaphus*), bison (*Bison bison*), and pronghorn (*Antilocapra americana*) were artificially reduced in Yellowstone National Park (YNP), particularly during 1942 through 1967 (Meagher 1973; Houston 1982). Reductions were terminated in 1967, when an experimental management program of natural regulation was initiated (Cole 1971; Houston 1976, 1982). Elk and other ungulate numbers tripled after cessation from controls, and concerns were expressed over high ungulate densities (Chase 1986; Kay 1991). The appropriate numbers of ungulates for the park's ranges are unknown since no similar control area exists where wolves (*Canis lupus*) are present and where ungulate migrations are completely unrestricted by humans (Cayot et al. 1979, Peek 1980). Ungulate densities are likely slightly above natural conditions, in that 3 independent computer models suggest 8–15% fewer elk and 10–25% fewer bison would occupy the system if wolves were recovered (Garton et al. 1990, Boyce 1993, Mack and Singer 1993).

Early workers expressed concern about the apparent overbrowsing and declines in big sagebrush (*Artemisia tridentata*) due to possible over-abundant populations of elk and pronghorn. As early as the 1930's, Rush (1932) and Cahalane (1943) reported losses of big sagebrush over lower elevation areas of the northern winter range. Rush (1932) reported that less palatable rabbitbrushes (*Chrysothamnus* spp.) were increasing. Kittams (1950) concluded big sagebrush numbers were declining at both lower and the higher elevations of the northern winter range. He felt physical disturbances by elk of big sagebrush during cold periods (shattering and trampling) and an absence of big sagebrush reproduction contributed to the decline. Declines in big sagebrush at the lower elevation Boundary Line Area (BLA) were attributed to excessive levels of browsing by pronghorn by Kittams (1950). Park management established a goal to reduce the pronghorn herd by 50% (Kittams 1959); by 1969 pronghorn numbers were artificially reduced from 600–800 to less than 200 through a combination of artificial reductions and severe winters (Barmore 1980).

Houston (1982) provided alternative interpretations concerning big sagebrush. He reported big sagebrush numbers increased over all the northern winter range except for the BLA near Gardiner, Montana, where numbers declined. Houston's (1982) compared photos taken during the 1860's to photos retaken in the 1970's. Houston (1982) attributed the increase in big sagebrush at higher elevations to fire suppression. He attributed the decline in big sagebrush in the BLA to a return to more natural conditions following the removal of intense grazing by livestock in the early 1930's when the area was added to the park. In 1986, the U.S. Congress directed the NPS to conduct a study to evaluate whether native ungulates were overgrazing the northern winter range (Congressional Record—Senate S.12613, 1986).

Our objectives were to document trends in big sagebrush abundance on a series of permanently marked plots from 1958 to 1990. Height, canopy size, twig lengths and annual production of shrubs were compared between browsed and unbrowsed sites.

THE STUDY AREA

Shrub sampling was conducted on unbrowsed (exclosed) and paired browsed sites at eight ungulate exclosures erected in 1958 and 1962 on Yellowstone's northern winter range. The eight exclosures were 2 ha in size and were located on gently rolling upland steppe ridge and the intervening swale habitats (Fig. 1). We divided the study area into a low elevation stratum (the BLA of Houston 1982) with two exclosures, and a much larger, high elevation stratum (n = 6 exclosures), based upon large differences in ungulate species, elevation, snowpack, precipitation and big sagebrush subspecies (Fig. 1).

Underlying soils are typic calciborolls, aridic haploborolls, and aridic calciborolls (Lane 1990). Precipitation averages 30 cm at the low elevation exclosures and 55 cm at the high stratum exclosures (Houston 1982; Despain 1991). The northern winter range is approximately 1100 km^2 and is located along the upper Yellowstone River drainage. Elevations range from 1500 m at the low stratum exclosures to about 2200 m at the highest exclosure. The northern winter range is lower, warmer, and drier than the remaining higher plateaus of YNP (Houston 1982). As a result, 80% of the ungulates in the park during winter are found on the northern winter range (Singer 1991).

Fig. 1. Map of the northern Yellowstone ungulate winter range, and the high elevation stratum (6 exclosures) and low stratum (2 exclosures) big sagebrush study sites. Pronghorns, mule deer, and the Wyoming subspecies of big sagebrush were found only at the low elevation stratum.

Dominant shrubs at all the study sites include two subspecies of big sagebrush at the high elevation stratum, nearly all mountain big sagebrush (*A.t. vaseyana*) with some basin big sagebrush (*Artemisia tridentata tridentata*), while only Wyoming big sagebrush (*A.t. wyomingensis*), occurs in the low stratum study sites. The big sagebrush subspecies vary markedly in their site requirements, growth, and preferences by ungulates (Beetle 1960; Beetle and Johnson 1982; Welch et al. 1981; McArthur and Welch 1982). Rubber rabbitbrush (*Chrysothamnus nauseosus*), green rabbitbrush (*Chrysothamnus viscidiflorus*), and horsebrush (*Tetradymia canescens*) are found at all the study sites. *Grayia spinosa* and *Atriplex canescens* occur at the low stratum study sites (Houston 1982). Dominant grasses are bluebunch wheatgrass (*Pseudoroegneria spicata*), Idaho fescue (*Festuca idahoensis*), junegrass (*Koeleria macrantha*), bluegrasses (*Poa compressa*, *P. sandbergii*, or *P. pratensis*), and thick-spike wheatgrass (*A. dasystachyum*; Houston 1982; Wambolt et al. 1987; Despain 1991).

Pronghorn and mule deer occupy only the low elevation stratum of approximately 52 km^2 within Yellowstone National Park (Barmore 1980; Houston 1982; Singer 1991). About one-half of the pronghorn population also summers in the low elevation stratum. The lower elevation (about 1,500 m), exclosures are located in typically, nearly snow-free, rolling xeric shrub and mixed grassland habitats. Elk occupy both strata and the entire winter range of 810–1000 km^2 (Houston 1982; Singer 1991). Only elk and bison winter near the high elevation stratum exclosure sites. Winter snow depths near the higher exclosures (1,639–2,200 m) are typically 0.4–0.6 m, which are excessive for pronghorn and deer. The abrupt elevation rise for Mt. Everts separates the high and low strata. The bison winter range expanded from about 130 km^2 in the 1960's in the higher stratum only to about 460 km^2 in the late 1980's, during a period of bison population and range expansion (Meagher 1989; Singer and Norland 1995). Periodic bison use of the low elevation stratum occurred following the population expansion in the late 1980's (Meagher 1989); the vegetation measures reported here were mostly taken prior to any bison use of the low elevation stratum.

Elk numbered about 8,000 in 1959–62 when initial monitoring of the sagebrush belt transects began. Elk were subsequently further reduced by artificial controls to less than 5,000 in 1967 (Houston 1982). After cessation of controls, elk steadily increased and counts ranged from 16,000 to 19,000 from 1982 to 1989 (Singer et al. 1989; Singer 1991). Bison were also artificially controlled until 1967. After cessation of controls, bison on the northern range increased from less than 100 to 850 by 1988 (Houston 1982; Meagher 1989). Pronghorn were artificially reduced from 600–800 to less than 200 (Barmore 1980) and pronghorn numbers remained less than 200 until about 1981. During the 1980's—apparently due to milder winters—pronghorn increased to about 600 (Singer 1991). Mule deer counts increased from 1,000 in 1985 to 2,300 in 1988 over the entire deer winter range, the majority of which lies north of the park boundary (Singer 1991). Conversely, mule deer counts just within the park boundaries declined from 230 in the 1960's (Barmore 1980) to about 100 in 1988, in spite of the overall herd increase.

METHODS

Ungulate Densities and Diets

Average ungulate densities based on actual aerial counts near the exclosures were based upon actual counts made from fixed-wing aircraft as described in Barmore (1980), Houston (1982), Meagher (1989), Singer (1991) and Singer and Norland (1995). Densities are uncorrected for visibility bias (Samuel et al. 1988) and they, therefore, represent minimum average densities for the study periods—undoubtedly some animals were missed on the counts (Singer et al. 1989). Diets of all four ungulates found near the study sites were estimated for each of three winters, December–March, 1985–1988, on the northern winter range from microhistological analysis of fecal samples (Washington State Univ., Wildlife Habitat Laboratory, Pullman). Each sample was a composite of 5 g of fresh dung material from 6–12 dung piles. Aggregate average percentages are reported for significant species and plant groups. Fresh samples were collected for groups of animals immediately after the groups had vacated an area to avoid confusion between similar species. Bighorn sheep (*Ovis canadensis*) use steeper terrain on the northern range, and moose (*Alces alces*) are found at the higher elevations; neither species were observed near the study sites.

Shrub Utilization Rates

Winter ungulate herbivory rates were sampled on the browsed transects in late winter–spring before leaf emergence (usually late April) in 1963–69, 1987, 1989, and 1990. Percent twig utilization was obtained from counts of all browsed and all unbrowsed twigs on each shrub located in the transect. Diameters at basal point and browsing point were measured on 20 random shoots on every 5th shrub of every browsed shrub individual of each species and bite sizes were estimated following Pitt and Schwab (1990).

Trends in Big Sagebrush, 1958–90

Five exclosures were erected in 1957 and three more were erected in 1962 (n = 8 total). The exclosures were placed in sites representative of mixed big sagebrush/bunchgrass communities. Paired belt transects (each 1.5 m × 30.5 m = 46.5 m^2) were permanently located inside and outside of eight of the exclosures (1 per exclosure treatment) in big sagebrush communities (Canfield 1941; Parker 1954). Each matched pair of transects was as nearly comparable as possible in terms of in slope, aspect, elevation, shrub species, and shrub cover (Barmore 1980, Houston 1982), but nevertheless, differences might have occurred. Sampling of the transects occurred at the date of exclosure, which should reveal any initial site differences. The transect for exclosure was selected arbitrarily. Heights and species of all shrubs found on the belt transects were recorded in 1958, 1962, 1967, 1974, 1981, 1986, and 1990. Numbers of individual shrubs and any shrub seedlings were tallied. The aerial cover of all shrubs was mapped on graph paper, and shrub cover was later estimated using a grid (Barmore 1980, Houston 1982).

Detailed Site Comparisons in 1986 and 1987

The shrub belt transects were not replicated at a site (n = 1 transect per treatment per location, 13 transects total) and were useful primarily for long-term trends and assessment of pre-treatment conditions (Parker 1954). In 1986 and 1987, more intensive and better replicated measurements (n = 15 plots per treatment) were gathered; 15 circular plots each 1.7 m in radius (9.3 m^2) were randomly located in big sagebrush stands both inside and outside of six exclosures. The tallest height, widest diameter, and perpendicular diameter were recorded for each shrub within each plot. The number of totally dead shrubs was recorded. The percent of dead material on partially live shrubs was estimated. At every fifth shrub of each species, lengths and diameters of 10 randomly sampled twigs were measured, and every vegetative twig and reproductive stalk was counted. A minimum of 100 twigs of each species from each site was collected, dried, and weighed. Canopy area for each individual shrub was estimated from the formula for the area of an ellipse (area = $(\pi/4)d^1d^2$ where d^1 = largest diameter and d^2 = its perpendicular diameter) following Peek (1970). All plots and long-term transects were located more than 25 m from the exclosure fences to avoid the effects of snowdrifts or ungulate trails along the fences.

Mean shrub height, largest crown area, shoot numbers and lengths, and total shrub cover were compared using a 2-way ANOVA with browsing and exclosure location as treatments. The six exclosures were considered as replications of one treatment (browsing) with five d.f. used to test for differences among the treatment and among replications. Replications at a location included the 15 random plots in each treatment (15 × 2 × 8 locations = 240 plots of 9.3 m^2). Non-parametric procedures were used for percent twig utilization comparisons between the 1960's versus the 1980's and for other data that were non-normal or with unequal variances (F-max tests; Sokal and Rohlf 1981). Frequency distributions of shrubs in browsed and unbrowsed plots were compared using the Kolomogorov–Smirnov test (Zar 1974). All differences discussed are significant at the $P < 0.05$ level unless otherwise indicated.

Aboveground biomass production of shrubs was estimated from the numbers of shrubs per plot times the average number of reproductive and vegetative shoots per plant times the average dry weight of shoots. Regression equations for dry weight of shoots (independent variable) were calculated from diameters at base (dependent variable) and length (dependent variable) of shoots following MacCracken and Viereck (1990). Separate regression equations were calculated for reproductive and vegetative shoots of big sagebrush, green rabbitbrush, and rubber rabbitbrush. The regressions on dry weight were applied to the sample of all twig diameters and lengths to estimate average twig biomass.

RESULTS

Ungulate Densities and Diets

Ungulate densities approximately doubled during the study period on the low elevation stratum (Table 1). Ungulate densities approximately tripled on the high elevation stratum during the same period (Table 1). Pronghorn consumed 81% shrubs in their diet, followed by mule deer 50%, elk 8%, and bison 1% (Table 2). Pronghorn diets were 49% big sagebrush; mule deer consumed 23%; and elk diets were only 4%. The higher combined ungulate densities and the presence of pronghorns and mule deer, both of which eat more big sagebrush all suggest ungulate herbivory on big sagebrush will be greater on the low elevation stratum study sites. Since pronghorns consume 12× more big sagebrush in their diets compared to elk, and 2× more than mule deer, and since pronghorns also spend summers in the low elevation stratum, we suspect pronghorns were the most important herbivore on big sagebrush on the low elevation stratum.

Table 1. Average minimum densities of elk, pronghorns, mule deer, and bison near the lower and higher elevation exclosures on the northern winter range of Yellowstone National Park. The reported densities are based upon actual counts from fixed-wing aircraft (Houston 1982, Meagher 1989, Singer 1991a), and are uncorrected for visibility bias.

Ungulate	Ungulate Density (no./km^2) Lower Exclosures	Ungulate Density (no./km^2) Higher exclosures
1965–1968		
Elk	6	6
Pronghorn	3	0
Mule Deer	4	0
Bison	0	1
Total	13	7
1985–1988		
Elk	16–19	16–19
Pronghorn	7–10	0
Mule Deer	2	0
Bison	tr	2
Total	25–31	18–21

Table 2. Mean percent of shrubs in the winter diets of 4 ungulates on Yellowstone's northern winter range, 1985–1988 determined by microhistological analysis of feces ($\bar{x}$ ± S.E.).

Ungulate (No.	Big Sagebrush		Rabbitbrushes[a]		*Eurotia lanata*		Fringed Sage		Total Shrubs[b]	
Aggregate Samples)	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Elk (28)	3.8	3.1	1.6	2.7	0.4	1.0	1.0	2.0	7.8	4.1
Bison (25)	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0	1.3	1.6
Mule Deer (21)	23.2	15.1	7.2	4.6	0.7	1.0	17.9	16.7	49.7	20.9
Pronghorn (20)	48.7	18.0	5.3	3.5	5.8	6.0	18.5	13.7	80.5	15.7

[a] Rabbitbrushes include *Chrysothamnus nauseosus*, and *C. visidiflorus*.
[b] Total shrubs also includes *Populus spp.*, *Salix spp.*, and *Atriplex spp.*

Table 3. Percent of twigs browsed in big sagebrush communities on Yellowstone's northern range. Total ungulate numbers increased 2-fold at the lower exclosures and 3-fold at the higher exclosures between 1963–69 compared to 1985–88. The same transects of 46.5 m^2 each (n = 5) were sampled both periods; only these 5 browsed transects were sampled 1963–69.

Location Shrub Species (n = transects)	1963–1969		1985–1988	
	$\bar{x}$	SE	$\bar{x}$	SE
Low elevation (n = 2)				
Big sagebrush	88.0	4.2	86.8	7.2
Green rabbitbrush[1]			70.1	10.5
Spiny hopsage[1]			14.8	4.3
High elevations (n = 3)				
Big sagebrush	1.9	0.8	11.6	3.5*
Green rabbitbrush	6.7	3.6	8.9	2.9
Horsebrush			46.6	11.4

[1] Only big sagebrush utilization was sampled 1963–1969, and green rabbitbrush at only the higher exclosures.

*$P < 0.05$, according to Mann–Whitney U tests.

Shrub Utilization Rates

Big sagebrush utilization rates were consistently high (87%) and did not differ between 1963–69 and 1985–88 at the low elevation stratum study sites dominated by the more palatable (to pronghorns) Wyoming big sagebrush (Table 3, Mann–Whitney U tests, $P > 0.05$). The pronghorn and elk reductions during 1962–67 apparently did not result in any decrease in percent leader use of Wyoming big sagebrush on the low stratum. Green rabbitbrush was also used heavily at the low stratum sites where deer and pronghorn occurred (Table 3). Utilization rates of big sagebrush at the higher sites dominated by mostly mountain big sagebrush, however, increased about 6-fold after ungulates increased 3-fold (Table 3, $P < 0.05$). Use of green rabbitbrush did not increase significantly at the high stratum during this period of ungulate increase. Percent leader use of big sagebrush at the lower elevation sites averaged 87%, but leader use averaged only 11% at the higher sites. Bite sizes averaged 73% of vegetative shoots and 83% of reproductive shoots (n = 180 measured diameters of browsed shoots and 540 unbrowsed vegetative and reproductive shoots). Consumption of annual aboveground biomass of big sagebrush by ungulates averaged about 68% at the low elevation stratum sites, and 9% at higher elevation stratum sites.

Big Sagebrush Trends in Densities, Heights and Cover, 1958–90

Big sagebrush on belt transects in the lower stratum differed at the time of exclosure in 1958–62. Densities were similar, but average heights were one-half and cover about 60% those values on transects selected for exclosure (Table 4). Big sagebrush densities, heights and cover, however, were similar between browsed and unbrowsed transects at the time of exclosure on the high elevation stratum.

Apparently, ungulates were suppressing Wyoming big sagebrush on the low elevation stratum during the study period. Wyoming big sagebrush densities decreased 43% and big sagebrush cover decreased 29% on the low stratum browsed site over the 31-year period (Table 4). Density and cover of Wyoming big sagebrush increased dramatically (350% and 830%, respectively) in the unbrowsed sites of the low stratum. Big sagebrush individuals were taller on unbrowsed sites (Table 4).

Table 4. Changes in density, heights and canopy cover of individual big sagebrush shrubs between time of exclosure placement in 1958–1962 and 1990 on permanently-marked 46.5 m^2 shrub transects, Yellowstone's northern winter range.

	Density of shrubs				Heights (cm)				Canopy Cover (m^2/46.5 m^2)			
	1958–62		1990		1958–62		1990		1958–62		1990	
Treatment	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Lower exclosures[1]												
Browsed	21	7	12	2	0.7	0.03	0.5	0.1	19	4	16	4
Unbrowsed	23	15	103	27	1.8	0.6	16.7	0.9	28	7	50	9
Higher exclosures[2]												
Browsed	67	18	41	1.7	1.9	0.9	5.9	1.6	12	2	42	7
Unbrowsed	72	34	37.8	6.2	1.6	0.2	8.6	0.9	10	2	82	9

[1] Big sagebrush subspecies in these transects, mostly *A. t. wyomingensis*, is apparently highly palatable to pronghorns.

[2] Big sagebrush subspecies include mostly *A. t. vaseyana*.

Herbivory effects were less on the high elevation stratum study sites and all trends were similar for browsed and unbrowsed sites. Mountain and basin big sagebrush density declined, and canopy cover increased on both browsed and unbrowsed belt transects, 1958–90 (Table 4). Wyoming and basin big sagebrush density declined 39%, but cover increased 39% on browsed sites over the 31 years. Heights of big sagebrush increased on both browsed and unbrowsed sites, but more on unbrowsed sites (Table 4).

Detailed Site Comparisons of Densities, Cover, and Biomass Production in 1986 and 1987

Densities of big sagebrush ($F = 50.9$), total canopy cover of big sagebrush ($F = 8.1$), individual shrub crown area ($F = 22.5$), and heights of big sagebrush ($F = 79.8$, $P < 0.05$) differed between a much larger sample of browsed (n = 15) and unbrowsed plots (n = 15 per location, n = 180 total) sampled in 1986 and 1987. In each case, however, location was also significant and the interaction between location and browsing was significant. For example, sagebrush individuals were 59% taller on unbrowsed at six exclosure sites, but at the Blacktail exclosures sagebrush plants were taller on browsed plots. Heights of big sagebrush, green rabbitbrush and horsebrush increased with elevation in both treatments. As a consequence of this exploratory analysis and significant interactions with location, our division of plots into a high and low strata appeared justified, and we analyzed data from the lower and higher study sites separately in all subsequent analyses.

Big sagebrush individuals were shorter and crowns were smaller in browsed versus unbrowsed exclosure sites at low elevations (F = 29.8,14.3, respectively), but there was no difference in heights or crown sizes due to browsing at the high elevation sites ($P > 0.05$, Table 5). Horsebrush was shorter and crowns were smaller on browsed and unbrowsed exclosure sites at the higher elevations only ($F = 14.5$, 4.6, Table 5). Common rabbitbrush was shorter on browsed plots at the lower elevations, but it was taller on browsed plots at the higher elevation exclosure sites (Table 5). Density of Wyoming big sagebrush were less on browsed versus unbrowsed plots at the lower exclosures ($F = 14.7$), but there was no effect of browsing at the higher exclosures (Table 6). No difference in the number of dead big sagebrush individuals was observed between browsed and unbrowsed plots at either elevation category ($P > 0.05$). Twenty-two times more seedlings of the year were observed on browsed in comparison to unbrowsed plots at higher elevations ($F = 2.7$, Table 6).

Big sagebrush contributed 82–99% of the annual aboveground shrub production in these shrub communities. Browsing did not consistently influence the production of big sagebrush or green rabbitbrush at higher exclosure sites, but browsed rubber rabbitbrush produced less biomass at higher elevation sites (Table 6). Both big sagebrush and rubber rabbitbrush

Table 5. Individual shrub crown and heights of shrubs in browsed and unbrowsed areas (protected) sites on Yellowstone's northern elk winter range. Samples were drawn from 180 plots of 9.3 m^2 each located randomly in browsed and unbrowsed sites in 1986 and 1987.

Shrub Species:	Crown area (cm^2)				Heights (cm)			
	Unbrowsed		Browsed		Unbrowsed		Browsed	
Location	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Big Sagebrush[1]:								
Lower (Artrwy)	678	85	347	66*	50	2	37	4*
Higher	798	90	524	51	79	3	71	2
Horsebrush:								
Lower	45	7	37	13	15	1	11	2
Higher	575	222	71	93*	63	10	27	3*
Common Rabbitbrush:								
Lower	287	109	278	85	78	8	43	3*
Higher	196	42	881	590*	59	5	50	11
Green Rabbitbrush:								
Lower	76	13	104	55	36	11	28	3
Higher	742	70	392	42	79	3	53	2*

* Significant difference between grazed and control means using ANOVA, $P < 0.05$.

[1] Big sagebrush subspecies included: lower exclosures—*A. t. wyomingensis* only; higher exclosures—mixed populations of *A. t. tridentata* and *A t. vaseyana*, but nearly all *A. t. vaseyana*.

Table 6. Estimated annual production (g/m^2) of the most common shrubs in browsed and unbrowsed big sagebrush communities at six exclosures on Yellowstone's northern winter range (n = 15 plots each in both browsed and unbrowsed treatments at each site). Wyoming big sagebrush is only found at the lower stratum exclosures and mixed populations of nearly all mountain with some basin big sagebrush at the higher exclosures.

	Lower Elevations				Higher Elevations			
	Unbrowsed		Browsed		Unbrowsed		Browsed	
Exclosure location	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Estimated Biomass (g/m^2)								
Big sagebrush	18		1.9		73.6		72.6	
Green rabbitbrush	0.1		1.5		3.1		5.8	
Common rabbitbrush	0.6		0.3		5.9		4.1	
No. Big Sagebrush Individuals/9.3 m^2								
No. alive	16	2	2	1*	13	2	15	2
No. dead	1.3	0.4	0.6	0.5	3.3	0.8	5.9	1.9
No. seedlings	0.8	0.3	0.2	0.1	0.2	0.1	4.4	1.4*

*$P < 0.05$ according to t-tests. No tests were conducted on biomass since it was estimated from a product of no. of plants × average no. of shoots × average weight of shoots. Tests were conducted on each of those parameters separately, however (see text and Table 7), suggesting statistically significant differences at the lower elevations.

produced much less aboveground biomass on browsed sites on the low study sites (Table 6).

There was no influence from browsing on the number of vegetative or reproductive shoots per shrub for big sagebrush or green rabbitbrush. Reproductive shoots averaged 42% longer (Friedman test, $\chi_r2 = 38$, n = 6 locations, $P < 0.05$), and vegetative shoots averaged 45% longer on browsed versus unbrowsed big sagebrush (Friedman test, $\chi_r2 = 42$, n = 6 locations, $P < 0.05$, Table 7). There was no effect of browsing on length of reproductive shoots of green rabbitbrush ($P > 0.05$).

DISCUSSION

Other studies indicate mountain big sagebrush is preferred and eaten at a higher rate by mule deer and elk than the Wyoming big sagebrush, while basin big

Table 7. Numbers and lengths of reproductive and vegetative stalks on shrubs in browsed and unbrowsed plots in big sagebrush communities on Yellowstone's northern range (n = No. shrubs).

	No. reproductive flowers/shrub				Length (cm) of flower stalks			
Species:	Unbrowsed		Browsed		Unbrowsed		Browsed	
Locations	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Big sagebrush								
Lower (Wyoming spp. only)	15	6	13	10	4	0.2	8	0.6**
Higher (Basin and Mountain spp.)	21	7	17	6	14	0.7	18	0.6**
Green rabbitbrush								
Higher	10	3	16	10	11	0.4	12	0.4
	No. vegetative shoots/shrub				Length (cm) of vegetative shoots			
Big sagebrush								
Lower	99	23	88	18	2	0.1	3	0.4
Higher	83	31	59	12	5	0.5	7	0.5**
Green rabbitbrush								
Higher	33	7	52	20	6	0.2	8	0.4**

*$P < 0.05$, **$P < 0.01$. Differences between numbers in browsed and unbrowsed plots were tested with t-tests and lengths with Mann-Whitney U tests.

sagebrush is the least preferred (Sheehy and Winward 1981; Welch et al. 1981; Personius et al. 1987). Our observations initially appear in contrast with this generalization; we observed 70% more winter utilization on Wyoming big sagebrush than mountain big sagebrush. Too few basin big sagebrush occurred on the study sites to draw any conclusions. Our data does not constitute a palatability test, however, in that the mountain and Wyoming subspecies did not occur at the same study sites. We suspect pronghorns were the primary herbivore on Wyoming big sagebrush in lower study sites, and pronghorns find the Wyoming subspecies highly palatable (Beetle 1960, Beetle and Johnson 1982), and the Wyoming subspecies was more available to all ungulates due to shallow snows and more winds in the low stratum. Ungulate preferences for big sagebrush subspecies also varies between locales (Welch et al. 1981, McArthur and Welch 1982), for example, Dietz and Nagy (1976) found Wyoming big sagebrush was preferred by mule deer in Colorado.

Mountain and basin big sagebrush seedling germination, establishment, and survival were apparently enhanced by browsing and ungulate grazing, (possibly due to secondary effects such as the reductions of herbaceous vegetation competition, and ungulate hoof action) at the higher winter range, but the opposite trend was observed on the lower sites. McArthur et al. (1988) also observed more big sagebrush seedlings on a site browsed by mule deer in winter than on an unbrowsed site. The physical action of ungulate grazing due to hoof action, greater soil disturbance, more bare ground, and less standing dead vegetation and litter may provide conditions more suitable to big sagebrush germination. Big sagebrush individuals are smaller on browsed sites which may also benefit establishment and survival of seedlings due to reduced competition for light, soil moisture, and other resources.

Ungulate herbivory suppressed big sagebrush on the lower elevation sites, where almost no recruitment of Wyoming big sagebrush occurred on browsed sites. Apparently few seedlings survive the intense browsing. Wyoming big sagebrush reproduces more successfully than the other subspecies on xeric sites (Welch and Jacobson 1988), and the xeric, sodic, clay soils of the low stratum are clearly more suitable to Wyoming big sagebrush. At high levels of ungulate herbivory we observed (roughly 68% biomass removal), the Wyoming subspecies is presently suppressed by ungulates.

The ability of Wyoming big sagebrush to recover from herbivory is less than for mountain and basin big sagebrush. Wyoming big sagebrush is shorter (individuals often do not exceed 0.3 m), seedling growth rates are lower, and current annual growth is less than for the other two subspecies (McArthur and Welch 1982; Booth et al. 1990). The approximately 66% decline in the numbers of mule deer using the lower stratum within the park over the past 2 decades may be due to the localized Wyoming big sagebrush decline. Pronghorn did not decline in the lower stratum during the same period, but pronghorn, unlike mule deer, were artificially reduced well below carrying capacity levels during the 1960's (Houston 1982), and pronghorns may still be recovering from the reductions.

Increases in height and cover of big sagebrush are reported after protection from ungulates. Robertson et al. (1970) reported big sagebrush cover increased 76% after 30 years of protection from browsing, although mean heights declined 12%. Heights and crown sizes were similar, but live cover by big sagebrush was greater on unbrowsed sites on a mule deer winter range, primarily due to a greater dieback of browsed big sagebrush (McArthur et al. 1988). Average crown dieback was 64% in the browsed area and 17% in the unbrowsed area (McArthur et al. 1988). Mule deer use was heavy (370 deer-use-days/ha), and the dieback of big sagebrush occurred after two successive winters of heavy snowfall (McArthur et al. 1988).

Browsing by native ungulates stimulated the seedstalks and leaves of big sagebrush and the leaves of green rabbitbrush on the study sites. Stagnation of shrubs occurred inside big game exclosures after only two years of exclosure—non-use of big sagebrush resulted in an average 36% reduction in biomass production over clipped plants (Tueller and Tower 1979). Numbers of sprouts of green rabbitbrush were similarly increased by clipping (30% herbage removal), and the new growth was longer, leaves were larger, and leaves remained green for one month longer (Willard and McKell 1978). On the other hand, browsing of more than 80% of the leaders of mountain big sagebrush by mule deer resulted in a reduction of 50–93% in the total number of seedstalks per plant and a reduction of 0–53% in the length of seedstalks (Wagstaff and Welch 1991). Grazed grasses on the northern Yellowstone winter range have higher protein levels (Coughenour 1991), and grazing stimulates aboveground growth of grasses (Frank and McNaughton 1993). Increased vigor in new growth of browsed shrubs on the Yellowstone northern winter range is consistent with these observations of grasses and the growth may be due to increased rates of nutrient cycling due to ungulate defecation and urination (McNaughton 1979). In addition, plant competition is reduced and water availability is increased on browsed sites on the northern winter range due to smaller crown sizes and less transpiring tissues for individual shrubs.

Historic mean duration between fires was 25 years on the Yellowstone northern winter range, but due to fewer fire starts and active fire suppression, no significant burning of the grasslands occurred between 1870 and 1988 (Houston 1973; Romme and Despain 1989). Big sagebrush communities had not yet achieved climax post-fire state on the northern winter range as indicated by increases in heights and cover of both browsed and unbrowsed big sagebrush individuals, 1958–90. Browsed big sagebrush communities on the higher elevation ranges were replacing themselves; many successful seedlings and small individuals were observed on browsed versus unbrowsed sites. Lomasson (1948) observed almost no reproduction for 40 years in a stand of big sagebrush, but then reproduction increased as the original population began dying. Average life span of big sagebrush is 53–72 years, and in a mature, undisturbed stand, most big sagebrush individuals were in the 55–59-year age class (Roughton 1972). Sagebrush recovery following fire varies from a few years to 30 years depending upon environmental conditions for reestablishment (Harniss and Murray 1973, Sneva 1972). If most big sagebrush communities we studied on the northern winter range last burned in the 1840–90 period (Houston 1973), then most big sagebrush populations should have approached senescence and population turnover at the time of the 1986–87 sampling.

Ungulate herbivory levels on the lower study stratum restricted growth, establishment, and survival of big sagebrush at the time of this investigation, although browsed big sagebrush communities were stable or increasing at the higher elevation. Suppression of growth and reproduction of plants by increasing native ungulates can result in a new, altered plant–ungulate equilibrium (Caughley 1981; Sinclair 1977). If unnatural (human-caused) concentrations of ungulates cause the plant alterations, the situation is not acceptable under National Park Service policy (U.S. Department of the Interior 1988). Houston (1982) concluded densities of ungulates in the BLA were unnatural and artificially high due to animal avoidance of hunting outside the park. If so, some form of ungulate management—control, encouragement of migrations—is justified on the BLA. Elk and pronghorn reductions in the 1960's, however, did not reduce the percent leader use or improve the declining status of big sagebrush in the BLA. Either effective ungulate densities remained the same near the big sagebrush study sites, the ungulate reductions did not go on long enough, or high preference of the Wyoming subspecies by pronghorns maintained high levels of herbivory in the area during the control period. The elk reductions apparently did result in less big sagebrush use at the higher elevations.

We caution we were unable to calculate appropriate or recommended ungulate herbivory levels or ungulate densities for the northern winter range. Our data included 2 dichotomous periods in ungulate management. The first period of our study, 1958–68, was clearly a period of ungulate underpopulation during which time elk, bison, and pronghorns were controlled far below ecological carrying capacity (ECC) densities (Barmore 1980, Houston 1982, Boyce 1994, Mack and Singer 1994, Singer and Norland 1995). The second period of our investigations, 1986–88, likely was a time of ungulate densities in excess of natural conditions, at least for elk and bison. This statement is not based upon any comparisons to control conditions (no similar ecosystem exists with wolves and nondisrupted migrations for a comparison), but upon the conclusions of Houston (1982) that elk concentrations were unnaturally high in the low elevation, BLA stratum, and the computer predictions that elk and bison would number 8–25% less following wolf restoration (Garton et al. 1990, Boyce 1994, Mack and Singer 1994). Pronghorn densities in relation to ECC are unknown—one author feels coyotes (*Canis latrans*) are suppressing pronghorns on the northern Yellowstone winter range, and that following wolf restoration, coyotes will decline, and pronghorns will further increase (Berger 1991). At the time of this publication, wolf restoration was proposed for the study area for the winter of 1994–95, providing an opportunity to test the effects of wolves upon ungulate–plant interactions in the Yellowstone ecosystem (Cook 1993).

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COMPARATIVE EFFECTS OF ELK HERBIVORY AND THE FIRES OF 1988 ON GRASSLANDS IN NORTHERN YELLOWSTONE NATIONAL PARK

F. J. Singer

Yellowstone National Park[1]

and

Natural Resource Ecology Laboratory
Colorado State University
Fort Collins, CO 80523
Fax (970) 491–1965

and

M. K. Harter

Research Division[1]
Yellowstone National Park, WY 82190

Abstract. The drought, frequent lightning strikes, and resultant large fires of 1988 in Yellowstone National Park were considered a several century event for the area, resulting in an unparalleled opportunity to document the effects of large fires on forage production, forage quality, and herbivory for the largest, elk (*Cervus elaphus*) population in a natural area in North America. We documented elk–grassland dynamics on the Blacktail Plateau on Yellowstone's northern elk winter range following the burning of 25% of the study area in 1988.

Contrary to the predictions of earlier scientists, grazing of the grasslands by elk before the fires did not result in warmer, drier, or less productive bunchgrass communities. Soil moisture was equivalent, soil temperatures were cooler, aboveground grass biomass was equivalent 2 of 3 years, and N, macronutrients (Ca, Mg, P, K), and digestibility concentrations were higher on grazed than ungrazed grasslands. Forb biomass, *Poa sandbergii* biomass, and litter accumulations, however, were less on grazed sites, and more bare ground occurred (35 versus 24%) on grazed grasslands ($P < 0.05$). Elk herbivory resulted in more documented ecosystem effects for elk on the Blacktail Plateau than did burning.

Burning increased aboveground biomass of grasslands by 20% 2 years postfire, but digestibility of only 1 of 3 grass species (*Festuca idahoensis*) was enhanced. N, cellulose, and macronutrient concentrations in grasses and digestibility in 2 other grasses (*Pseudoroegheria spicata*, *Koeleria macrantha*) were unaffected by the fires. Grazed areas, on the other hand, had an average 21% higher N concentration in all 3 grasses, digestibility averaged 7% higher in grasses, aboveground herbaceous biomass was greater in 1 of 3 years, and total aboveground N yield was greater in 2 of 3 years. Forage biomass did increase postfire and could have benefited elk foraging efficiency. Elk use of burned grasslands increased following the fires ($P < 0.05$). Elk avoided burned forests the first 3 winters postfire ($P < 0.05$), but elk obtain few of their forages from forest communities on the northern Yellowstone winter range (<10% of feeding observations prefire). The possibility exists that shrub and herbaceous biomass in

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[1] Now with the new National Biological Service.

forest understories will increase ≥3 years postfire. Other studies suggest slower recovery or increases to preburn levels in forests by about 6–8 years, and eventually the elk might be benefited by increased quality and biomass of forages in burned forests. Grazing, by reducing fuels, can alter the extent of burning and create a more patchy fire pattern than occurs on ungrazed areas, thereby, grazing can conserve N which is otherwise volatilized by burning. We observed no such interaction between elk herbivory and burning, in spite of a sixfold reduction in litter on grazed sites. Burning did not affect N concentrations on either grazed or ungrazed study sites, apparently because dead aboveground plant material accumulations were still very light on both treatments compared to, for example, tallgrass or mixed grass prairies in the Great Plains. The relatively minor effects of the fires of 1988 on the grassland study sites were likely a result of the relatively fast, front fires, with little residual burning, and the relatively small dead plant accumulations in bunchgrass communities.

Key words: Burning, *Cervus elaphus*, fire effects, grazing, herbivory, ungulate winter range.

Introduction

The large fires in Yellowstone National Park (YNP) in 1988 provided the opportunity to study the effects of a large wildfire on a relatively self-regulated population of elk (*Cervus elaphus*). Effects of the elk on park vegetation are equivocal and controversial (Skinner 1928; Cole 1971; Beetle 1974; Houston 1982; Chase 1986; Baur 1987; Patten 1993). Artificial controls on elk were terminated in 1968 under the assumption that the ungulates, even in the absence of gray wolves (*Canis lupus*), would be naturally regulated within acceptable effects on the park vegetation (Cole 1971; Houston 1976, 1982). Some critics have argued that the park's "natural regulation" experiment has failed—the elk population has grown without constraint and the vegetation has been severely affected by ungulates (Beetle 1974; Chase 1986; Kay 1987, 1990; Patten 1993). Others suggest that the experiment is incomplete without gray wolves or wildfires (Peek 1980) or that no scientific experiment exists but rather a paradigm in management (Kay 1990; Chadde and Kay 1991). Here, we present data on the effects of elk herbivory and the fires of 1988 on aboveground biomass production, nitrogen (N) and macronutrient concentrations, percent digestibility, and plant species composition in bunchgrass and big sagebrush (*Artemisia tridentata*) communities, and on effects of the fires on elk habitat preferences. Frank and McNaughton (1992) documented plant responses to elk and bison grazing on Yellowstone's northern range, but they studied more mesic meadows, mostly on higher elevation transition and summer ranges where elk densities were only about one-tenth of the ungulate densities of our study area, but herbaceous biomass production is much greater. Bison consumption was approximately equivalent to elk on their study sites, while our sites were nearly exclusively affected by elk herbivory, and ungulate herbivory occurred during the growing season on their sites, while we studied only winter grazed sites. Coughenour (1991) studied plant responses to ungulates on lower elevation, semiarid portions of the winter range, but he studied only major plant groups. Neither author studied burning effects.

The climatic, lightning, and wind patterns of 1988, which ultimately led to the burning of 1,405,775 ha in the Greater Yellowstone area, were considered a 250–400 year event for the area (Despain et al. 1989; Schullery 1989; Millspaugh 1995). The low winter snowpack of 1987–88 was only 31% of normal, and the June–July–August rainfall was only 36% of normal—the lowest precipitation for those months recorded in 112 years of park records (Singer et al. 1989). Temperatures were elevated in June and July (2.7° C above normal), and moisture levels in fine fuels were reduced to only 2–3% by late July (Schullery 1989). Nearly all of the burn on the northern range occurred during a single 24-h period on the afternoon and night of 9 September and the morning of 10 September 1988 during a spectacular, fast moving, 34 km run of the North Fork fire. About 27,000 ha (27%) of the 140,000-ha ungulate northern winter range burned, including about 11,427 ha of grasslands and 15,580 ha of forest. The Blacktail Plateau study area was burned mostly by an accidental human-caused fire (North Fork fire) that could not be suppressed, and by a naturally ignited fire that was suppressed (Lava Creek fire).

The large Yellowstone fires of 1988 presented the opportunity to evaluate a number of questions dealing with the management of fire and elk in large natural areas. The elk population was suspected to be at or above ecological carrying capacity (ECC) in 1988 (Boyce and Merrill 1989; Merrill and Boyce 1991). The immediate decline of elk following the fires and subsequent predicted increase in elk due to increased biomass and quality of forages presented an opportunity to evaluate the ECC for the population (Boyce and Merrill 1989; Christensen et al. 1989).

Increases in grassland biomass and plant tissue concentrations, forage digestibility, diet quality, and body condition were predicted for elk following the fires (Rowland et al. 1983; Hobbs and Spowart 1984; Christensen et al. 1989; Boyce and Merrill 1989). The fires might alter elk–grassland interactions. For example, elk diets might change following the fires as previously unpalatable forages might become more palatable to elk following burning (Leege 1969; Asherin 1976), green-up might occur earlier and senescence might occur later (Peet et al. 1975; Hobbs and Spowart 1984), and N may be more concentrated in grass biomass on burned areas. Although elk might prefer burned grasslands, elk might avoid burned forests during winter because of deeper snows and more crusted snows under burned canopies (Mieman 1968; Skovlin and Harris 1970; Jones 1974; Davis 1977).

Most studies in grasslands have investigated the effects of prescribed burns that are typically slow burning, hot backfires, conducted during spring (Hobbs and Spowart 1984; Seip and Bunnell 1985; Canon et al. 1987). Wildfires in grasslands are more typically fast frontfires that are cooler than backfires (Daubenmire 1968). Burning in fall typically results in less enhancement of aboveground herbaceous plant production when compared to spring burning (Anderson 1965; Owensby and Anderson 1967). Greater enhancement of production from spring burning is likely due to larger increases in soil temperatures.

Our objectives were to document elk herbivory on grassland species composition, biomass production, and forage quality, and to document any changes in ungulate–grassland interactions caused by the fall wildfires of 1988.

We hypothesized:

1. Herbivory by elk at densities of 14–19 elk/km^2 will result in a warmer, drier grassland with more bare ground, reduced plant biomass, and altered plant species composition (Beetle 1974; Chase 1986; Kay 1990).
2. Burning of Yellowstone's grasslands would increase biomass, nutritional quality, and digestibility of forages consumed by elk (DeWitt and Derby 1955; Miller 1963; Lyon and Stickney 1976; Keay and Peek 1980; Rowland et al. 1983). As a consequence, elk should prefer burned over unburned grassland habitats (Rowland et al. 1983; Hobbs and Spowart 1984; Canon et al. 1987) and elk diets would be altered as some burned forages become more palatable (Leege 1969; Asherin 1976).
3. The fall Yellowstone fires of 1988 (all frontfires) should increase quantity and quality of grassland forages relatively less than prescribed spring burns (mostly backfires; Anderson 1965; Owensby and Anderson 1967; Smith and Owensby 1972; Canon et al. 1987) due to cooler burning of frontfires, a longer interval between fall burning and initiation of plant growth, and less enhancement of the soil temperatures during the growing season (Aldous 1934; Smith and Owensby 1972).

Study Area

The northern Yellowstone elk herd is one of eight migratory elk herds that spend part of the year in Yellowstone National Park (YNP) and is one of only two elk herds that winter primarily within the boundaries of YNP (Singer and Mack 1994). The northern Yellowstone elk herd is one of the most populous in North America, and it is the largest elk herd in Montana. Harvest of elk (mostly antlerless), which occurs when elk migrate north of the park, averaged 1,056 ± 725 per year from the northern elk herd ($\bar{x}$ harvest of adult cows = 559 ± 467 each year), 1975–90, or 5–8% of the population each year, have been insufficient to limit or regulate the elk population (Houston 1982; Merrill and Boyce 1991; Singer and Mack 1993). The northern Yellowstone elk herd is presumed to be regulated primarily by natural processes (Houston 1982; Coughenour and Singer 1995). The combination of the events of 1988–89—including the most severe drought on record, the fires of 1988, and a severe winter (rated –2.5 on a scale from +4 [mildest] to –4 [most severe; Farnes 1995]) with three arctic storm fronts—contributed to unprecedented elk migrations, large elk harvests outside of the park, and a large winterkill of elk. About 38–43% of the northern elk population died during winter 1988–89. About 14–16% of the population was harvested north of the park (typical harvests are 6–8%), and 24–27% of the population died of winter malnutrition both within and north of the park (Singer et al. 1989).

Our study was conducted on the 97.7-km^2 Blacktail Plateau, located in the approximate geographic center of the northern winter range. Elevation is approximately 2,040 m and average annual precipitation at the nearest weather station at Mammoth, 8 km distant, is approximately 400 mm/yr. Aerial counts of the northern Yellowstone elk herd ranged from 14,800 to 18,900 during the winters of 1985–90, and an average of 1,470 ± 345 elk ($\bar{x}$ ± SE, range 223–2,969) were counted on the Blacktail Plateau area during that period. Average elk densities on the Blacktail Plateau during this study, 15.0 ± 3.6 elk/km^2, were representative of densities (13–16 elk/km^2) on the entire northern range at the same time (Singer 1991; Singer and Mack 1993).

The Blacktail Plateau is composed mostly of open grassland habitat types (e.g., Idaho fescue–bearded wheatgrass *Festuca idahoensis–Agropyron smithii*, *Geranium* phase (8.5%), Idaho fescue–bluebunch wheatgrass *Pseudoroegneria spicata* (1.4%), Idaho fescue–bearded wheatgrass (1.5%), big sagebrush *Artemisia tridentata* types, mostly big sagebrush-Idaho fescue (11.1%), big sagebrush–Idaho fescue, *Geranium* phase (8.5%), and of coniferous forest types, mostly Douglas-fir/snowberry *Pseudotsuga menziesii–Symphorocarpus albus* (16.9%), and Douglas-fir/pinegrass, *Calamogrostis rubescens*; 4.5%; Despain 1991). The remainder of the study area is a variety of wet coniferous forests (*Pinus contorta*, *Picea engelmannii*) little used by elk. Dominant grasses are Idaho fescue, bluebunch wheatgrass, prairie junegrass (*Koeleria macrantha*), bearded wheatgrass–wildrye (*A. smithii–Elymus cinereus*), and Sandberg's bluegrass (*Poa sandbergii*). Dominant shrubs are big sagebrush, common rabbitbrush (*Chrysothamnus nauseosus*), and green rabbitbrush (*C. viscidiflorus*). A variety of forbs exists on the sites, but forbs are apparently of limited availability to elk during winter because of their desiccation and the extensive snow cover. Forbs comprised only 3% of the winter diet of elk from 1985 through 1988, while grasses and sedges comprised 83% and shrubs 8% (Singer and Norland 1994). Soils at the Blacktail sites are Pinedale glacial till derived from Absaroka volcanics, limestone, Precambrian crystalline rocks and tuff (Pierce 1973; U.S. Geological Survey 1975).

Two 2-ha ungulate exclosures were erected (1 in 1958, 1 in 1962) near Blacktail Deer Creek to evaluate the effects of elk grazing (Barmore 1980; Houston 1982). Both are located on open, rolling, shrub–steppe habitats. Most winter ungulate herbivory on Blacktail Plateau is by elk; a few bison seen on the area concentrated their feeding in the swales and sedge meadows (Barmore 1980; Meagher 1989). Winter consumption by elk on similar grassland sites averaged 55% over 8 winters, 1971–79 (Houston 1982:147). A few elk linger each spring in the vicinity of the exclosures to graze on early green-up of grasses before migrating to subalpine summer ranges.

Measurements of aboveground biomass and forage quality were obtained from a series of marked plots located in grazed and ungrazed sites in 1986 and 1987. Some of these plots opportunistically burned when 49% of the Blacktail Plateau study area burned on 9 September 1988 as the North Fork fire made its last major run (Despain et al. 1989). Extensive mosaics of unburned areas occurred within the fire perimeter (Despain et al. 1989) and provided representative burned and adjacent unburned plots both inside and outside of the exclosures. The burning mosaic pattern was primarily due to erratic winds at the time of the fires; no known differences existed between the burned and unburned patches (D. Despain, personal communication, Nov. 1988, Yellowstone National Park).

Methods

Sampling Design and Biomass Measures

Different, but comparable, sample designs were used before and after the fires to measure the effects of the treatments on plant biomass. In 1986 and 1987, before the fires, 20 1- × 1-m plots were randomly located on ungrazed (= exclosed) sites and 20 plots on grazed sites adjacent to the 2-ha elk exclosures ($n = 40$ total). Percent cover of plant basal area, bareground, rocks (>6 cm diameter), pebbles (<6 cm diameter), pavement, moss, lichens, elk dung, litter, and dead bunchgrass clumps were sampled on each plot using a 1-m^2 gridded frame. All herbaceous and subshrub aboveground biomass was then clipped from the 1-m^2 plots at peak standing crop (late July), sorted by species, and green vs. dead oven-dried for 48 h at 60° C, and weighed.

During the fires of 1988, about half of the ungrazed and half of the grazed areas burned. Following the fires, a 20-ha area in and near the exclosures was stratified into burned and unburned of grazed and ungrazed sites within two habitats, grass and big sagebrush. Twelve 1-m^2 plots were randomly located within each strata for a balanced ANOVA design of the 2 treatments (burning and grazing; $n = 48$ plots total). Temporary grazing cages (1.5 m^2) were placed at each of the grazed plots, and 1990 offtake was sampled from paired plots using the difference method. Plots within the burn were separated by either a swale, fire boundary, or both, and the plots were treated as independent samples under the assumption that movements by elk between sites required a foraging decision. Plant species biomass in 1990 was sampled three times during the growing season using the canopy intercept method with hits by a pin passed through vegetation (Frank and McNaughton 1990).

We clipped 12 plots in 1990 to calibrate number of hits with clipped biomass, and we compared 1990 to prefire sampling because plot size was identical (1-m^2) and because Frank and McNaughton (1990) reported good correlations between biomass and pin hits of narrow-bladed ($r = 0.846$) and medium-bladed grasses ($r = 0.896$) from the area using this technique. All subsequent samples of morphology, forage quality, and soil were taken from these same plots, unless otherwise indicated.

Grass Morphology

Vegetative and reproductive culm numbers and heights were recorded for bluebunch wheatgrass in 1986, 1987, 1989, and 1990 on 20- × 30-cm subplots located within the same 48 1-m^2 plots sampled for biomass. The circumference and heights of the tallest vegetative and reproductive culms were measured, and the number of vegetative and reproductive culms and seeds of each individual plant were counted.

Forage Quality

Forage quality was sampled in mid-July 1986, 1989, and 1990 for *Pseudoroegneria spicata*, *Festuca idahoensis*, and *Koeleria macrantha* by collection of randomly located grass clumps in each treatment (n = 24 clumps/species). Fiber (analyzed by proximate analysis—Van Soest 1981), total ash, gross energy, and N, Ca, Ph, K, Mn, and Mg concentrations of the grasses were analyzed by the Composition Analysis Laboratory, Colorado State University, Fort Collins, Colorado (Association of Official Analytical Chemists 1970). In-vitro digestible organic matter (hereafter digestibility) was determined by the method of Tilley and Terry (1963) as modified by Pearson (1970). These grasses were the 3 most common grasses in the elk diet (*P. spicata*—12%, *F. idahoensis*—18%, *K. macrantha*—7% of elk diets; Singer and Norland 1995).

Soil Moisture and Temperature

Soil moisture and temperature were recorded biweekly from late April through early September of 1990 within the same 48 plots sampled for biomass. Soil moisture was measured gravimetrically from 3 random points at 5 and 15 cm depths within the same plots. Soil temperatures were obtained using a soil thermometer at three random points at 12 cm depth within the plots.

Statistical Analyses

Nutritional levels of grass forages and standing crop biomass were first compared among years with ANOVA. Burning and grazing treatments were compared with a 2-way (burning × grazing) ANOVA. Three-way ANOVA's (month × grazing × burning) were used to compare production between treatments within each habitat type. The Bartlett's test was conducted to test for equal variances; normality and equal variances were found except where otherwise noted. Tukey's w procedure was used for pairwise comparisons in those cases when variances were equal, F statistic was significant, and interaction was not significant. Numbers, heights, and seed production of bluebunch wheatgrass were tested among treatments with a 2-way ANOVA. All statistical differences were at the $P < 0.05$ level, except where otherwise indicated.

Soil moisture and temperature data were analyzed using 2-way ANOVA (date and burning) for each habitat type. Soil measurements on permanently exclosed grass sites were compared to grazed sites with a 3-way ANOVA (date × burning × grazing).

Elk Selection for Habitats

Seven aerial counts of elk were made from fixed-wing aircraft (Super Cub) during midwinter (Dec.–Feb.) two winters prefire (1986–87, 1987–88) and three winters postfire (1988–89, 1989–90, 1990–91). The entire Blacktail Plateau elk study area was censused during each survey, and group size and location (UTM) of each elk group was plotted on a topographic map (1:62,500). Elk were counted in the mornings mostly between the hours of 0730–1030; nearly all elk groups were feeding or were located near feeding sites. Habitat preference tests, therefore, largely represent feeding habitats. Elevation, slope, aspect, vegetative cover type, habitat type, and burn category (burned, unburned, mosaic burn; Mattson and Despain 1984; Despain et al. 1989) were later generated for each elk location using YNP Geographic Information System (GIS). The availability of each cover type and burn category type on the study area was generated from the GIS system. We used the Bonferroni approach (Neu et al. 1974; Miller 1981; Byers et al. 1984) to calculate confidence intervals on the proportional use of vegetation cover and burn areas by elk. The technique is used in conjunction with a chi-square test, after the chi-square has led to the rejection of the null hypothesis that a set of observations does not follow an expected occurrence pattern. The technique involves the use of a

Bonferroni z statistic used in estimating whether the number of elk groups occurs more or less frequently in a habitat than expected from its availability. Confidence intervals on elk use were compared to availability of habitats to evaluate disproportionate use by elk. Elk "selection," use "less than," or use "equal to" availability were tested at the $P < 0.10$ level, following suggestions of Neu et al. (1974).

Results

Elk Herbivory in Grasslands

In contrast to our hypotheses, mostly winter-grazed bunchgrass communities on the Blacktail Plateau were not less productive, and with a few exceptions, plant species composition was not altered by elk herbivory restricted mostly to the winter period. Less total aboveground standing green biomass, total grass biomass, and *Pseudoroegneria spicata* biomass were produced in grazed areas in 1986, but there were no other consistent trends due to elk herbivory ($P > 0.05$; Fig. 1) in these variables in 1987 or 1990. Less forb, *Poa sandbergii*, and litter and standing dead biomass were sampled on grazed versus ungrazed sites during all 3 years (Fig. 1). Less *Koeleria macrantha* was produced on grazed sites (both burned and unburned) in 1990, but there was no difference the other 2 years ($P > 0.05$; Fig. 1). More *Festuca idahoensis* was produced on grazed sites in 1987 and 1990, but not in 1986, and more total grasses was produced on grazed sites in 1987 ($P < 0.05$; Fig. 1). No consistent trend was observed in the production of subshrubs, or of any of the other 19 grasses, 87 forb species, or 22 shrubs and subshrubs present on the study sites.

Elk herbivory did not influence total species richness; an average of 4.5 grasses, 17.5 forbs, and 3.5 shrubs and subshrubs were identified on each 1- × 1-m plot (t-tests, $P > 0.05$). Three forbs (*Tragopogon dubius*, *Arabis holboelii*, *Allium cernum*) were found more often than expected on ungrazed sites (χ^2 tests, $P < 0.05$), although none of these species were eliminated from grazed sites. Two grasses (*P. spicata*, *A. dasystachum*) were found more often than expected on grazed sites ($P < 0.05$).

Ground cover was altered by elk herbivory. Moss cover was significantly greater on ungrazed sites (10.4 ± 3.9) than on grazed sites (1.7 ± 0.2, $P < 0.05$). All unvegetated surfaces (bareground and pebble cover combined) averaged 35% cover on grazed plots versus 24% cover on protected plots (Fig. 1, $P < 0.05$). Litter and standing dead vegetation biomass amounts averaged 6.0 times more on ungrazed than grazed plots ($P < 0.05$), which explained differences in estimates of bare ground cover (Fig. 1). Lichen cover did not differ due to elk herbivory ($P > 0.05$). Animal dung from ungulates and rabbits provided a minor amount of ground cover (1–4%) on both grazed and ungrazed sites.

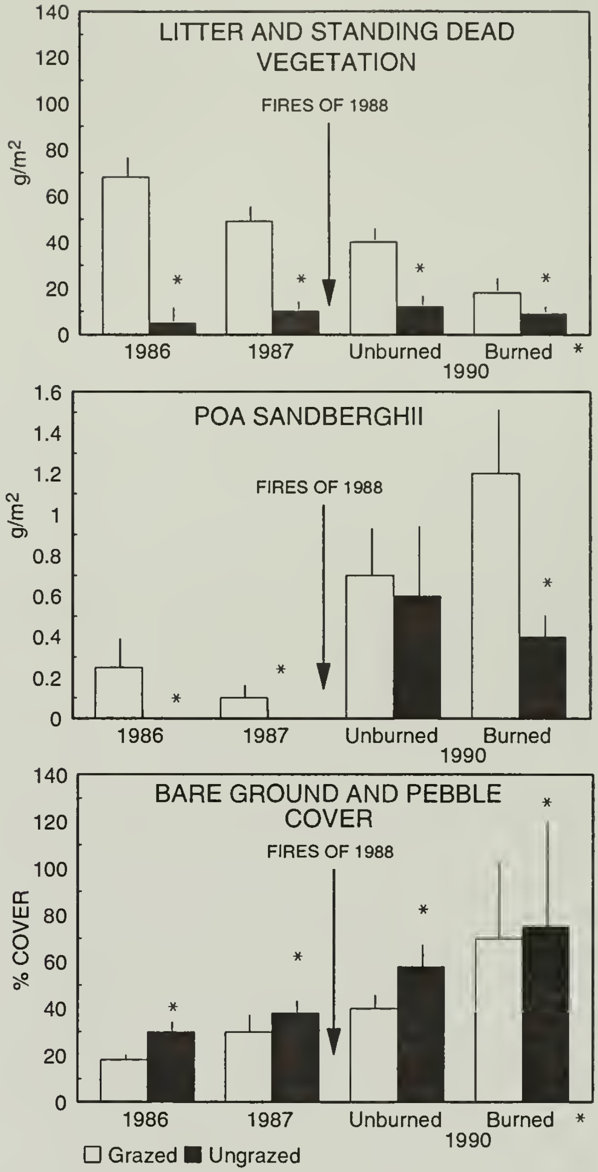
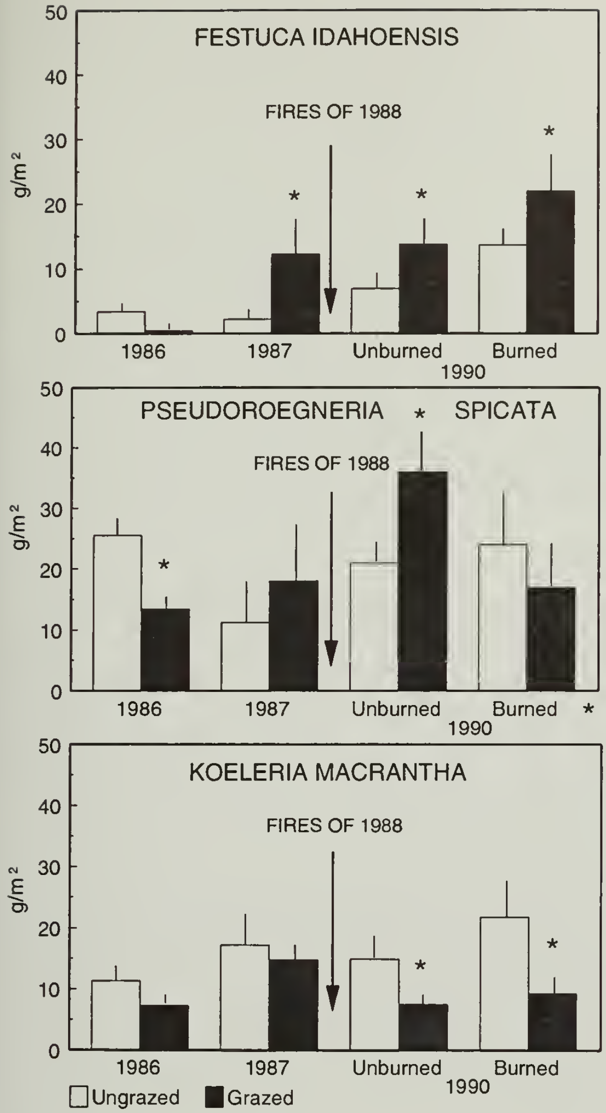


Fig. 1. Aboveground standing crop biomass in late July for functional plant groups, plant species, and ground cover in bunchgrass communities inside (ungrazed) and outside (grazed) of 2 large ungulate exclosures on the Blacktail Plateau, 1986, 1987 and 1990. An * above means indicates significant different due to grazing, while an * next to the B label denotes a difference in biomass due to burning (P, ANOVA).



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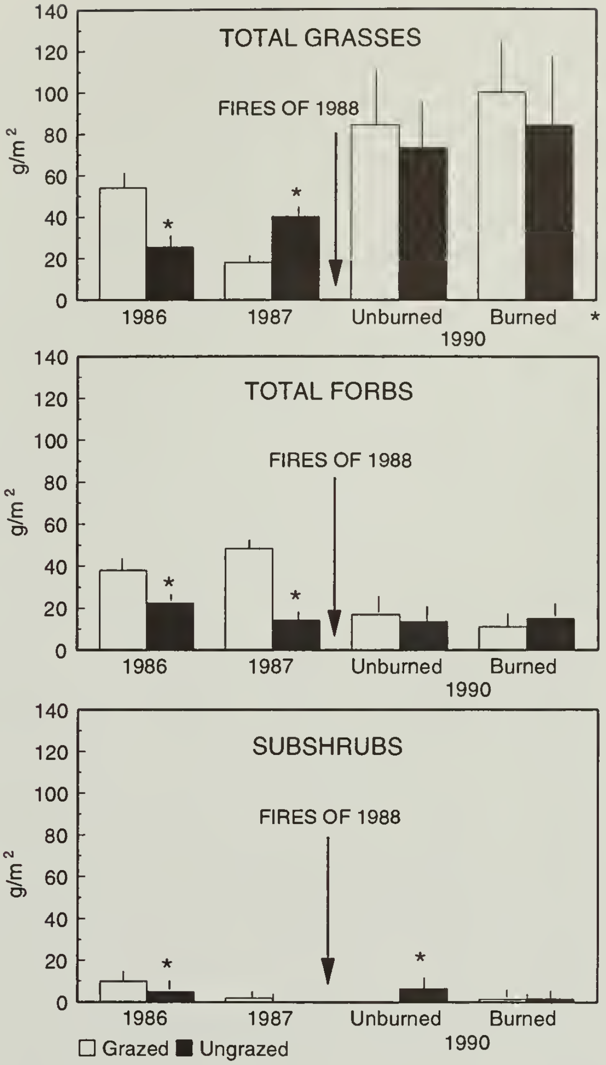

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Although recently overgrazed ranges typically possess large numbers of dead bunchgrass clumps (Mueggler 1969), we observed no significant increase in bunchgrass mortality due to elk herbivory ($t = 0.54$, $P > 0.05$). Dead bunchgrass clumps averaged 4.3% of groundcover on both treatments.

Effects of Burning on Plant Biomass

The effects of habitat, burning, and date on plant production were significant (3-way ANOVA, $P < 0.05$). Burning enhanced total plant and grass production in both grass and sage habitats by about 20% ($P < 0.05$). Burning enhanced grass production in May and June in grass habitats and in July in sage habitats (Tukey's multiple comparison tests, $P < 0.01$). Burning did not affect forb production in either habitat ($P > 0.05$).

Spring and summer consumption by elk were zero in 1990 ($P > 0.05$) according to our sampling program. At least one group of elk was seen feeding in the area during spring 1990, however, and limited spring consumption was known to occur.

Effects of Elk Herbivory and Burning on Forage Quality

Grazed grasses were more nutritious, elemental concentrations were higher, and total nitrogen yield was enhanced by elk herbivory during 2 of 3 years. Percent N was higher in *P. spicata* and *F. idahoensis* on grazed than on ungrazed sites ($P < 0.05$) but there were no differences for *K. macrantha* ($P > 0.05$). Nitrogen yield (biomass × %N) in 1986 on grazed sites was only 50% of that on ungrazed sites, but in 1987 grazed sites yielded 56% more N than ungrazed sites, and in 1990 grazed sites yielded 10% more N than ungrazed sites. Nitrogen concentration varied amongst years for all three grasses ($P < 0.05$). Each grass species contained higher N concentration in 1989 than in 1986 or 1990 (Fig. 2). Elk herbivory did not influence fiber, lignin, cellulose, or ash concentration in any of the grasses (Table 1). Calcium, phosphorus, magnesium, potassium, and manganese levels were higher in grazed *F. idahoensis*. Potassium levels were also higher in grazed *P. spicata*, but manganese levels were lower in grazed *P. spicata*. No differences due to elk herbivory were observed in element concentrations in *K. macrantha*.

Burning influenced grass nutritional and elemental concentrations far less than did grazing. Percent N in grasses on the study sites was not influenced by burning (2-way ANOVA, burning × grazing, $P > 0.05$). Burning elevated digestibility in both grazed and ungrazed *F. idahoensis* ($P < 0.05$), but we did not find evidence that burning influenced IVDOM levels in either *P. spicata* or *K. macrantha* ($P > 0.05$). Burning increased fibrous constituents in grasses. Cellulose and ash levels were higher in burned than unburned samples of grasses (Table 1; $P < 0.05$). Burning increased lignin and fiber in *P. spicata* and *F. idahoensis* ($P < 0.05$). Nutrient

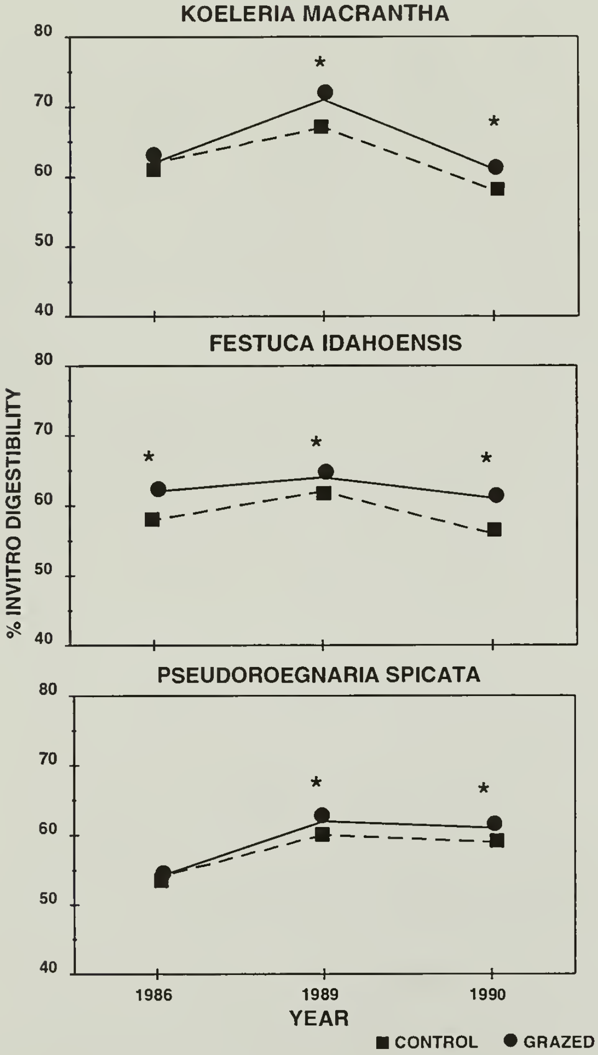

Fig. 2. Nitrogen content and in vitro digestible organic matter (IVDOM) content of unburned *Pseudoroegneria spicata*, *Festuca idahoensis*, and *Koeleria macrantha* forages in grazed and ungrazed sites, 1986, 1989 and 1990. Means with * above are different at *P* level.

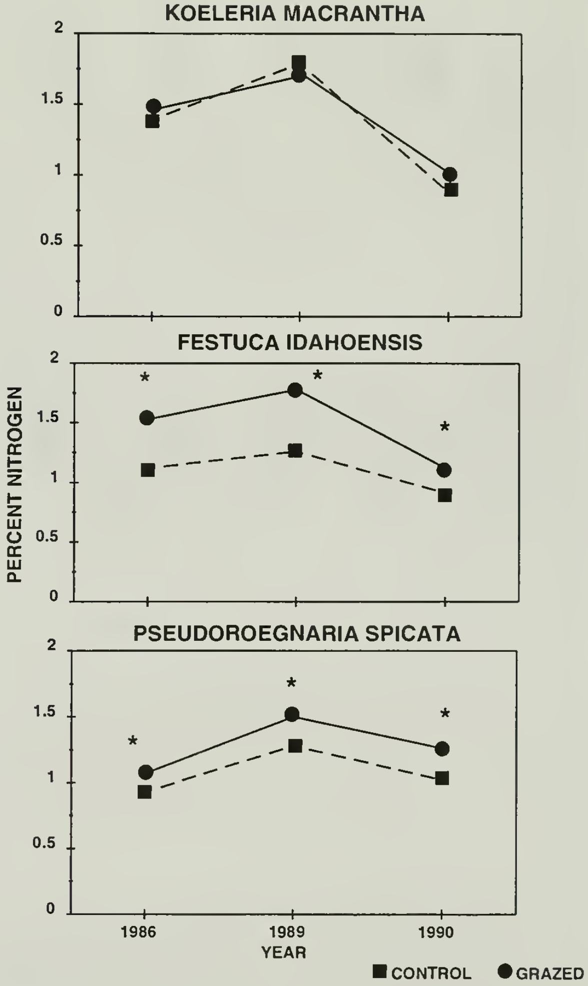

Fig. 2. Continued.

Table 1. Fibrous concentrations (% dry mass) of three grass species from grazed and protected grassland sites in 1990 influenced by burning in the Yellowstone fires of 1988. Significance level was $P < 0.05$ = *, $P < 0.01$ = **.

	UNGRAZED		GRAZED		2-WAY ANOVA *P*		
	Unburned	Burned	Unburned	Burned	Grazing	Burning	Interaction
Lignin							
Pseudoroegneria spicata	5.3	6.5	5.2	7.0	0.78	0.03*	0.66
Festuca idahoensis	4.1	6.1	3.6	6.1	0.72	0.001**	0.68
Koeleria macrantha	5.4	6.0	5.5	7.3	0.26	0.08	0.27
Cellulose							
P. spicata	16.2	29.0	18.0	28.9	0.74	0.000**	0.72
F. idahoensis	12.9	29.6	15.7	28.8	0.76	0.000**	0.56
K. macrantha	17.0	26.9	20.1	30.1	0.26	0.002**	0.95
AD Fiber							
P. spicata	33.8	37.9	33.4	38.2	0.98	0.03*	0.87
F. idahoensis	24.7	38.9	29.2	38.2	0.56	0.000**	0.56
K. macrantha	31.1	34.9	35.9	39.4	0.09	0.20	0.95
Ash							
P. spicata	4.0	7.2	4.2	10.0	14.00	0.005**	0.04
F. idahoensis	2.1	5.6	1.9	6.2	15.63	0.05*	0.18
K. macrantha	3.8	7.7	5.2	8.3	17.74	1.44	0.07
Ca							
P. spicata	0.3953	0.4222	0.4332	0.3712	0.04*	0.32	3.71
F. idahoensis	0.3525	0.2911	0.4079	0.3684	6.08	3.52	0.17
K. macrantha	0.4756	0.4254	0.4817	0.4533	0.18	0.95	0.07
Mg							
P. spicata	0.0734	0.1010	0.0798	0.0751	1.86	1.34	3.71
F. idahoensis	0.0766	0.0853	0.0976	0.0940	0.12	0.04*	0.69
K. macrantha	0.1141	0.1157	0.1218	0.1098	0.22	0.01*	0.38
K							
P. spicata	0.8307	0.9586	1.0242	0.8370	0.41	0.28	7.91
F. idahoensis	0.8790	0.6890	1.0373	1.0302	12.18	1.90	1.63
K. macrantha	1.0689	1.0144	1.0828	1.1639	0.93	0.02*	0.64
P							
P. spicata	0.1060	0.1218	0.1367	0.1091	1.31	0.56	7.6
F. idahoensis	0.1370	0.1367	0.1591	0.1689	9.88	0.31	0.34
K. macrantha	0.1554	0.1392	0.1789	0.1834	8.73	0.26	0.81
Mn							
P. spicata	0.0030	0.0032	0.0029	0.0021	3.97	1.28	2.68
F. idahoensis	0.0014	0.0025	0.0018	0.0018	1.23	9.68	11.29
K. macrantha	0.0046	0.0034	0.0041	0.0030	1.27	7.57	0.01**

levels were largely unaffected by burning. Calcium, Mg, K, and P levels did not differ between burned and unburned grasses ($P > 0.05$; Table 1), except that K increased in burned and grazed *K. macrantha*. Magnesium levels were lower in burned *F. idahoensis* and *K. macrantha* ($P < 0.05$).

Effects of Elk Herbivory and Burning on Grass Morphology

The height of reproductive culms of *P. spicata* was increased by both elk herbivory and burning (3-way ANOVA, year × burning × grazing, $P < 0.05$; Fig. 3), but there was no effect of either treatment on heights of vegetative culms (3-way ANOVA, year × burning × grazing, $P > 0.05$). Reproductive heights of *P. spicata* were shorter in 1986 than during the other 3 years ($P < 0.05$; Fig. 3). Reproductive culm heights were taller on grazed than ungrazed sites ($P < 0.05$). Burning increased reproductive culm heights on both ungrazed and grazed sites in 1990 ($P < 0.05$; Fig. 3) but not in 1989 ($P > 0.05$).

There was a lower density of *P. spicata* clumps on grazed than ungrazed sites ($F = 18.5$, $P < 0.001$; Table 2), but burning did not effect density of bunchgrass clumps ($F = 0.03$, $P = 0.86$, 2-way

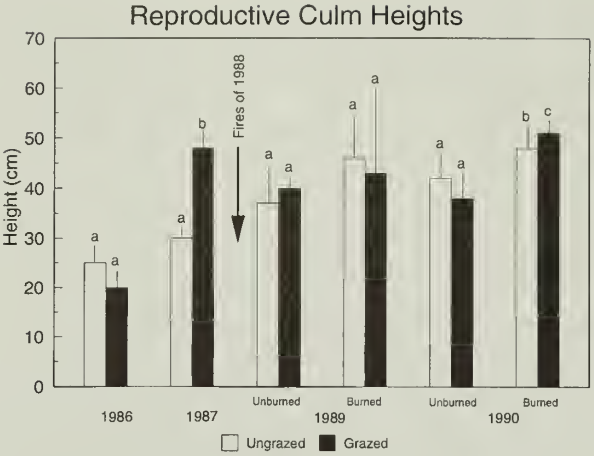

Fig. 3. Vegetative and reproductive culm height, July 1986–90, on long-term exclosed sites and grazed sites. Years 1989 and 1990 include burned plots. Different letters (a,b,c) denotes statistically different means using ANOVA (*P*).

ANOVA). Seeds produced per *P. spicata* bunchgrass clump were not influenced by elk herbivory ($F = 1.5$, $P = 0.23$), but burning increased seeds produced per clump 2-fold on grazed sites and 4-fold on ungrazed sites ($F = 10.8$, $P < 0.01$, 2-way ANOVA; Table 1). Circumference of clumps did not differ due to elk herbivory or burning ($P > 0.05$).

Soil Microclimate

Soil temperatures were higher on ungrazed than grazed sites (3-way ANOVA, elk herbivory, burning, and month, $P < 0.05$; Fig. 4). Soil moisture levels were not influenced by elk herbivory, burning or habitat (3-way ANOVA, $P > 0.05$).

Elk Use of Burned Areas

Elk use of the Blacktail Plateau dropped drastically during the first postfire winter. About 15% of the northern Yellowstone elk herd wintered on the Blacktail Plateau study area before the fires of 1988. Following the fires, only 8% of the elk population used the area in January 1989, and only 3% of the population was present in April 1989 (Fig. 5). By the second and third postfire winters, proportional elk use of the study area recovered and averaged 14% of the counted population. These year to year differences in elk use of the study area were significant ($\chi^2 = 1{,}721$, $P < 0.0001$).

Elk selected burned grasslands the prefire winter of 1986–87, but elk use was equal to availability during the prefire winter of 1987–88 (Neu et al. 1974 test, $P \leq 0.10$; Fig. 6). These same grasslands were used less than availability during the first postfire winter (1988–89), but were used more than availability during the second postfire winter (1989–90), and during February of the third postfire winter (1990–91). Forests that later burned were used less than and equal to availability during prefire winters, but burned forests were used less than availability during all three postfire winters. Elk selected unburned grasslands during all 3 winters postfire, while unburned forest–grassland mosaic was used less than availability during both pre- and postfire winters.

Discussion

Effects of Elk Herbivory on Grasslands

Contrary to the hypotheses, winter elk herbivory of about 55% consumption of the aboveground herbaceous standing crop on Yellowstone's northern winter range did not cause grasslands to be drier, warmer, less productive or altered in species composition. The exception was 1986 when total herbaceous and grass biomass amounts were less on grazed versus ungrazed sites. Heights of grass reproductive culms, an index of grass vigor, were

Table 2. Numbers of *Pseudoroegnaria spicata* clumps and numbers of seeds per clump on grazed and burned treatments, Blacktail Plateau study area in 1990. Different letters indicated significant differences with 2-way ANOVA and pairwise Tukey's comparisons at $P < 0.05$.

	Ungrazed				Grazed			
	Unburned		Burned		Unburned		Burned	
Pseudoroegnaria spicata	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
No. clumps per 1 m^2	13.9^a	1.0	16.7^a	1.8	10.6^b	1.8	7.2^b	1.3
No. seeds per clumps	85^a	25	392^b	115	209^a	74	481^b	111

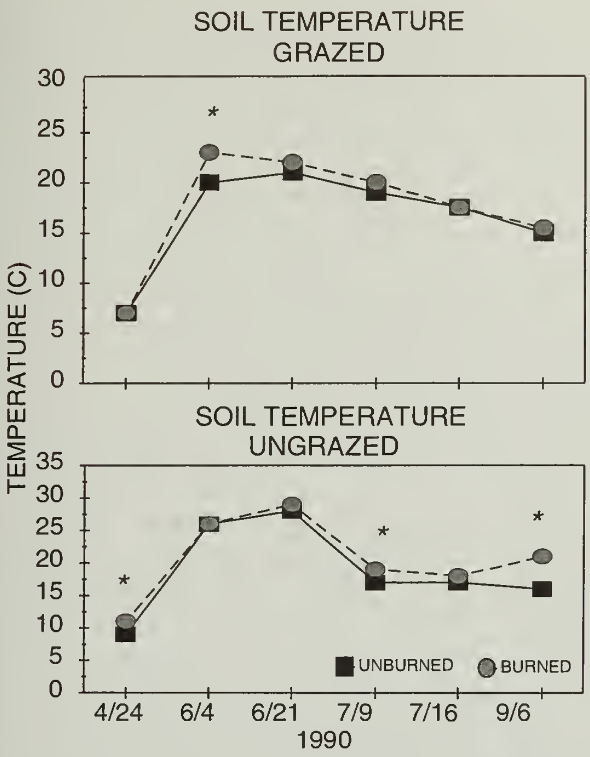

Fig. 4. Mean daily soil temperatures from burned and unburned (control) grazed and ungrazed sites on the Blacktail Plateau. An * denotes statistical differences between dates using Tukey's multiple comparisons (*P*).

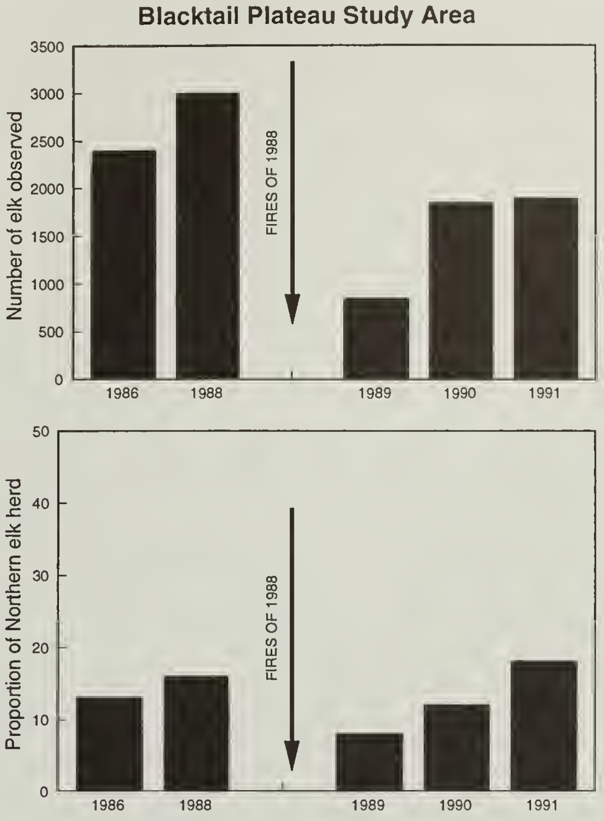

Fig. 5. Number and proportion of total northern Yellowstone elk herd observed on the Blacktail Plateau study area during the winters 1986–91.

shorter on grazed sites during only 1 of 4 years in 1986, suggesting that 1986 was suboptimal for grass growth. No increases in bunchgrass mortality , no differences in species diversity, and no difference in soil moisture due to winter elk herbivory were documented. Reproductive stalks of *P. spicata* were taller on grazed sites 2 of 4 years, and numbers of individuals of *P. spicata*, and biomass of *F. idahoensis*, a grazing sensitive grass (Daubenmire 1940; Young 1943; Evanko and Peterson 1955; Pond 1960), were more abundant on grazed sites. Soil temperature responses were the opposite of the predictions (Beetle 1974)—soils were warmer on ungrazed sites. We speculate that warmer soils on ungrazed sites were due to lower wind speeds and resultant lower heat loss rates caused by more standing dead vegetation (Old 1969; Smith et al. 1983; Knapp 1984). Cooler soil temperatures on grazed sites might counteract the drying effects of 11% more bare ground and resultant increases in solar radiation on grazed soil surfaces.

Maintenance of aboveground biomass on grazed sites in Yellowstone may be due to (1) reduced competition from adjacent grazed plants (Mueggler 1969, 1975; Archer and Detling 1985), (2) grazing during winter when plants are senescent (Mueggler 1975), (3) the positive effects of ungulate herbivory, defecation, and urination on nutrient cycling rate (Williams 1966; McNaughton 1979), and (4) decomposition of plant material (Gusev and Gusev 1983).

Several lines of evidence suggest grass growth was even stimulated by elk herbivory. Reproductive culms of *P. spicata* were taller on grazed sites 2 of 4 years, and seed production was greater on grazed sites during 1 of 4 years when seeds were counted. Heights of reproductive culms and production of seeds are indicators of vigor in grasses and grazing typically reduces both (Jameson 1963; McNaughton 1979; Owen and Wiegart 1981). In addition, N concentrations in 3 grasses were an average 21% higher on grazed areas during 3 years, and total N yield was greater on grazed areas during 2 of 3 years of study. Increased foliar concentrations of N on grazed areas (Jameson 1963; Eversion 1966; Chapin 1980; Detling and Painter 1983) may be due to greater proportions of younger shoots that tend to be higher in N (Jameson 1963; Owensby et al. 1970), higher uptake rates of N by grazed plants (Wallace et al. 1982; Ruess

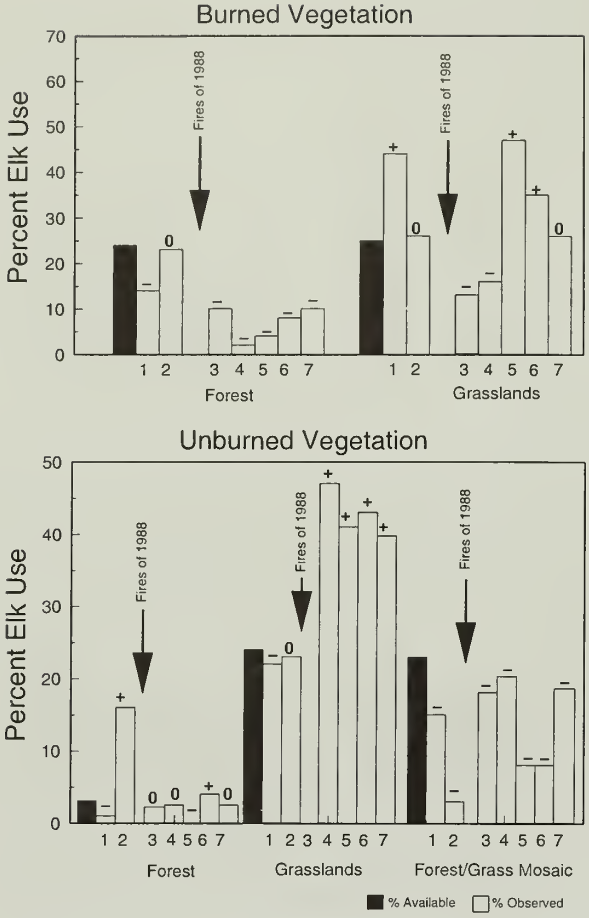

Fig. 6. Percent available habitat compared to elk use of habitats using the Neu et al. (1974) procedure before and after the fires of 1988 on the Blacktail Plateau study area. The symbols +, 0, and – refer to use greater than expected, proportionate use, and less use than expected, respectively, at the *P* level. Flight dates were: (1) 10 Dec 1986, (2) 19 Jan 1988 (Fires of 1988 = 9 Sep 1988), (3) 26 Jan 1989, (4) 11 and 14 April 1989 (pooled), (5) 18 Jan 1990, (6) 6 Feb 1991 and (7) 22 Apr 1991.

et al. 1984), and higher rates of decomposition (Holland and Detling 1990). Frank and McNaughton (1993) reported the promotion of aboveground grassland production by elk and bison herbivory in Yellowstone National Park. The average protein content of the three most common grasses averaged 7.6% on ungrazed sites but 9.1% on grazed sites. Mould and Robbins (1981) indicated dry matter intake of forage by elk (initially) increased rapidly when dietary protein fell below 8%, suggesting that grazing enhancement of protein on Yellowstone's northern range might enhance elk winter survival, since elk are under nutritional stress during winter (DelGiudice and Singer 1994) in certain threshold situations. We observed enhanced mineral concentrations (Ca, Mg, K, P) in grazed grasses as did Georgiadis and McNaughton (1990). These increases will also likely benefit elk. Ca and P metabolism are closely related and both are essential to elk (Robbins 1983). P is often limiting to elk and can limit N cycling in elk.

In agreement with the hypothesis, we sampled less forb biomass on grazing sites during 2 of 3 years of study. Also, there was less litter and standing dead, and there was 11% more bareground. *Poa sandbergii*, a grazing sensitive grass (Smith 1960), was also less abundant on grazed sites. In agreement with our findings, Jameson (1963) concluded forbs were more sensitive to grazing and clipping than were grasses. Removal of accumulated litter and standing dead vegetation might reduce the growth of grasses and forbs (Weaver and Rowland 1952; Jameson 1963), although alternatively, litter removal might benefit the growth of grasses and forbs (Dahl and Hyder 1977; Hulbert 1969).

Effects of Burning on Grasslands

Contrary to the hypotheses, soil moisture was not reduced by burning, burning only slightly increased aboveground biomass of grasses, and burning did not affect percent N, macronutrient concentrations, or digestibility of grasses. Most authors report warmer soils (Aldous 1934; Ehrenreich and Aikman 1963; Anderson 1965; West 1965), large biomass increases of grasses (Blaisdell 1953; Mueggler and Blaisdell 1958), increased forb biomass (Antos et al. 1983), increased concentrations of Ca, P, Mg, and K (Old 1969; Lloyd 1971; Willms et al. 1981; Umoh et al. 1982; Ohr and Bragg 1985) and higher digestibility in grasses following burning (Daubenmire 1968; Pearson 1970; Grelen and Whitaker 1973; Rowland et al. 1983). Rowland et al. (1983) and Seip and Bunnell (1985), however, also reported no effect of burning on crude protein concentrations in grasses. The higher fiber and lignin levels we observed following burning are in contrast to most reports of lower levels (Willms et al. 1981). We speculate that the relative lack of positive benefits from burning on forages on the Blacktail Plateau were due to the rapid speed (2.4 km/hr), relative coolness (100 BTU/ 0.09 m^2), and lack of residual burning of the fires of 1988 in grasslands (P. Perkins, unpublished data, Yellowstone National Park, Wyoming). The Yellowstone fires were cool, fast frontfires—most other comparative studies report on hot, slow backfires (prescribed burns) and most other published studies are in grassland regions (tallgrass, mixed grass prairie) with greater litter accumulations than for the northern Yellowstone winter range (Old 1969; Lloyd 1971;

Uresek et al. 1975; Umoh et al. 1982). We observed enhanced seed production in grasses due to burning, as do many workers (Uresk et al. 1975; Patten et al. 1988).

Condition of wintering ungulates is typically enhanced on burned grasslands, even when burning does not increase protein concentrations in grassland forages (Rowland et al. 1983; Hobbs and Spowart 1984; Seip and Bunnell 1985). Spring grass growth was initiated 1 week earlier, forage abundance was greater, the horns of mountain sheep grew faster, and sheep had fewer lungworm larvae on a burned range in British Columbia (Seip and Bunnell 1985). Elk ate more grass and less browse, and they weighed more and were in better condition on a burned winter range in New Mexico (Rowland et al. 1983), even though neither protein concentration nor digestibility of the grasses was enhanced by burning. Foraging efficiency of elk was enhanced in burned aspen forests, even though forage nutritional concentrations were not enhanced by burning (Canon et al. 1987). Diet quality of mountain sheep and mule deer (*Odocoileus hemionus*) was substantially higher on burned grassland–shrubland due to an increased proportion of green grasses in their diets (Hobbs and Spowart 1984), though N concentration of grasses was unaffected by the burning. Turner et al. (1994) and DelGiudice and Singer (1995) reported improved condition of Yellowstone elk following the fires of 1988, and we observed elk preference for burned grasslands, both of which suggested elk derived some benefits from the fires.

Elk Use of Burned Forests

Elk avoided burned forests the first 3 winters postfire, apparently because of deeper, more dense accumulation of snow, and because of reduced forage biomass. Snow depths were greater in total canopy burns than in partial canopy burns in conifer forests on the northern Yellowstone winter range, and snow was more dense in burned than unburned forests, as Skovlin and Harris (1970) and Meiman (1968) observed, although the differences were small during our study (2.5 cm deeper snows and 11% greater density; Norland et al. 1995). The herbaceous biomass declines in the hotter burned conifer forests on the study area were still dramatic during the second postfire winter; 61% less herbaceous biomass was sampled in burned forests versus unburned forests (Norland et al. 1995). Elk almost completely avoided the Blacktail Plateau during the first postfire winter (winter 1988–89 when 25% of the available foraging area burned). Those animals that remained, mostly adult bulls, died at a high rate (Singer et al. 1989). Turner et al. (1994) and Coughenour and Singer (1995) concluded that the severe winter of 1988–89 and the mosaic burning pattern of the fires contributed to the high mortality in elk during the first postfire winter. They concluded that winter severity was the dominant influence on ungulate survival.

Elk use of burned forests, however, will likely increase ≥4 years postfire following recovery of the herbaceous biomass, at least during periods of shallow snow. Protein concentrations in burned conifer forest understory forages from burned forests were 12.5% higher than in unburned forages in the northern Yellowstone winter range, and dry matter digestibilities were 4.6% higher (Norland et al. 1995), suggesting considerable advantages to elk for foraging in the forests. Forest understories recover more slowly following fire than do grasslands. Forests possess higher fuel loadings, greater fire intensity and more residual burning occurrs; 6–8 years were required for herbaceous biomass in burned forests to equal or exceed unburned forests (Vogl and Beck 1970; Lyon and Stickney 1976) and increased herbaceous biomass over preburn levels continued at least 12 years in one case (Bartos et al. 1994). Since our observations ended at only the third postfire winter, greater use of burned forests by elk will likely be observed in subsequent years, especially when snow depths are not excessive.

Conclusions

The ecological effects of the fires of 1988 on elk forages were minor. Grass biomass increased about 20% and digestibility increased in 1 of 3 grasses. Protein, cellulose, and macronutrients in grasses were unaffected by fire. Elk preference for burned grasslands during the second and third winters following the fires, however, suggested that elk gained some benefits from burned grasslands, perhaps due to greater foraging efficiency. Canon et al. (1987) reported greater foraging efficiency by elk in burned versus unburned habitats—more bites per minute, larger bite sizes, and less travel time by elk were observed in burned habitats.

Elk herbivory caused more documented ecological effects on vegetation of the Blacktail Plateau than did burning. Protein concentration was enhanced an average of 21%, digestibility was increased 7%, macronutrients concentrations were increased, and N yield was increased an average of 22% on grazed versus ungrazed areas. Forage quality of 5–7% is needed for maintenance of elk during winter (Robbins 1983). The increases in forage quality we observed on elk-grazed areas might therefore raise elk forages above critical levels in some winters. The enhanced digestibility of grasses due to elk herbivory could also be ecologically important for elk during critical periods on the Blacktail Plateau; an increase in dietary digestibility from 50 to 55%, an increase similar to what we observed, increased body weight gain almost 100% in domestic sheep (Blaxter et al. 1961).

No interactions were observed between elk herbivory and burning on the Blacktail Plateau. Frequent, hot fires in ungrazed or lightly grazed shortgrass and tallgrass prairie, with much heavier litter accumulations than our study sites, reduce N (Parton and Risser 1980; Ojima 1987). Grazing on tallgrass prairie, by reducing litter, reduces the extent of burning and creates a patchy fire pattern (Hobbs et al. 1991), therefore, grazing can conserve N. Burning did not affect N levels in either grazed or ungrazed grasslands on the Blacktail Plateau, probably because litter accumulations on our study sites, even unprotected sites, were still far less than in tallgrass prairie. Hotter fires result in a larger increase in nutrient enhancement of forages (Dewitt and Derby 1955). We attribute the lack of nutrient enhancement by the fires of 1988 on the Blacktail Plateau to elk herbivory, the relatively low accumulation of aboveground material, the relative high speed of the frontfire, and the resultant cool burning.

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Changes in Grazed and Protected Plant Communities in Yellowstone National Park

James J. Reardon

Intermountain Research Station
Fire Sciences Laboratory
P.O. Box 8089
Missoula, Montana 59807

Abstract. Eight permanent ungulate exclosures were constructed in 1958 and 1962 at five winter range sites in northern Yellowstone National Park, Wyoming. Paired quadrats inside and outside the exclosures were examined five times over the subsequent 32 years for changes in species composition and shrub, forb, and grass cover. Total vegetative cover increased on all sites from 1958 to 1990 both inside and outside the exclosures. Although there was a site by grazing interaction for forb cover in 1990, the exclosure of ungulate herbivores did not significantly affect the changes in vegetative cover. Plot and sample size limitations may have influenced the vegetative cover results. Species composition and rankings of dominant species fluctuated during the study period, and the changes were not attributable to herbivore exclosure. The lack of stable or predictable species rankings may be indicative of the dominance of stochastic processes over other deterministic community regulation mechanisms.

Key words: Exclosure, forb, grass, herbivore, shrub, ungulate.

Herbivory influences the species composition and structure of plant communities (Begon et al. 1990), and the removal of herbivores from grasslands that coevolved with grazers greatly alters the community (Belsky 1986). Changes in species composition can result from long-term selective grazing (Crawley 1983), whereas the development of homogeneous communities can result from the absence of grazing (Harper 1977). The reported responses of total basal cover, community biomass, and community productivity to herbivory or exclusion of vertebrate herbivores are controversial (Belsky 1986; Pacala and Crawley 1992).

Grazed vegetation may be optimally adapted for hebivory and the abiotic environment and show closer linkages between abiotic and biotic variables than ungrazed vegetation (Sims et al. 1978). The complete exclusion of herbivores from plant communities that coevolved with ungulate herbivory is considered ecologically unrealistic (Belksky 1986), and the removal of hebivores may be an insensitive way to study herbivory and plant community dynamics (Pacala and Crawley 1992). The comparisons of long-term changes in plant community characteristics that developed with and without herbivory may, however, allow limited inference about the influences of hebivory and time on community structure and composition.

In response to concerns about elk population size and the condition of Yellowstones's winter range vegetation, the National Park Service constructed exclosures on the northern winter range in 1957 and 1962. One objective of the original design was to establish vegetative standards useful for the evaluation of ungulate management activities (Houston 1982). Detailed data on plant characteristics and the species composition of these sites were collected at approximately 5-year intervals from 1958 until the present. This report is a description of the analyses of the 1958–90 chart quadrat data conducted to examine changes in basal cover and species composition.

Study Sites

Six ungulate species use the northern winter range: elk (*Cervus elaphus*), bison (*Bos bison*), pronghorn (*Antilocapra americana*), mule deer (*Odocoileus hemionus*), bighorn sheep (*Ovis canadensis*), and moose (*Alces alces*). Populations of the most numerous species, elk and bison, were regulated by Yellowstone National Park managers until 1968. In 1968, natural regulation was adopted as the preferred management alternative (Houston 1982).

Elk, the predominant herbivore on the northern winter range, had a population of 6,963 in 1956, down to 3,172 in 1968, and up to 19,000 in 1988. Other ungulate populations on the northern range also increased during the study period. Population estimates in 1988 were 2,500 bison, 2,500 mule deer, 400–500 pronghorn, 250–400 bighorn sheep, and 200 moose (Singer et al. 1988)

The grassland–shrub–steppe communities that make up 22% of Yellowstone's northern winter range were chosen as exclosure study sites because they receive the heaviest winter use by ungulates and were thought to show significant grazing influences (Houston 1982). Each November, elk migrate from summer and transitional ranges to the winter range and remain there until greening of the vegetation in May (Houston 1982). Other ungulates use the northern range from spring to fall, but the heaviest grazing occurs while the plants are dormant. Herbivory while grasses and forbs are dormant is not detrimental (Mueggler 1967).

The five sites selected for exclosure construction were Gardiner, Montana (1,676 m elevation), Mammoth, Wyoming (1,951 m), and Lamar Valley (1,973 m), Junction Butte (1,890 m), and Blacktail Plateau (2,042 m) in Yellowstone National Park. The first exclosures were constructed in 1958 at Gardiner, Lamar Valley, Mammoth, and Blacktail Plateau. Three additional exclosures were constructed in 1962 at Gardiner, Lamar Valley, and Blacktail Plateau, and one at Junction Butte. The Gardiner study site is dominated by sagebrush (*Artemisia tridentata*), bluebunch wheatgrass (*Agropyron spicatum*), and junegrass (*Koeleria macrantha*), while Mammoth, Junction Butte, Blacktail Plateau, and Lamar Valley are dominated by sagebrush, bluebunch wheatgrass, Idaho fescue (*Festuca idahoensis*), and junegrass.

Characterized by long, cold winters and short, cool summers, the climate of the northern winter range is influenced by regional physical geography (Dirks and Mather 1982). The long-term mean annual temperatures range from 4.3° C in Gardiner to 1.8° C in the Lamar Valley, and long-term mean annual precipitation values are 277 mm in Gardiner, 317 mm in Lamar Valley, 350 mm at Blacktail Plateau, and 421 mm at Mammoth. On a smaller scale, the local temperature and precipitation vary significantly both spatially and temporally.

The soils at the Mammoth, Junction Butte, Blacktail Plateau, and Lamar Valley sites are derived from glacial till, and the substrate is composed of Absaroka volcanics, Precambrian crystalline rocks, tuff, breccia, sandstone, and detrital material. These soils vary in texture from loams to sandy loam soils. In contrast, the soils in Gardiner were formed from mudflows primarily composed of sandstones and shales, and the soil texture varies from gravelly clays to sandy clay loams (Lane 1989).

Methods

The study sites were stratified by vegetative cover, edaphic characteristics, and topographic features. Sampling was limited to the sparse grassland–shrub–steppe communities on the drier upland sites. Overall, 36 quadrats on 5 sites were established. On each site, four paired chart quadrats (81.28 × 81.28 cm) were permanently established in similar strata on exclosed and nonexclosed sites. Each site was sampled in 1958, 1962, 1967, 1986, and 1990. The vegetation of each quadrat was mapped, basal cover was recorded by plant species, and the areal cover and the species of individual shrubs were recorded. During the 32-year period, 180 samples were obtained.

Because of the small sample size and high variability, cover data were analyzed by growth form rather than at the species level. All cover data were log transformed for analysis. Basal cover and areal cover of each quadrat were summed by grass, forb, and shrub categories. A total cover category was created by the addition of data for the grass, forb, and shrub components. To ensure consistent treatment effects and establish equal sample size between treatments, data for 1962 exclosures were excluded from the analysis of variance and repeated measures analysis. The Mammoth and Junction Butte sites were also excluded due to lack of replication within these sites. The analysis of the cover data was done using 22 quadrats on 3 sites: Gardiner, Blacktail Plateau, and Lamar Valley ($n = 110$).

Analysis of variance (ANOVA) was used to separately examine cover data from 1958 and 1990. These results served as an assessment of within and between site differences in 1958 and a measure of site, grazing, and the interaction influences on the vegetative cover present in 1990.

A number of studies have reviewed the analysis of experimental designs using the repeated measurement of sample units (Rowell and Walters 1976; Evans and Roberts 1979; Simms and Burdick 1988). Repeated measures analysis was used to investigate the influence of site and herbivory factors on the changes in cover over time. The results of the repeated measures analysis consisted of two related parts: a between-subject and a within-subject analysis. The between-subject analysis is a univariate measure of site, grazing, and interaction effects on the average cover during the study period. The within-subject analysis is a multivariate measure of the effects of site, grazing, and time interactions between years.

The number of individuals per species was considered an inappropriate variable for the analysis of species composition change. Species frequencies for each sample (quadrat/year) were calculated by overlaying a 10- × 10-unit grid on the vegetation map and recording the total number of grids in which each species was present (Smartt et al. 1974). Those species present on less than 5% of the quadrats were excluded from the analysis. This removed the effects of species that appeared random in nature or were influenced by sample size (Gauch 1982).

The species frequencies were analyzed with cluster and ordination techniques. TWINSPAN (Hill 1979b) classified individual samples (quadrat/year) into clusters with similar vegetative characteristics. DECORANA (Hill 1979a; Hill and Gauch 1980) was used to examine the patterns of change in the grassland community over time (Austin 1977; Collins et al. 1987; Cramer and Hytteborn 1987). Site and quadrat indicator values were created to relate environmental variables to changes in vegetation during the study period (Curtis 1959; Persson 1981).

Mechanisms of community regulation were investigated using concordance analysis with Kendal's *w* as an estimate of the correlation in the ranking of species over the years (Grossman et al. 1982; Moyle and Vondracek 1985). Tests for concordance during the study period were done using the 10 most dominant species present in 1958.

The influence of weather was examined with precipitation, mean monthly temperature values, and a drought index constructed with available temperature and precipitation data (Martner 1976). Correlations between the available weather data and plant community characteristics were examined.

Results

The small plot and sample size, missed sampling intervals, and limited number of plots prevented the reliable assessment of species-specific changes or species diversity or richness on a landscape scale. These data are more representative of site-specific change—inference to other plant communities and sites is limited.

The analysis of vegetation cover present in 1958 found no difference in the amount of cover present both within or among the exclosure sites for the four vegetation components tested (Table 1). There were total and grass cover differences among the sites in 1990 (Table 2). Gardiner had the lowest grass and lowest total cover. Lamar Valley had the greatest total cover while Blacktail Plateau had the greatest grass cover (Table 3). There were no differences in cover between the grazed and ungrazed areas, but there was a significant site by grazing interaction found for the forb component (Table 2). This interaction effect is

Table 1. Analysis of variance (ANOVA) mean-square values for 1958 data.

Source	df	Total	Grass	Forb	Shrub
Site	2	0.017	0.814	3.289	5.454
Grazing	1	0.097	0.061	0.001	0.708
Site × grazing	2	0.077	0.365	3.705	0.232
Error	16	0.132	0.672	1.678	3.021

Table 2. Analysis of variance (ANOVA) mean-square values for 1990 data.

Source	df	Total	Grass	Forb	Shrub
Site	2	1.596**[a]	4.987**	2.65**	2.497
Grazing	1	0.730	0.025	0.106	5.519
Site × grazing	2	0.260	0.292	2.78**	7.532
Error	16	0.260	0.319	0.732	3.756

[a] ** indicates significance at the 0.05 level.

possibly the result of the forb response at the Gardiner site. Forb cover at the Blacktail Plateau and Lamar Valley sites is greater on the ungrazed sites, but at Gardiner forb cover is greater on the grazed sites (Figs. 1, 2, and 3).

The between-subjects portion of the repeated measures analysis shows the average grass, forb, and shrub cover present during the 32 years were not influenced by either site or herbivory factors (Table 4). Grazing was statistically significant, however, at the 0.1 level for average total cover. The average total cover was lower on the grazed areas of all three sites (Table 3).

The growth of total grass, forb, and shrub cover from 1958 to 1990, represented by the within-subject portion of the repeated measures analysis, showed a positive trend on all sites (Figs. 1, 2, and 3) and appeared sensitive to site differences (Table 3). Blacktail Plateau and Lamar Valley showed the greatest rates of change, and Gardiner showed the least change in total cover during the study period.

Overall, the grazed and ungrazed sites have shown similar total, forb, and shrub cover responses during the study period. When considered at a lower level of statistical significance (0.1), the results suggest the changes in grass cover are sensitive to herbivory (Table 3), and it seems that the changes in grass cover are greater on the grazed sites.

Two distinct site groupings with similar species composition were determined by cluster analysis. The first group consisted of quadrats from four sites (Mammoth, Junction Butte, Blacktail Plateau, and Lamar Valley). The species that dominated these sites included *Artemisia tridentata, Koeleria macrantha, Festuca idahoensis, Agropyron spicatum, Astragalus miser,* and *Antennaria microphylla.* The other group contained quadrats from the Gardiner site and was dominated by *Artemisia tridentata, Koeleria macrantha, Agropyron spicatum, Artemisia frigida,* and *Phlox hoodii.* Site was the major factor influencing the clustered groups, and there was no evidence of herbivory or temporal effects among or within clusters.

Species changes at the Blacktail Plateau, Mammoth, Junction Butte, and Lamar Valley sites show considerable overlap in the composition of the quadrats through time. There was no consistent pattern or directional trend attributable to either herbivory or time, but the composition did fluctuate between measurements. The first two ordination axes account for little of the variation in composition, and correlations of site scores with a number of biotic and abiotic factors were not significant. The eigenvalues of the first 2 axes were 0.361 and 0.268, and the gradient lengths were 2.854 and 2.548 units of standard deviation.

Changes in species composition at the Gardiner site show a considerable overlap in the composition of the quadrats. There was no clear pattern or trend attributable to either time or herbivory, but the composition did fluctuate during the study. The first two ordination axes account for a considerable amount of the variation in composition. Initial densities (total cover) of the quadrats may have influenced species composition changes over time, but there was no significant correlation between site scores and initial densities. Other correlations of the site scores with biotic and abiotic factors were not significant. The eigenvalues for the first two axes were 0.501 and 0.405, and the gradient lengths were 3.4 and 3.17 units of standard deviation.

The tests of the mechanisms of community regulation and stability revealed no significant correlations existing within the clusters over the

Table 3. Repeated measures analysis for 1958–1990. Mean square values for between subject analysis and Pillai trace values for within-subject analysis.[a]

Source	df	Total	Grass	Forb	Shrub
Between-subjects					
Site	2	0.934	2.957	7.906	4.252
Grazing	1	1.581**[b]	0.500	0.0181	4.881
Site × grazing	2	0.069	0.520	8.458	8.246
Error	16	0.359	1.666	4.8461	2.51
Within-Subjects					
Site	8, 26	0.581	0.963**	0.850**	0.970**
Grazing	4, 13	0.068	0.437*[c]	0.297	0.121
Site × grazing	8, 26	0.236	0.498	0.417	0.350

[a] Probabilities for multivariate analysis were calculated using the Pillai Trace method.

[b] ** indicates significance at the 0.05 level.

[c] * indicates significance at the 0.1 level.

30-year period (Table 5). Because of the absence of significant correlations in the clusters, no tests were conducted to compare the grazed and ungrazed sites.

Climate

No significant correlations were found between the weather parameters and plant community characteristics.

Discussion

The lack of significance for site and herbivory factors in 1958 suggests there was no immediate response to exclusion from grazing and there was no bias in site and quadrat selection. These results are informative about the cover present on the plant communities in 1958 but are not a valid assessment of existing site differences or long-term herbivory influences on the vegetative cover of communities at that time.

The cover values reported for 1958 are comparable with values reported in other studies at that time. Envanko and Robertson (1955) studied long term records of a *Agropyron spicatum–Festuca idahoensis* habitat west of Yellowstone National Park. These sites were similar in composition to the exclosure sites and had a documented history of both protection from grazing and different intensities of domestic grazing. The cover ranged from 13 to 17%, and the researchers concluded that cover on grazed and protected areas was not significantly different. A comparison of the 1958 cover data with that study shows the percent cover at the exclosure sites lower but comparable to areas outside Yellowstone National

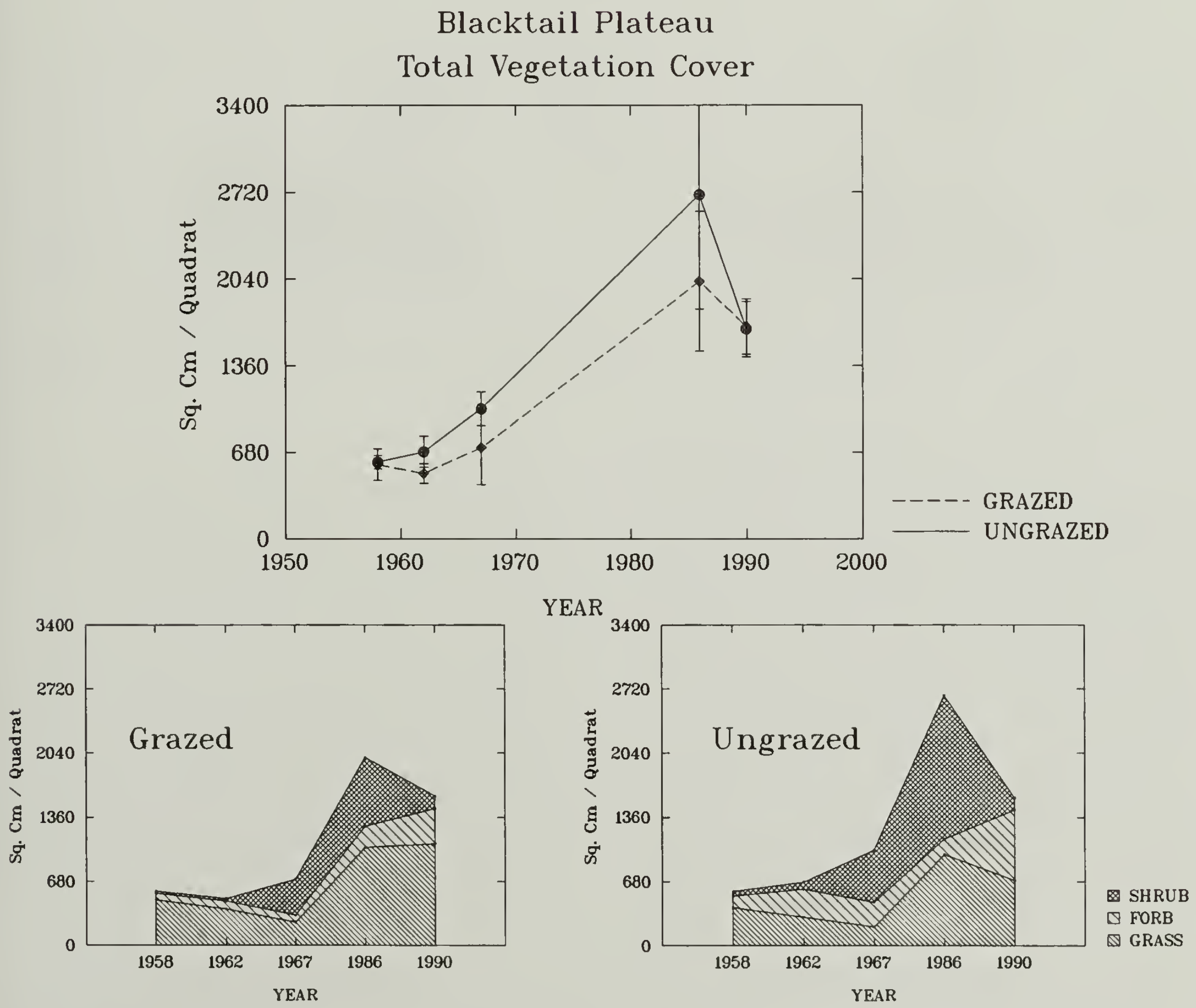

Fig. 1. (a) Blacktail Plateau mean total cover and standard errors for grazed and ungrazed sites. (b) Grass, forb and shrub cover on grazed and ungrazed sites.

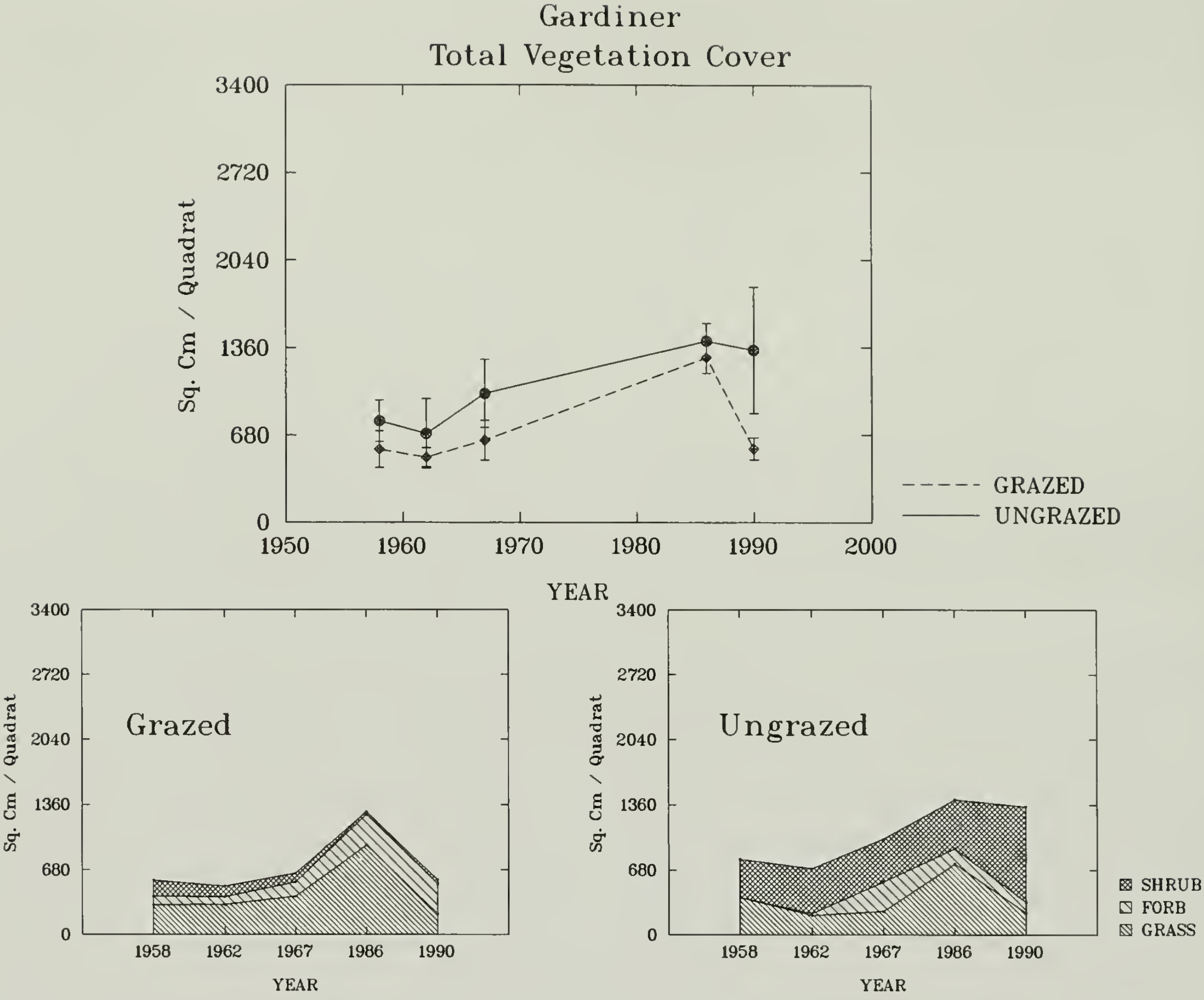

Fig. 2. (a) Gardiner mean total cover and standard errors for grazed and ungrazed sites. (b) Grass, forb and shrub cover on grazed and ungrazed sites.

Park subjected to varying intensities of grazing and protection.

During the study period there were significant changes in ungulate numbers on the winter range. The elk population was actively controlled until 1968 when management policy changed and elk were subjected to natural regulation. Other ungulate populations on the northern range also increased during this period (Houston 1982). Visual trends in the data suggest cover increased substantially on all sites after 1968 (Figs. 1, 2, and 3). A lapse in sampling from 1967 to 1986 prevents the assessment of the relation between either the timing or magnitude of cover changes and elk population changes or abiotic influences.

Site-related factors were responsible for most of the changes in the cover of grass, forb, and shrub components during the study period. The differences in the growth of cover between sites are the result of a number of factors. Climate, geologic parent materials, and the time of formation have strong influences on soil properties such as texture, mineral stability, and clay formation; they are also important factors influencing the nature of plant communities (Birkeland 1974; Grime 1979; Tillman 1988). Considerable variability in soil characteristics was found both within and between sites (Lane 1990). Previous analysis of the 1958 to 1967 quadrat cover data showed no significant differences on these sites by 1967 (W. J. Barmore, Population characteristics, distribution and habitat relationships of six ungulates in northern Yellowstone National Park. Unpublished final report, Yellowstone National Park files). This lack of an increase in total cover during a 9-year period of low elk numbers is not unexpected. A slow response to exclusion from grazing on sagebrush–grassland sites has been reported in other studies (Robertson 1971; Harniss and West 1973). In contrast, rapid changes were found on grassland sites in the absence of grazing

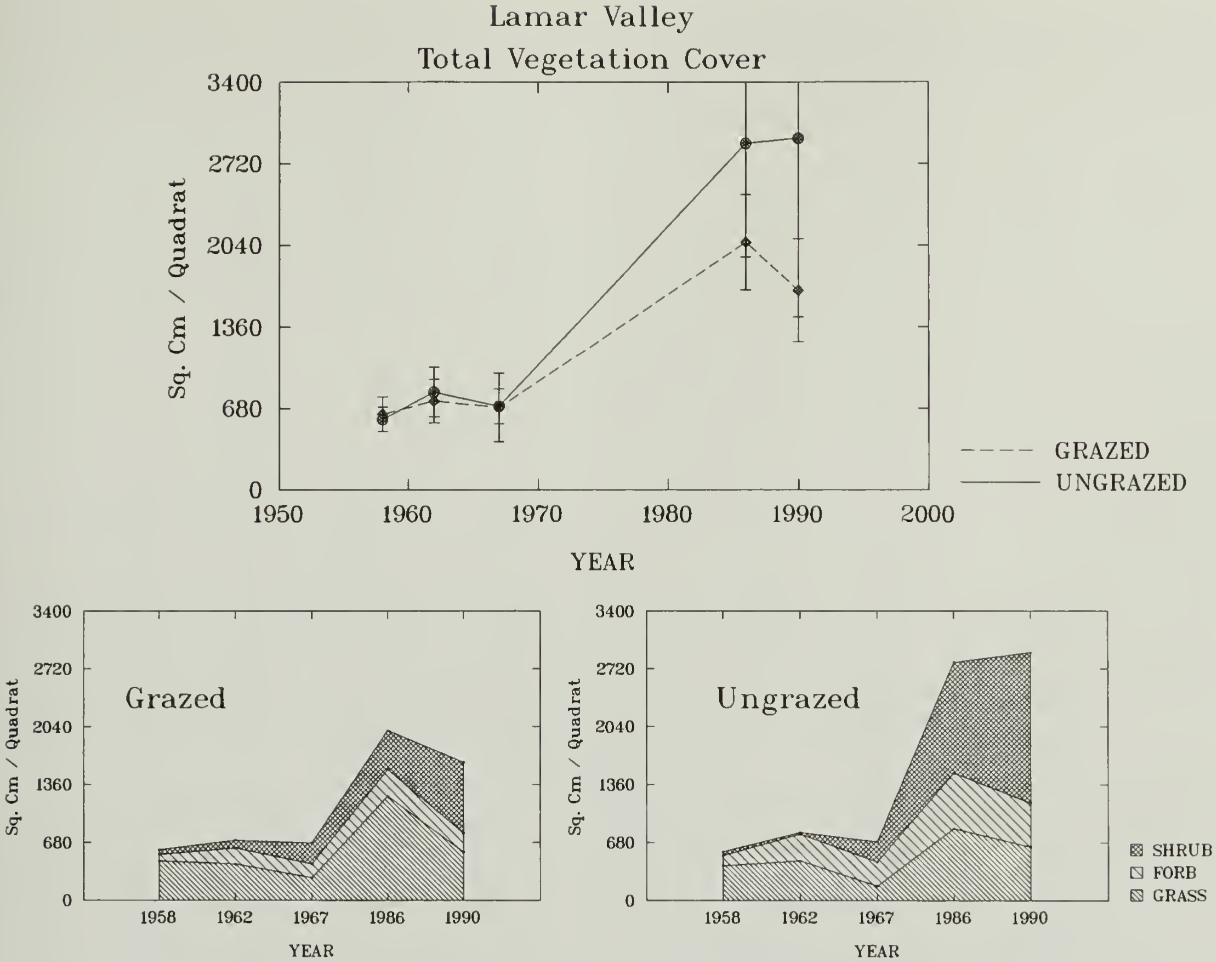

Fig. 3. (a) Lamar Valley mean total cover and standard errors for grazed and ungrazed. (b) Grass, forb and shrub cover on grazed and ungrazed sites.

(Collins and Adams 1983; Biondini et al. 1985). The differences in the rate of the response are influenced by the type and intensity of disturbance (Denslow 1980; Collins et al. 1987; McLendon and Redente 1990) and community productivity and dependence on grazers (Oksanen 1988).

The comparison of the changes in total cover between the exclosure sites shows the response at the Gardiner site seems lower than the responses at the other sites. The differences may reflect site factors and the effects of past manipulations. The Gardner site receives the least precipitation and was acquired by Yellowstone National Park after a period of domestic grazing. Trends in the data also suggest there may have been insufficient time for the exclosed sites to fully respond to the removal of grazing pressures.

Several important points should be considered when interpreting the significance of the betweensubject grazing factor for average total cover (Table 3). The presence of serial correlations between measurements may result in the loss of efficiency in the estimation of treatment means and bias in the estimation of the error terms (Simms 1988). Additionally, a significant within-subject time factor suggests a moving or nonstationary average and that average cover is not a reliable predictor of the effect of herbivory on vegetative cover.

Accepted at a reduced level of statistical significance (0.1), the within-subject herbivory factor (Table 3) for grass cover suggests that grazing or exclusion from grazing has influenced the growth of grass cover. Barmore (W. J. Barmore. Population characteristics, distribution and habitat relationships of six ungulates in northern Yellowstone National Park. Unpublished final report, Yellowstone National Park files) reported that grass cover was consistently less on the ungrazed sites by 1967, but the difference was not statistically significant. Numerous studies have shown grass cover and productivity influenced by sage cover and have shown grass cover significantly greater on grazed sites (Robertson 1947; Ries and Fisser 1979; Collins et al. 1987). Although not statistically

Table 4. Mean cover (cm^2/quadrat) and standard errors for Gardiner, Lamar Valley and Blacktail Plateau exclosure sites.

Location		Total cover		Grass cover		Forb cover		Shrub cover	
Treatment	Year	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Gardiner									
Ungrazed	58	790.1	160.6	388.2	138.6	3.2	1.29	397.9	258.0
	62	692.0	268.9	203.2	39.3	22.0	14.2	466.9	301.8
	67	1,002.3	264.4	245.7	69.6	308.3	199.3	448.3	301.8
	86	1,413.2	136.1	744.3	146.0	159.3	89.0	509.5	279.9
	90	1,340.9	491.5	230.9	61.9	110.9	49.6	999.1	523.7
Grazed	58	568.2	141.9	311.5	157.4	87.7	54.8	169.0	96.1
	62	506.9	73.5	314.7	134.2	81.3	19.3	110.9	58.7
	67	639.8	156.1	399.2	207.7	150.9	82.6	89.7	49.7
	86	1,284.2	121.3	935.2	172.3	318.6	171.6	30.3	17.4
	90	573.4	86.4	216.1	114.2	313.5	88.4	43.2	25.1
Lamar									
Ungrazed	58	588.9	101.9	410.2	129.0	119.3	137.4	237.4	278.6
	62	815.9	207.7	467.0	218.6	311.5	104.5	21.3	21.3
	67	697.9	145.1	170.9	80.6	280.6	218.0	240.6	238.6
	86	2,888.9	935.2	844.3	220.6	651.4	490.2	1302.9	1279.0
	90	2,930.2	1488.7	628.9	191.6	516.6	265.7	1766.0	1667.3
Grazed	58	630.8	143.8	461.8	179.3	80.0	40.6	53.5	53.5
	62	741.1	179.9	427.0	225.1	187.7	78.0	92.2	90.3
	67	688.7	286.4	269.6	72.2	158.7	69.0	247.0	243.2
	86	2,065.3	396.0	1,222.9	539.2	316.7	59.3	435.4	370.9
	90	1,664.1	429.6	568.9	100.0	221.2	105.8	832.0	418.0
Blacktail Plateau									
Ungrazed	58	603.0	52.9	403.1	81.9	122.7	74.5	48.4	21.9
	62	685.0	121.9	304.4	85.1	295.4	219.3	75.5	25.1
	67	1,022.3	130.9	199.9	58.0	262.5	197.4	550.2	263.2
	86	2,697.4	891.4	966.8	411.5	163.2	111.6	1523.5	823.7
	90	1,646.7	216.1	694.7	143.2	744.3	35.7	128.3	80.0
Grazed	58	583.7	122.5	483.7	74.2	67.7	59.3	27.1	15.5
	62	514.7	78.0	387.0	42.6	80.6	65.8	29.0	16.8
	67	716.6	290.9	245.7	12.9	74.2	61.3	383.8	305.7
	86	2,019.5	546.3	1,040.4	200.6	222.5	93.5	730.1	409.6
	90	1,666.7	215.4	1,081.0	104.5	372.2	105.8	131.1	43.9

significant in this study, the greater level of shrub cover inside the exclosures may be responsible for the smaller increases in grass cover on the ungrazed sites.

While general trends in the data show total and shrub cover consistently greater on the ungrazed sites (Figs. 1, 2, and 3), there is a lack of statistical significance in the repeated measures analysis (Table 3). This apparent contradiction may reflect a true lack of significance or confounding biological factors such as undetected pretreatment differences and the elimination of shrub cover from the Blacktail Plateau site during the fires of 1988. Nonbiological

Table 5. Results of concordance testing.

Site cluster	Treatment	Kendals coefficient	Chi-square probability
Gardiner	Grazed	0.5811	0.002
	Ungrazed	0.589	0.002
Mammoth–Blacktail Plateau–Junction Butte–Lamar	Grazed	0.710	0.000
	Ungrazed	0.655	0.001

factors influencing the statistical results may include the possibility of inconsistent measurement techniques, the conservative nature of this test, or inadequate sample and plot size. Overall, the large variances and small sample size of this study suggest the statistical power of this analysis is low. A similar analysis of data from sage belt transects established on the same sites and at the same time show changes in sage cover influenced by site differences and herbivory (Norland and Reardon 1991).

In a study of the dynamics of a sagebrush–grassland, West (1979) found considerable variance in total community basal area between years. Evanko and Robertson (1955) reported the measurements of the cover occupied by species and groups of species varied among sites and within grazed and ungrazed areas and concluded that measurement variation reflected treatment irregularity. The variance of the cover measurements in this study may also reflect the patchy nature of grasslands (Belsky 1983) or differences between the spatial or temporal scales of grazing and quadrat size or sampling interval (Brown and Allen 1990).

The comparisons of cover changes between growth form categories and the analysis of cover changes in categories formed from the cover of different growth forms may be misleading. On quadrats of small size, the changes in shrub cover and the responses of grass or forb cover may involve comparisons at different scales. Interpretation of these comparisons is limited because changes in total cover are a combination of the responses of individual shrubs and the responses of grass and forb populations. These comparisons might lead to inconsistencies such as the significance of a within-subject site factor for grass, forb, and shrub categories but a lack of significance in the total cover.

Although there was equal cover across all sites in 1958, there were differences in species composition among the sites. The initial analysis separated the Gardiner site from the Mammoth, Blacktail Plateau, Junction Butte, and Lamar Valley sites for all years. The species differences appeared as a result of the dissimilarity in edaphic variables and long-term precipitation and temperature trends. Gardiner is the lowest and driest of the sites and has a history of domestic grazing. The other sites have soils formed from similar parent materials, are higher in elevation, have lower long-term mean temperatures, and receive more long-term precipitation.

The lack of species composition change in this study is comparable to the results of other long-term exclosure studies (West et al. 1972; Sneva et al. 1984; Collins et al. 1987). Fluctuations in the species composition of the sites may be the result of differences in site factors or reflect the influence of abiotic factors such as short-term variations in weather.

Patterns in the changes and relative abundance of species are related to community persistence and stability (Connel and Sousa 1983) and mechanisms of community regulation (Strong 1983). Species replacement in communities not influenced by disturbance should show significant correlation among the ranking of the most dominant species over the time. Disturbances that operate at a community level, such as herbivory (Collins and Glenn 1990), should be reflected in changes of species composition and abundance and in the community correlation structure. Stable or persistent communities should also show significant correlations reflecting little change in the ranking of the most dominant species. Other deterministic or density-dependent mechanisms such as competition are also hypothesized to show strong correlations in the ranking of species over time.

The negative results of concordance tests within similar sites support the conclusion that communities were regulated by stochastic processes. This lack of significance does not prove the absence of deterministic mechanisms of community regulation mechanisms, but it does emphasize the strong influence of stochastic or density independent processes on the community composition and structure.

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EFFECTS OF GRAZING BY UNGULATES ON UPLAND BUNCHGRASS COMMUNITIES OF THE NORTHERN WINTER RANGE OF YELLOWSTONE NATIONAL PARK

Francis J. Singer

Yellowstone National Park
P.O. Box 168
Yellowstone National Park, Wyoming 82190

Abstract. Herbivory by native ungulates, primarily elk (*Cervus elaphus*), was studied on xeric, bunchgrass-dominated slopes on the Northern Yellowstone ungulate winter range of Yellowstone National Park. Plant cover, standing green biomass, and nutrient concentrations were compared between grassland sites protected from grazing for 24–27 years and adjacent plots grazed mostly during winter by elk, and to some extent by bison (*Bison bison*). Accumulated litter and standing dead vegetation were four times more abundant on the ungrazed plots. However, few consistent differences were observed in grass or forb biomass from elk herbivory. There was no overall effect of grazing treatment on forbs or other nongrasses ($P < 0.05$). Total grass biomass was less on grazed than ungrazed sites in 1986, after a dry, warm spring, but there was no difference in 1987 ($P < 0.05$). Biomass of junegrass (*Koeleria macrantha*) and thick-spiked wheatgrass (*Agropyron dasystachyum*) was greater on grazed than ungrazed sites. Three nongrasses (*Artemisia frigida, Phlox hoodii, Antennaria microphylla*) were more abundant on some ungrazed sites although the effect on grazing treatment was not significant ($P > 0.05$). The numbers of grasses ($\bar{x} = 4.5$), forb (17.5) and shrub ($\bar{x} = 3.5$) species did not differ between grazed and ungrazed plots ($P < 0.05$). Vegetative culms of bluebunch wheatgrass (*Pseudoroegneria spicata*), Idaho fescue (*Festuca idahoensis*), bluegrasses (*Poa* spp.), needle-and-thread grass (*Stipa comata*), junegrass, and thick-spiked wheatgrass were shorter on winter grazed plots ($P < 0.05$), but grazing did not affect the numbers of vegetative culms or the height or numbers of reproductive culms of grasses ($P > 0.05$), with the single exception that more vegetative culms of junegrass occurred on grazed sites. Protein content averaged 16% higher in bluebunch wheatgrass, 36% higher in Idaho fescue, and 10% higher in junegrass ($P < 0.05$) on grazed sites. Bare ground averaged 38% more on grazed sites than on ungrazed sites ($P < 0.05$), but pebble cover was 50% less on grazed sites (probably because of hoof compaction); as a result all bare surfaces (bare ground plus pebble cover) averaged only 18% greater on grazed sites. Dead clumps of the grazing sensitive bluebunch wheatgrass and Idaho fescue can be expected on an overgrazed range, but dead bunchgrass clumps did not vary between grazed and ungrazed sites ($P < 0.05$). The effects of herbivory by native ungulates was observed in swale sites that had been disturbed by agricultural activities until the 1930s. Three grasses (*Stipa viridula, Poa pratensis, P. compressa*) possessed greater cover on grazed swales, but one forb, field pennycress (*Thlaspi arvensi*), was less abundant on grazed sites. Herbivory by native ungulates greatly stimulated grass but not forb cover on these productive swale sites (grass cover was double that of ungrazed sites) ($P < 0.05$), and grazing mostly by elk contributed to the continued dominance of these sites by the exotic, grazing resistant *Poa pratensis* even 54 years following cessation of agricultural activities.

Key Words: *Cervus elaphus*, elk winter range, natural regulation hypothesis, northern Yellowstone elk.

INTRODUCTION

Caughley (1970, 1976, 1979) and Sinclair (1977) suggested that free-ranging ungulates reach an equilibrium with their vegetative food base. Beginning in 1967, Yellowstone National Park embarked upon an experimental program of "hands-off" or natural regulation management of the large ungulates within the park's boundaries (Cole 1971, Houston 1976), although harvest of migratory elk north of the park was encouraged to the greatest extent possible. Cole (1971) stated that over a period of years, naturally regulated ungulate populations were self regulating units. Yellowstone ungulates regulated their own mortality and compensatory natality in relation to available winter food and their population size, and predation seemed a nonessential adjunct. Prior to 1967, elk (*Cervus elaphus*), bison (*Bison bison*), and pronghorn (*Antilocapra americana*) were reduced by park staff (Craighead et al. 1972, Meagher 1973, Houston 1982, Coughenour and Singer 1991). Elk numbers were reduced to below 5,000 by 1967, and after cessation of artificial controls in 1969, elk increased dramatically (Houston 1982, Merrill and Boyce 1991). Harvests of the northern Yellowstone elk that migrated north of the park averaged only 9% of the herd during the years 1967–88 (Houston 1982, Singer 1991), a level insufficient to control the herd's growth.

Yellowstone's ungulate management since 1967 can not be regarded as a scientific experiment in that there is no ecosystem replication, no control situation(s) with similar climate where wolves exist, where ungulate migrations are uninfluenced by human activities, and where natural fire is unregulated (Cayot et al. 1979, Peek 1980, Kay 1987). Yellowstone National Park's climate is different this century than last—summer temperatures are increasing and January–June precipitation levels are decreasing (Balling et al. 1992). The climatic changes alone might alter vegetation–ungulate relations. Evaluations of the park's management program have been limited mostly to monitoring of range plots (mostly 1958 to present), comparisons inside and outside of ungulate exclosures, and comparisons of current photos to those taken 100–120 years ago (Houston 1982, Houston and Meagher in prep.); inferences from these kinds of monitoring studies are limited (Platt 1964). Few precise criteria for testing hypotheses were provided during the original statement's of the ungulate management experiment (Houston 1976, 1982; Cole 1971), overgrazing was not defined, and equilibrium theories prevalent for the time, which have since been questioned (DeAngelis and Waterhouse 1987), are central to the hypothesis (Coughenour and Singer 1991).

Houston (1982:125) who used Parker transect and chart quadrats for his analysis 1957–74, concluded there were "... little or no consistent differences between the treatments of nongrazing and grazing by native ungulates on plant species abundance, basal area, or composition. Differences over time appeared to be related more to fluctuations in growing conditions." Comparative photos from the 1970s compared to historic photos from the 1860-80s suggested no increase in gross evidence of erosion such as in visible erosive rills, exposed tree roots, or bare ground (Houston 1982). Houston (1982) concluded the effects of elk on vegetation did not exceed those expected from a population near ecological carrying capacity; fluctuations in abundance of perennial grasses were influenced more by fluctuating growing conditions, especially rainfall, than ungulate densities.

Several serious questions were raised, however, concerning ungulate densities on the northern Yellowstone winter range following Houston's (1982) study which ended in 1979. Elk counts increased to 16,000 in 1982 and then to 19,000 in 1988 (Singer 1991), raising concerns for overgrazing of the winter range (Chase 1986, Kay 1987). Bison counts also increased 154%, mule deer (*Odocoileus hemionus*) 126%, and pronghorn 215% on the northern Yellowstone winter range during the 1980s (Meagher 1989, Singer 1991), and contributing to the concerns. Alternatively, the winter range might not be overgrazed. Useable elk winter range may have increased during mild winters of the 1980s (seven of the 8 winters between 1980 and 1988 received less than the average amount of snowfall), ungulates ranged over a wider area, forage was more accessible because of the shallower snows, and elk more regularly migrated north of the park boundary beginning at about 1980, thus effectively adding 18% to their area of winter use and dispersing grazing pressures (Singer 1991).

To resolve the controversy, in 1987 the U.S. Congress directed the National Park Service to "start a study on Yellowstone to see whether there is evidence of overgrazing (Congressional Record—Senate S.12613, 1986)."

Studies published from this large research initiative, 1986-88 did not document overgrazing of grasslands by native ungulates. Parker transect data sampled in and out of exclosures 1962-89 suggested vegetation responses to climate were much more significant than changes due to exclosure from grazing. Grasses increased in frequency of abundance until 1986 (in spite of increasing elk numbers) and forbs decreased, reverse trends were observed after 1986, apparently in response to drier conditions (Coughenour et al. 1995). Changes in plant frequency were parallel inside and outside of the ungulate exclosures. Coughenour et al. (1995) concluded elk grazing has not degraded the herbaceous vegetation of the northern winter range, but the authors pointed out problems with the sampling including: no correlation of Parker hits to plant biomass, high variances, and small sample sizes. Coughenour (1991) reported grass and forb biomass production inside and outside of exclosures was largely uninfluenced by elk grazing in 1987, but both were reduced on grazed sites in 1988, a dry year. Root biomass and soil moisture were not affected by grazing. Coughenour's (1991) sampling, however, was restricted to plant groupings; he did not separate herbaceous biomass to the species level.

The purpose of this investigation was to evaluate differences in aboveground biomass production by plant species between grazed and ungrazed sites on Yellowstone's northern elk winter range.

METHODS AND STUDY AREA

The Yellowstone northern winter range consists of about 100,000 ha, of which about 82% lies within Yellowstone National Park and 18% lies north of the park on Gallatin National Forest and private lands. The Yellowstone northern winter range is lower (1,500 m–2,400 m), warmer, and receives less precipitation than the higher plateaus of the park. Total precipitation averages less than 75 cm for most of the northern winter range. Mean annual precipitation at the lower elevations (1,620 m) at the park boundary near Gardiner, Montana, is 30 cm, but precipitation is 55 cm at 2,000 m near the Lamar Ranger Station.

The majority of the winter range is undisturbed by human activities with two major exceptions:

(1) The 4,900 ha Boundary Line Area described by Houston (1982) was subjected to a livestock grazing, irrigation and haying of meadows and swales, and the introduction of a variety of exotic hay meadow plants (timothy, *Phleum pratense*; Kentucky bluegrass, *Poa pratensis*; smooth brome, *Bromus inermis*; quackgrass, *Agropyron repens*; cheatgrass, *Bromus tectorum*). Houston (1982) felt that prior to the agricultural activities the Boundary Line Area was dominated by needle-and-thread grass (*Stipa comata*) and bluebunch wheatgrass (*Pseudoroegneria spicata*). I studied swales and the intervening rolling grasslands in this area, near the two Gardner ungulate exclosures.

(2) Bison were largely restricted in the park to the Lamar Valley from about 1904–52, when bison were fed hay cut from both the native meadows, and from irrigated, cultivated fields of exotic grasses (Meagher 1973, Houston 1982). Exotic grasses that still persist in the Lamar Valley area include smooth brome, timothy, Kentucky bluegrass, and quackgrass.

About 41% of the northern winter range is forested, largely with Douglas-fir (*Pseudotsuga menziesii*) stands and a grass understory (Houston 1982, Despain 1991). About 55% of the area is grassland, especially Idaho fescue (*Festuca idahoensis*) and big sagebrush (*Artemisia tridentata*) habitat types (Mueggler and Stewart 1980), about 2% is aspen (*Populus tremuloides*) stands, and about 0.4% is willow (*Salix spp.*) and riparian shrub stands. My investigation focused on two plant community types used mostly by elk: (1) upland bunchgrass communities (ridge and slope) never subjected to agricultural activities, and (2) lower elevation, swale winter range sites grazed mostly by elk, but subjected to cattle grazing and haying activities until 1932 on the Boundary Line Area (since my study, these swales are being grazed by the park's expanding bison population (Meagher 1989).

Upland Bunchgrass Communities Never Disturbed by Haying Activities

Sampling was conducted within upland bunchgrass communities both inside (ungrazed) and immediately adjacent (grazed) to 8 2-ha exclosures for ungulates. The exclosures were erected in 1957 and 1962 between Gardiner and the Lamar Ranger Station. All 8 exclosures are on dry, upland ridges or slopes within a complex of gently rolling swales and ridges. These ridges and slopes are windblown and receive high use by elk, especially in late winter (Houston 1982). The ridges and slopes at the Gardiner exclosures were grazed by livestock until 1932, but were not subjected to the seeding or haying of grasses—no soil disturbances occurred on these sites.

Measurements in bunchgrass communities in 1986 and 1987 included biomass and cover in 10 pairs of 10 × 10 m macroplots (grazed and ungrazed) located with similar slope, aspect, and soil characteristics at each exclosure site. Sampling of paired plots was conducted simultaneously. Lane (1991) described the soils at the macroplot sites as Typic Calciborolls, Aridic Haploborolls, and Aridic Calciborolls. Lane (1991) found no consistent trends in soil organic matter, nitrogen, sulfur, electrical conductivity, iron, and zinc between grazed and ungrazed plots. Slopes between paired sites varied less than 6%, and aspects varied less than 18%. Ten 1 × 1-m quadrats or 15 0.25 × 0.25-m quadrats were located randomly within each larger (10 × 10 m) macroplot. Percent cover of each plant species, along with cover of dead litter, dung, bare ground, rocks (>6 m diameter), pebble (<6 m diameter), and pavement was estimated with a grid frame placed on the quadrats. Percent cover by dead bunchgrass clumps was estimated from the grid frame. All herbaceous and subshrub aboveground biomass was then clipped and frozen, later sorted into green and dead material by species, oven-dried for 48 hours at 60° C and weighed.

Swale Communities Subjected to Haying Activities

Swale communities in the Boundary Line Area were studied inside and outside of the two Gardiner exclosures, but sampling was restricted to measurements of percent plant cover only. I selected 5 paired macroplots (10 × 10 m) located inside and outside of each exclosure in swales. Each swale site was separated from the other by rolling ridges and slopes ($n = 10$ paired macroplots total). Since these swales were small in size (about 0.1 ha) and since they were separated spatially by intervening rolling steppe vegetation, I treated each swale as an independent replicate sample, but I pooled the data within each swale. A single mean value from all the plots in each swale was used in a 1-way ANOVA with grazing as the treatment and individual swales as replicates. Physical evidence (farm parts, ditches) indicated these swales were seeded and grazed by livestock, and some were irrigated prior to 1934, but these swales were probably not plowed under.

Nutritional and fibrous constituents were sampled after senescence in August at 2 of the eight total exclosures. The two exclosures sampled were located on the Blacktail Deer Creek. Crude protein, fat fiber, Van Soest fibers, total ash, gross energy, in vitro digestibility (IVDDM, Tilley and Terry), and Calcium, Phosphorus, Manganese, Potassium, and Magnesium levels were determined (Wildlife Management Habitat Lab, Pullman) for the three most common forage grasses, bluebunch wheatgrass, junegrass (*Koeleria macrantha*), and Idaho fescue. Heights and numbers of reproductive culms and vegetative leaves were counted and measured for the same three grasses on a 20 × 30 cm subplot within each quadrat.

Each exclosure represented one replicate (Hurlbert 1984) of the grazing treatment (grazed vs. ungrazed). One mean value for each exclosure was compared for only the most common species and plant categories (forb, subshrub, total grasses) that were present at all locations with 1-way ANOVA. Percent ground cover categories were compared between grazed and ungrazed sites, with the non-parametric Kruskal-Wallis test. The data was not transformed because of the large number of small and zero values of cover categories and biomass.

Grass morphology and reproductive characteristics were compared with Mann-Whitney U tests because the data were not normal (Kolomogorov–Smirnov test), and the variances were heteroscedastic (F-max test, Sokal and Rohlf 1969). Nutritional and fibrous constituents were compared between grazed and ungrazed sites with the t-test.

RESULTS

Most of the ungulate herbivory near the eight exclosures was attributed to elk, with some herbivory by bison. Herbivory by pronghorn and mule deer occurs at the Boundary Line Area near the Gardiner exclosures, but these ungulates are primarily browsers in the study area (Singer and Norland 1995). Elk outnumber other ungulates on the northern Yellowstone winter range by ratios of 100 elk:14 mule deer:3 bison:2 pronghorn:2 bighorn sheep (*Ovis canadensis*):1 moose (*Alces alces*) (Singer 1991). Bighorns and moose were not observed near the exclosures. Rodents (*Lepus townsendi, L. americanus, Spermophilus armatus*) occur near the exclosures and pass freely in and out of the fences.

Ungulate herbivory at the exclosure sites was restricted almost entirely to winter, but some grazing of early spring grass occurs just prior to elk leaving the winter ranges (Houston 1982). Spring off-take was zero near the Blacktail exclosure in 1990 (Singer and Harter unpubl. data), but spring off-take was more significant in the Lamar Valley (Frank and McNaughton 1992). Elk vacated the winter range sites during the remainder of the growing season (Houston 1982). Bison, however, recently shifted their area of winter range use westward (Meagher 1989) and began wintering near the Junction Butte in 1983, and to a limited extent near the Gardiner exclosures since 1988.

Comparisons of Herbaceous Biomass in Grazed and Ungrazed Bunchgrass Communities Not Subjected to Agricultural Activities

Less standing crop of annual green herbage biomass was collected on grazed sites than on ungrazed sites in 1986 ($F = 45.7$, $P < 0.01$, Table 1), but not in 1987 ($P > 0.05$). Forb biomass was not influenced by grazing in 1986 ($F = 2.0$, $P = 0.12$), but the difference due to grazing approached significance in 1987 ($F = 2.4$, $P = 0.10$). Less grass biomass was produced on grazed sites in 1986 ($F = 28.0$, $P < 0.01$),

Table 1. Comparisons of biomass between grazed and ungrazed bunchgrass communities on Yellowstone's northern elk winter range.

	1986 (n = 4 macroplots)				1987 (n = 6)			
	Ungrazed		Grazed		Ungrazed		Grazed	
	$\bar{x}$	± SE	$\bar{x}$	± SE	$\bar{x}$	± SE	$\bar{x}$	± SE
Bluebunch wheatgrass	13.4	6.6	8.3	2.9	7.6	2.8	7.6	2.8
Idaho fescue	8.3	2.9	5.9	2.7	7.2	1.6	10.0	2.0
Junegrass	7.3	2.5	4.7	1.4	4.8	1.6	10.0	2.0*
Total grasses	49.8	4.7	18.9	1.9**	24.4	5.6	31.6	5.2
Total sedges	0.2	0.1	0.4	0.1	0.4	0.3	0.4	0.2
Rosy pussytoes	1.0	0.2	0.9	0.4	10.8	6.8	0.8	0.4
Total forbs	22.5	6.6	10.9	2.5	26.0	8.8	10.8	3.6¯
Fringed sage	3.3	1.8	1.4	0.7	4.8	2.0	4.0	2.0
Total shrubs and subshrubs	3.8	2.0	2.0	1.0	10.8	1.6	6.4	2.8
Total green herbage production	76.1	4.3	31.8	3.8**	62.0	11.2	49.2	6.0

** $P < 0.01$, * $P < 0.05$, ¯ $P \leq 0.01$. Biomass differences were tested using 1-way ANOVA with location as replicates and grazing as the treatment.

[1] Does not include biomass of the perennial succulents, *Opuntia spp.*, which occurred at the lowest elevation, Gardiner exclosures, because I could not differentiate annual from perennial growth. *Opuntia spp.* biomass (annual plus perennial) was 19.2 ± 9.64 g/m^2 on protected sites and 9.6 ± 7.4 g/m^2 on grazed sites.

but not in 1987 ($P > 0.05$). Numerically, 85% less biomass of rosy pussytoes (*Antennaria microphylla*) and 33% less fringed sage (*Artemisia frigida*) was collected from grazed sites, but the differences were statistically not significant ($P > 0.05$).

Several other plant species were less ubiquitous in the study plots, and inferences concerning grazing treatment effects are tenuous. For example, thick-spiked wheatgrass (*A. dasystachum*) was found at only the two highest exclosure locations in the Lamar Valley where it was more abundant on grazed (6.2 ± 0.9 g/m^2) than on ungrazed sites (3.5 ± 0.7 g/m^2) ($P < 0.05$).

Elk herbivory did not influence the frequency of grass, forb or shrub species (Table 2, $P > 0.05$). An average of 4.5 grass species, 17.5 forb species and 3.5

Table 2. Number of grass, forb, and shrub species compared between 10 pairs of grazed and ungrazed macroplots, in 1986 and 1987 from upland bunchgrass communities on Yellowstone's northern range.

	1986							
No. plant species	Mammoth-W		Mammoth-E		Blacktail-W		Blacktail-E	
	Control	Grazed	Control	Grazed	Control	Grazed	Control	Grazed
No. grasses	6	4	4	5	4	4	6	3
No. forbs	8	7	15	10	26	25	16	21
No. shrubs	5	3	3	5	2	3	2	2
TOTAL	19	14	22	20	32	32	24	26

	1987					
No. plant species	Gardiner-E		Gardiner-W		Blacktail	
	Control	Grazed	Control	Grazed	Control	Grazed
No. grasses	2	2	4	3	4	4
No. forbs	11	16	21	17	10	12
No. shrubs	0	1	3	2	2	3
TOTAL	13	19	28	22	16	19
No. plant species	Junction Butte		Lamar-E		Lamar-W	
	Control	Grazed	Control	Grazed	Control	Grazed
No. grasses	3	8	5	5	3	4
No. forbs	19	17	22	21	27	32
No. shrubs	2	2	1	1	3	3
TOTAL	24	25	28	27	33	39

shrub species were identified on each 10 × 10 m macroplot in bunchgrass communities. One species, *Arabis holboelii*, was recorded from only grazed plots.

Lichen cover was not influenced by elk herbivory ($P > 0.05$, Table 3), but moss cover was significantly greater on ungrazed sites in 1986 ($P < 0.05$), but not in 1987 ($P > 0.05$). Litter and standing dead vegetation averaged 3.5 times more biomass on ungrazed plots ($P < 0.05$, Table 3), and as a result bare ground averaged 3.8 times more on grazed sites both years (Table 3). Pebble cover, however, averaged 50% less on grazed sites ($P < 0.05$), probably because pebbles were less obvious on grazed areas due to hoof action and soil compaction by ungulates. When bare ground and pebble cover were combined, all bare surfaces averaged only 18% more on grazed versus ungrazed sites in 1987 ($P < 0.05$), but the difference was not significant in 1986 ($P > 0.05$, Table 3). Small pebble cover was greater on ungrazed plots both years. Animal dung from ungulates and rabbits provided a minor amount of ground cover (1.2–4.1%) and its abundance was greater on grazed than ungrazed sites ($P < 0.05$) (Table 3).

I observed no evidence of any significant increase in bunchgrass mortality due to elk herbivory ($P > 0.05$, t-test, $t = 0.54$). Dead bunchgrass clumps averaged 4.3% cover for both treatments.

Grass Morphology

Numbers and heights of reproductive culms and numbers of vegetative culms did not vary between grazed and ungrazed paired plots for bluebunch wheatgrass, Idaho fescue, junegrass, thick-spiked wheatgrass, needle-and-thread grass (*Stipa comata*), or bluegrasses (Table 4). The single exception was more vegetative culms of junegrass were sampled per individual plant on grazed sites. Heights of vegetative leaves were shorter in grazed sites of bluebunch wheatgrass ($t = 5.7$, $P < 0.001$), Idaho fescue, junegrass, thick-spiked wheatgrass, and bluegrasses ($P < 0.05$). Reproductive ratio (the number of reproductive vs. the number of vegetative culms per plant) did not vary between grazed and ungrazed paired plots for any grass species ($P > 0.05$).

Nutritional Responses of Grasses to Grazing

Elk herbivory enhanced the protein content of live grasses. Protein content averaged 16% higher on grazed versus ungrazed paired plots for bluebunch wheatgrass ($t = 9.8$, $P < 0.0001$), 36% higher for grazed Idaho fescue ($t = 11.8$, $P < 0.001$), and 10% higher for grazed junegrass ($t = 6.8$, $P < 0.05$, Table 5). Grazing did not significantly influence digestibility (IVDDM) or fibers (NDF, ADF, ADL, $P > 0.05$). Ash content was significantly higher in grazed Idaho fescue and junegrass ($P < 0.05$, Table 5).

Grazing resulted in a minor enhancement of macronutrients. Calcium levels were higher in grazed than ungrazed Idaho fescue (0.56 ± 0.07 ppm vs. 0.41 ± 0.06 ppm, $t = 15.8$, $P < 0.001$, d.f. = 18) as were Phosphorous levels (0.16 ± 0.01 ppm vs. 0.14 ± 0.04 ppm, $t = 6.20$, $P < 0.01$) and Magnesium levels (0.14 ± 0.01 ppm vs. 0.09 ± 0.01 ppm, $t = 15.8$, $P < 0.001$). Potassium levels were higher in grazed bluebunch wheatgrass (1.14 ± 0.10 ppm vs. 0.99 ± 0.03 ppm, $t = 7.9$, $P < 0.001$). No other differences

Table 3. Ground cover categories and standing dead and downed litter on grazed and protected bunchgrass communities in Yellowstone National Park, 1986–87. Differences were tested using the Kruskal–Wallis 1-way ANOVA with grazing as treatment and locations ($n = 4$ or 6) as replicates.

	1986 (n = 4)				1987 (n = 6)			
	Ungrazed		Grazed		Ungrazed		Grazed	
	$\bar{x}$	+ SE	$\bar{x}$	+ SE	$\bar{x}$	+ SE	$\bar{x}$	+ SE
Lichen cover(%)	6.3	3.3	9.8	8.0	4.2	1.1	5.1	3.9
Moss cover (%)	10.4	3.9	1.7	0.2*	1.9	0.4	0.6	0.3
Bare ground (%)	11.7	5.1	20.2	2.5*	4.4	0.3	35.1	6.5*
Pebble cover[1] (%)	29.4	4.5	18.3	8.9	37.0	8.2	13.8	0.7**
All bare surfaces[2] (%)	41.1	5.1	38.5	2.5	41.4	4.1	48.8	2.7*
Animal dung[3] (%)	0.2	0.1	34.3	11.6**	1.2	0.3	4.1	1.2*
Litter and standing dead vegetation (g/m^2)	84.4	16.4	21.1	7.2**	67.0	9.3	23.3	3.9**
Dead wood[4] ($g/^2$)	2.1	0.6	1.7	0.5	3.2	0.7	2.0	0.7

[1] Pebbles were defined as <6 cm diameter.

[2] Bare ground and pebble cover combined.

[3] Elk, pronghorn, deer and rabbits pellets as percent of ground cover in 1987, and total number of pellets per m^2 in 1986.

[4] Dead stems of shrubs (big sagebrush, horsebrush, rabbitbrush) and subshrubs (fringed sage, Phlox) lying on the ground surface.

Table 4. Mean morphological measurements for 3 common grasses at 8 grazing exclosures on Yellowstone's Northern Winter Range (n = 130 grazed and 130 ungrazed plots, 1-m^2).

	Bluebunch wheatgrass		Idaho fescue		Junegrass	
	Ungrazed	Grazed	Ungrazed	Grazed	Ungrazed	Grazed
No. vegetative culms	15.4 ± 13.3	18.6 ± 15.8	94.0 ± 50.1	127.6 ± 107.2	23.1 ± 17.9	44.7 ± 21.4*
No. reproductive culms	2.0 ± 1.7	2.3 ± 2.1	4.2 ± 3.3	3.2 ± 2.9	2.5 ± 2.6	3.2 ± 2.7
Tallest vegetative culm (cm)	22.3 ± 2.5	18.0 ± 1.6*	15.4 ± 3.1	7.8 ± 0.4*	10.1 ± 2.3	7.6 ± 1.0*
Tallest reproductive culm (cm)	27.1 ± 13.7	29.5 ± 11.6	33.2 ± 9.6	24.4 ± 9.7	18.5 ± 10.1	13.9 ± 7.8

* Significant difference, $P < 0.05$, Mann-Whitney U tests.

attributable to elk herbivory were observed for 5 elements (Phosphorus, Calcium, Magnesium, Potassium, Manganese) in Idaho fescue or bluebunch wheatgrass, and no differences in any elements were observed in junegrass.

Effects of Native Ungulate Grazing in the Former Agricultural Zone

Bunchgrass communities formerly grazed by livestock. Vegetation on elk grazed and ungrazed rolling bunchgrass-dominated ridges and slopes in the Boundary Line Area was similar; apparently both treatments recovered in a parallel fashion from livestock grazing terminated 54 years before. No exotic plants were sampled on either treatment and no biomass differences by plant species occurred with the single exception that more biomass of *Phlox hoodii* was sampled on sites ungrazed by elk ($P < 0.05$).

Swales formerly hayed and grazed by livestock. Swale communities in the Boundary Line Area, however, where seeding and soil disturbance from agriculture occurred, differed on sites grazed by native ungulates during the 54 recovery period versus those sites ungrazed by native ungulates. The differences did not suggest decreased productivity on the elk grazed sites, in fact, grass cover was nearly double and bare ground less on the elk grazed sites (Table 6, $P < 0.05$). Three grasses (green needlegrass; Kentucky bluegrass; Canadian bluegrass, *Poa compressa*) were more abundant on elk grazed sites ($P < 0.05$, $F = 5.7, 5.1, 3.6$, respectively), but one of these grasses is an exotic (Kentucky bluegrass) suggesting elk grazing promoted continued dominance of the sites by an exotic grass. Field pennycress (*Thlaspi arvensi*), an exotic forb, however, was more abundant on sites ungrazed by elk ($F = 3.9$, $P < 0.05$).

DISCUSSION

Grass biomass on upland bunchgrass types was reduced in 1986 by grazing, but there was no effect from grazing in 1987. The winter of 1985–86 which preceded the 1986 growing season was characterized by an early spring snowmelt and less than normal spring precipitation (83% of average). Grazing effects on grasslands may be exacerbated during dry conditions (Coughenour 1991, Frank and McNaughton 1993) and recovery from a drought is slower on heavily-grazed sites (Young 1943). Growing season consumption by ungulates was negligible at the study sites in 1990 (F. Singer and M. Harter, unpubl. data) and growing season consumption was suspected to be negligible most other years, since so few elk were observed near the study plots. But spring consumption

Table 5. Nutritional values of grazed and ungrazed (exclosed) grasses on Yellowstone's northern winter range, 1986 (S.D.).

	Bluebunch Wheatgrass		Idaho Fescue		Junegrass	
	Ungrazed	Grazed	Ungrazed	Grazed	Ungrazed	Grazed
Protein (%)	7.74 ± 0.49	9.01 ± 0.80**	7.02 ± 0.56	9.58 ± 1.02**	7.95 ± 0.31	8.78 ± 0.75**
Digestibility (IVDMD, %)	60.98 ± 1.83	61.18 ± 2.46	60.06 ± 4.50	64.93 ± 3.08	61.74 ± 2.70	62.89 ± 3.26
Fiber (NDF, %)	68.69 ± 2.76	68.21 ± 1.09	73.15 ± 1.74	68.13 ± 3.69	69.63 ± 2.33	69.23 ± 2.93
Ash (AIA, %)	1.54 ± 0.32	1.49 ± 0.18	1.20 ± 0.36	2.15 ± 0.42**	0.78 ± 0.33	2.09 ± 0.57**

*Significant difference between grazed and ungrazed grasses, $P < 0.05$, ** $P < 0.01$, t-tests.

Table 6. Percent cover of common plant species in swale communities of the boundary line area (BLA) of Yellowstone's northern winter range. n = 10 plots of 1 m^2 randomly located in each of 10 swales within each treatment. Ungrazed sites were protected from grazing for 27 and 29 years. Each swale was considered 1 replicate sample and only 1 mean value from subplots in each swale (n = 10) was used a 1-way ANOVA with grazing as the treatment ($P < 0.05$). The BLA was grazed by domestic livestock until the 1930s and some areas were seeded with exotics for hay crops, thus exotic plants are more prevalent in this part of the winter range.

	Ungrazed		Grazed	
Plant species	$\bar{x}$	SE	$\bar{x}$	SE
Grasses				
Stipa viridula	0.4	0.4	5.5	2.0**
Bromus tectorum (exotic)	4.7	2.8	3.1	1.4
Poa pratensis (exotic)	17.1	6.2	43.8	9.1**
Poa compressa	0		4.5	3.1*
Hordeum jubatum	1.0	0.6	1.4	0.9
Koeleria macrantha	2.1	0.8	2.2	1.0
Agropyron spicatum	0.9	0.5	0.3	0.1
Other grasses[1]	5.2	2.8	3.8	1.8
Total grasses	31.4	1.8	64.6	19.4
Forbs				
Thlaspi arvensi (exotic)	2.9	1.2	0.9	0.6*
Taraxacum spp. (exotic)	1.0	0.5	0.3	0.2
Other forbs[2]	3.5	1.5	1.2	0.4
Total forbs	7.4	3.2	2.4	1.2
Mosses	5.1	2.2	0	

[1] Other grasses included *P. sandbergii, H. punctuata, A. smithii, S. comota, A. cristatum, A. caninum, Elymus cinerius, B. inermus, Sitanion hystrix* in frequencies too low for analysis.

[2] Other forbs included low frequencies of *Polygonum, Eurotia, Alyssum gabrum, Tragapogon dubius, Chenopodium, Descuainia richardsonii, Lappula redowskii.*

by elk was not sampled in 1986 or 1987, and it may have been more significant than I suspected.

The response of individual plant species to grazing were minimal. Only 4% (5 of 133) of the plant species found on the macroplots reflected biomass differences that might be attributed to grazing. Three species (rosy pussytoes, fringed sage, *Arabis holboelii*) might have decreased due to grazing (not statistically different, but a consistent trend), but two other species (junegrass and thickspiked wheatgrass) might have increased due to elk herbivory (statistical differences).

Smith (1960) rated junegrass as an increaser species in response to elk herbivory in the nearby Jackson Hole region of Wyoming and thickspiked wheatgrass was resistant to grazing; these observations are consistent with these Yellowstone northern range data. The lack of any consistent grazing responses in other grasses on the study plots is noteworthy since both Idaho fescue and bluebunch wheatgrass are sensitive to grazing and clipping experiments (Daubenmire 1940, Young 1943, Evanko and Peterson 1955, Pond 1960, Caldwell et al. 1981). However, most native ungulate herbivory of Yellowstone northern winter range occurred during winter when grasses are dormant and during the first 2 weeks of initial grass growth (Houston 1982). Other research suggests that winter combined with minimal spring grazing, as occurred on the study plots, might have few effects on grass production. For example, clipping of Idaho fescue and bluebunch wheatgrass after they had cured had minimal effects on future production (Mueggler 1969). Early spring grazing has minimal effects on production of many grasses and forbs (McCarthy and Price 1942, Stoddart 1946, Blaisdell and Pechanec 1949).

Total forb and subshrub biomass was not consistently influenced by elk herbivory. A few forbs and subshrubs were less abundant at some paired grazed sites (fringed sage, rosy pussytoes, phlox). Perhaps some of these sites received elk herbivory into the spring on newly growing forbs. Jameson (1963) concluded that forbs were more sensitive to grazing than were grasses, as my data indicates. Elk eat very few forbs during the winter months in Yellowstone National Park (only 3% of winter diets), apparently because of deep snows and forb desiccation (Singer and Norland 1995), but less litter and more bare ground on grazed sites may provide conditions that are more (or less) suitable to some plants' needs for seedling establishment, for example some forb species.

Grass cover was substantially greater on elk grazed swales in the BLA. These swales are more productive than bunchgrass communities (Houston 1982). High nutrient return in urine and feces, and stimulation of grass growth were likely in the more productive swale communities (Frank and McNaughton 1992, 1993). These swales were seeded to exotic hay grasses prior to inclusion in the park during the 1930's. Apparently, grazing by native ungulates, especially by elk, contributed to the persistence of exotic grasses, while complete protection from ungulates since 1958 contributed to their decline. The dominance of Lamar Valley study sites of Frank and McNaughton (1993) by exotic grasses also suggests heavy grazing by native ungulates, both elk and bison, contributes to the persistence of the Eurasian grasses.

The maintenance of aboveground and belowground biomass of grasses on heavily grazed sites on Yellowstone's northern range may be due to the benefits of ungulate defecation and urination (Williams 1966, McNaughton 1979) and to the accelerated decomposition of plant material (Gusev and Guseva 1983). Furthermore, grass meristems may be activated by grazing (McNaughton 1984), and the growing season may be extended by enhanced water availability (McNaughton 1983) and by higher early season soil temperatures on grazed sites (Whitman 1971, Archer and Detling 1985). Total protection of bunchgrass winter range sites from native ungulate grazing for 24–27 years resulted in a 4-fold increase in accumulated dead litter and standing dead vegetation. Excessive accumulations of mulch may reduce grass production (Weaver and Rowland 1952, Jameson 1963) due to a cooler soil surface (Johnston et al. 1971, Whitman 1971), but the addition of litter increased production in other studies (Ellison 1960). Whatever the mechanism, we observed no difference in total standing crop biomass between grazed and ungrazed sites during the first year, but only about one-half the total standing crop biomass was produced on grazed sites versus ungrazed sites the second year. In contrast, Frank and McNaughton (1993) reported more consistent and numerically more biomass increases due to grazing (47% more aboveground primary production from grazed) sites) in Yellowstone National Park. However, their study involved different years than mine (1988 and 1989) and they sampled primary production (I sampled standing crop only). Frank and McNaughton's (1992, 1993) study sites were more mesic, and more productive than mine. Five of their 12 study sites were dominated by grazing resistent, exotic grasses (timothy, Kentucky bluegrass, and/or smooth brome). Their study sites were located on summer range, transition range, and upper elevation–winter range, nearly all of their sites were located at higher elevations with more precipitation than my study sites. The swale sites I studied were more similar to study sites of Frank and McNaughton's (1992, 1993), i.e., depositional, productive sites and the swale comparisons were more supportive of their conclusions; apparently grasses were stimulated by grazing in swales, and the exotic grass, Kentucky bluegrass, continued to dominate sites grazed by elk following cessation of agricultural activities.

Grass heights and shapes did not differ following 28 years of protection from native ungulate herbivory, with the single exception that vegetative culms of most grasses were shorter in grazed areas. Grazing results in shorter, more prostrate forms of grasses (Jameson 1963, McNaughton 1984) and more horizontal leaf angles (Detling and Painter 1983). My study indicated no effect on the height or numbers of seed heads of grasses from winter and early spring grazing. In contrast, most clipping or grazing during the growing season reduced seed production of grasses (Jameson 1963, Mueggler 1975, Owen and Wiegart 1981, McNaughton 1983, Ruess et al. 1983). The effects of winter grazing on seed production, as occurred on the Yellowstone northern range study sites, are less significant than is grazing during the growing season.

Grazing enhanced protein content in grasses by an average of 21% on the study sites. Several macronutrient concentrations (Ca, Ph, Mg, K) averaged 13–36% higher in grazed versus ungrazed grasses. The average crude protein content on the northern winter range for 3 common cured grasses in early August was 7.6% on ungrazed sites and 9.1% on grazed sites. Mould and Robbins (1981) indicated dry-matter intake of forage by elk sharply increased when dietary protein concentration fell below 8%. Therefore, enhancement of protein content on the northern winter range from grazing thus may be critical to elk over-winter survival. Increases in foliage N concentrations of grasses in response to grazing have been reported elsewhere (Jameson 1963, Everson 1966, Chapin 1980, Detling and Painter 1983, Day and Detling 1990). Enhanced N content has been attributed to greater proportion of younger stems after grazing which are higher in N and other nutrients (Jameson 1963, Owensby et al. 1970). Uptake rates of N are higher after clipping (Ruess et al. 1983), soil nutrient pools may be enhanced by dung and urine deposition (Williams 1966, Ruess and McNaughton 1987), and increased net mineralization rates (Holland and Detling 1990).

Compensatory growth of grazed grasses (sensu Belsky 1986 = any positive increase in plant growth due to herbivory) may have occurred in years of adequate precipitation on the study sites (see also Coughenour's (1991) and Frank and McNaughtons' (1993) study sites). Total protein yield (biomass × % protein) produced in 1986 on grazed sites was only 50% that of ungrazed sites, but in 1987 grazed sites produced 156% of the total protein yield of ungrazed sites. Gordon (1988) observed greater biomass and a higher proportion of green grass available for red deer (*C. elaphus*) on sites grazed by cattle (*Bos taurus*) during the previous winter.

CONCLUSIONS

The upland bunchgrass sites under study on Yellowstone's northern winter range apparently were not overgrazed at the time of this investigation in 1986 and 1987, at least in terms of declines in aboveground biomass production, while only the most minor changes in species composition were observed. There were very few differences in plant species composition or numbers of plant species between grazed and ungrazed plots, and there was no evidence of accelerated mortality of bunchgrasses from elk herbivory. Protein concentrations and the concentrations of several nutrients were enhanced in grasses by elk herbivory. Very few differences were observed on the heights or growth form of grazed grasses. An increase in bare ground and a large decrease in accumulated litter and standing dead vegetation were observed on grazed sites which, combined with higher bulk densities, contributed to slightly lower soil infiltration rates on grazed sites (Lane 1991). Numerically less total forbs and shrubs were found on grazed sites, but the differences were not statistically significant. Less total grass biomass was found during 1 of 2 years on grazed sites. Limitations of the study include the small number of replicate comparisons (n = 10 paired macroplot comparisons) over only 2 years. Tedious hand sorting of all live and dead materials by species for this study was enormously labor intensive (1.3 person years) and limited the number of replicates. In addition, pre-exclosure differences in species abundance or microsite characteristics might have occurred, and possibly obscured real effects due to grazing. Parker transect data gathered at the time of exclosure in 1958 and 1962, however, does not suggest any consistent site differences at the time of exclosure (Houston 1982, Coughenour et al. 1995). Data from swale grassland types was limited to species cover data. Elk grazing on these more productive sites apparently resulted in stimulation of grasses (double the total herbaceous plant cover in grazed sites), but the elk herbivory also resulted in continued persistence of a grazing resistant exotic grass, Kentucky bluegrass, following cessation of agricultural activities. The work of Frank and McNaughton (1993) also suggests exotic grasses persist with intense elk and bison herbivory (45% consumption) in the Lamar Valley where haying activities persisted until 1952. Exotic grasses apparently declined more rapidly in ungrazed swales in the Boundary Line Area, but one exotic weed, field pennycress, was more abundant on ungrazed sites. National Park Service policy states that native animal populations be managed under conditions representing as near as possible natural conditions. Natural conditions include herbivory by native ungulates. At the time of this study, Yellowstone's northern elk winter range supported 21 elk/km^2 during the winter months (Singer 1991), yet only minor differences were detected between grazed bunchgrass sites and paired sites protected from native ungulates for nearly three decades. I propose the minimal number of grazing effects observed on the study plots are due to the restriction of direct and indirect effects from ungulate activity (grazing, trampling, bedding, trailing) to the winter season only. During the winter, plants are in senescence, the ground is frozen and, in most situations, the ground is also snowcovered, minimizing the effects from herbivory by elk. I stress these findings apply only to the upland bunchgrass sites under study and to sites where native ungulate herbivory was restricted to the winter period only.

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The Coincidence of Elk Migration and Flowering of Bluebunch Wheatgrass

Don G. Despain

National Park Service
Research Division
Box 168
Yellowstone National Park, Wyoming 82190

Abstract. Bluebunch wheatgrass (*Agropyron spicatum* Pursh) is a major grass species of the lower elevations and foothills of the Rocky Mountains. It is highly palatable and strongly affected by grazing during its flowering period. Bluebunch wheatgrass serves as a major food on winter ranges for elk (*Cervus elaphus*) and other ungulates migrating from higher elevations. Elk move off bluebunch wheatgrass ranges before the onset of flowering, thus allowing adequate time for regrowth of the grass before the next season of intensive grazing.

Key words: *Agropyron spicatum*, bluebunch wheatgrass, *Cervus elaphus*, elk, migration, phenology, Yellowstone National Park, winter range.

The physical parameters impinging on a great portion of the earth's surface are highly variable. In the interactions between organisms or between organisms and their environment, therefore, the timing of an event is often as important as the occurrence. Two species are major components of the interactions on the northern winter range of Yellowstone National Park. The elk (*Cervus elaphus*) is a major consumer of photosynthetically fixed carbon, and bluebunch wheatgrass (*Agropyron spicatum* Pursh) is a major supplier. The timing of the interaction of these two species could play a major role in ecosystem dynamics.

Bluebunch wheatgrass is a major overstory component on portions of the winter range of the northern Yellowstone elk herd (Houston 1982). It is a C3 grass that starts growth in early spring and reproduces in late May to early June before soil moisture becomes limiting. It is susceptible to damage by grazing during reproduction (McIlvanie 1942; Stoddart 1946; Wilson et al. 1966; Mueggler 1972). Plants clipped during the flowering stages failed to regrow significantly, and many died after 2 years of such treatment (Stoddart 1946). Plants clipped once during the susceptible period grew only 6–30% as much as unclipped plants the following year (Blaisdell and Pechanec 1946). Suppression of regrowth can last for several years (Mueggler 1975).

Members of the northern Yellowstone elk herd migrate seasonally, and on the winter range the highest densities occur from November through April (Houston 1982). The herd utilizes its range in Yellowstone National Park without significant competition from livestock and with only minor influences from hunting (Houston 1982). Elk wintering on the lower portion of the northern winter range graze primarily on plant communities dominated by bluebunch wheatgrass. National Park Service records of a winter count taken in January 1982 showed about 16,000 elk on the northern range. In addition, a relatively small number of other ungulates use the winter range, including mule deer (*Odocoileus hemionus*), pronghorn (*Antilocapra americana*), bison (*Bos bison*), and bighorn sheep (*Ovis canadensis*). These animals and the elk take nearly all the annual production of aboveground biomass during the winter.

Without some mechanism to mediate interactions between elk and bluebunch wheatgrass, grazing ungulates could possibly eliminate this species of grass from the winter range. The confinement of susceptibility of bluebunch wheatgrass to grazing to a short period and because elk migrate from their winter range provided an opportunity to look at the interaction between elk and bluebunch wheatgrass within a time context. My objective was to determine if migration of elk and bluebunch wheatgrass phenology were related in time. I tested the null hypothesis that they were related.

Study Area

The study area covered about 2,500 ha and bordered the north boundary of the park. The area is underlain by two major types of soil, a silt loam and a clay loam. The silt loam is derived from alluvial sand and gravel mixed with a silty matrix along the Yellowstone River. The clay loam is derived from mudflows on the open slopes of the valley side (Houston 1982).

Vegetation on the alluvial flats is dominated by needle-and-thread (*Stipa comata* Trin. & Rupr.) and junegrass (*Koeleria cristata* Pers.), with bluebunch wheatgrass, Hood's phlox (*Phlox hoodii* App.), and fringed sage (*Artemesia frigida* Willd.) as major components. Vegetation on the lower part of the mudflows is dominated by bluebunch wheatgrass and junegrass with needle-and-thread, fringed sage, Hood's phlox, and winter fat (*Eurotia lanata* (Pursh) Mog.) as major components. Vegetation on the upper part of the mudflows is dominated by Idaho fescue (*Festuca idahoensis* Elmer), junegrass, and bluebunch wheatgrass. Three subspecies of big sage (*Artemisia tridentata* Nutt. subspecies *vaseyeanna*, *tridentata*, and *wyomingensis*) are the major components of a sparse shrub overstory throughout and are severely browsed. The flat areas at the lower elevations were cultivated until 1932 when the fields were purchased by the National Park Service. These fields were planted to crested wheatgrass (*Agropyron cristatum* (L.) Gaertn.) about 1936.

Elevations range from 1,500 m at the river to 1,950 m at the lower tree line. Annual precipitation ranges from 257 mm at Gardiner (at the lower eastern end of the study area) to 403 mm at Mammoth (at the same elevation but 6.4 km south of the upper part of the study area). Approximately 35–40% falls in April, May, and June. Houston (1982) gives a more complete description of the area and its history.

Climatic factors differed each year of the study. Table 1 presents the precipitation and temperature for winter and spring. March is listed separately because it can be either winter or spring depending on the annual course of temperature. In general, 1978–79 was characterized by a slightly dry winter and a warm and extremely dry spring; 1979–80 had a dry cool winter that extended into March and a dry warm spring; 1980–81 had a warm, dry winter and a moist warm spring; 1981–82 had a fairly normal winter but a cold spring with normal precipitation.

Recession of snowline and new growth of plants are functions of temperature and incident sunshine. Lilac phenology follows closely the accumulated heat and total sunshine in the environment rather than day length (Caprio 1966) and can be used as an indicator of the progress of spring warming. It can be assumed that snowline recession and new plant growth at higher elevations are correlated with regional lilac phenology. Data from the 4 years of study also show great variation in regional lilac phenology. In 1979, lilacs were close to average in their phenology; in 1980 they were 10–15 days early; in 1981, about 5 days early; and in 1982, about 15–20 days late (Joseph Caprio, Montana State University, personal communication).

Methods

To assess the health of bluebunch wheatgrass relative to grazing, total green biomass and basal cover of both bluebunch wheatgrass and junegrass were estimated both inside and outside a 2-ha exclosure. The exclosure, established in 1957, was on one of the mudflows near the center of the elk-counting transect described below. The sites chosen were on a north-facing slope of a small ridge (approximately 50 m long) that was bisected by the exclosure fence. Basal area at each site was estimated in 20 2- × 5-dm plots placed at 1-m intervals along two 10-m lines running parallel to the slope. Green biomass was measured at 10 different points, both inside and outside the exclosure, using the ratio of red to infrared reflected radiation (Pearson and Miller 1973). Ten 1-m-square plots were clipped on 15 May 1979 to calibrate the radiometer. Five were inside and five were outside the exclosure.

As an index of the number of elk on the study area, elk were counted at sunrise on 2 consecutive days per week each spring from 1979 through 1982. Counting started on 1 May during the first 2 years. It then became obvious that an earlier starting date (1 March) was necessary. Counting was discontinued when only a few elk (about 50) remained in the study area. Counts were made along an 8-km transect beginning at the north entrance of Yellowstone National Park and ending at Reese Creek. Five counting sites were used to cover the entire area without overlap. Observers used a variable power (×15–60) zoom spotting scope.

Phenology and green biomass were monitored on the sites where basal area measurements were

Table 1. Seasonal precipitation and mean temperature at Mammoth Hot Springs, 1979–1982.

	Winter[a]		March		Spring	
Year	ppt (mm)	temp (°C)	ppt (mm)	temp (°C)	ppt (mm)	temp (°C)
1979	122		59	−1.8	36	+8.5
1980	68	−5.6	20	−2.8	121	+9.3
1981	56	−2.4	10	+0.9	168	+8.5
1982	138	−4.7	49	−1.9	147	+6.9
Normal	117	−4.8	27	+3.0	136	+7.9

[a] Winter = November–February; Spring = April–June; March can be either winter or spring.

taken. Observations were made weekly from early April through late July 1979–82. I recorded green leaf length and phenological stage, inflorescence detectable in the sheath (boot stage), heads out of sheaths, anthers shedding pollen, and seed shatter.

Results and Conclusions

Basal cover of bluebunch wheatgrass and junegrass was 4 and 12% on the inside and 3 and 16% on the outside. There seems to be little or no effect of grazing or protection from grazing near the exclosure. Despite the highly variable weather conditions, bluebunch wheatgrass flowered at the same time each year except 1979, when drought resulted in insignificant flowering of bluebunch wheatgrass.

By the end of the growing season each year, the total green biomass inside and outside the exclosure did not differ (Table 2). There was no significant difference (*t*-test, $P < 0.00$) in green biomass measured by clipping or biomass meter. The lowest values occurred during the dry spring of 1979 and the cold spring of 1982. The highest values occurred during the wet spring of 1981 and the warm moist spring of 1980.

The maximum number of elk was counted in 1982 (more than 1,000) during the preflowering stage. Elk began moving off the range coincident with inflorescences being detectable in the sheaths of bluebunch wheatgrass (Figure). The number of elk seen from the transect in early May was only 50% or less of the number seen during the preflowering stage and decreased to less than 10% by mid- to late June each year.

The movement of elk from this portion of their winter range at this time releases bluebunch wheatgrass from grazing during a critical period in its life history. Absence of grazing at this time allows it to regrow and thus to persist.

Table 2. Maximum green biomass and the date on which it occurred inside and outside an exclosure on the lower winter range for the northern Yellowstone elk herd.

		Outside		Inside	
		Mean[a]	SE[b]	Mean	SE
Year	Date	(g/m^2)		(g/m^2)	
1979	06/25	33.0	1.1	34.7	1.1
1980	07/01	34.0	0.5	36.0	0.9
1981	07/06	40.5	0.8	42.6	1.8
1982	06/21	31.7	0.7	34.0	2.4

[a] There are no statistically significant differences between outside and inside means.

[b] SE = standard error of the mean, $n = 10$.

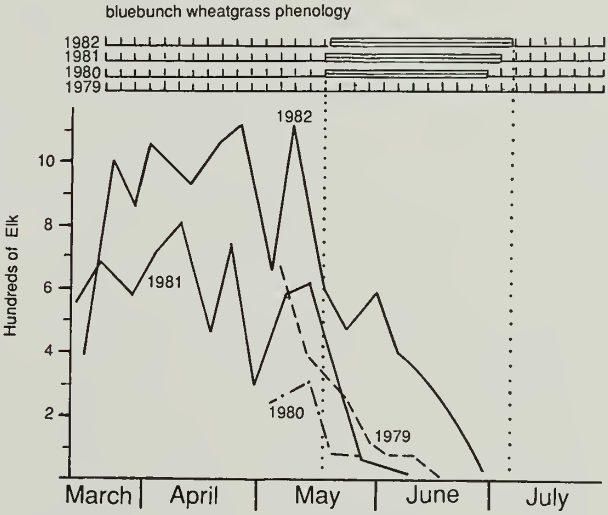

Figure. Relation of elk counted on the study area to phenology of bluebunch wheatgrass. *Horizontal bars* indicate reproductive period from the time the inflorescence is first detectable in the sheath (boot stage) of the flowering culm through the end of pollen dispersal. The number of flowering culms produced in 1979 was insignificant.

Discussion

The minor difference in basal area of both bluebunch wheatgrass and junegrass between the protected and grazed areas indicates little or no long-term effect on these species from grazing pressure. The study area has been under heavy grazing pressure for more than 50 years, and the exclosure has been in place since 1957 (Houston 1982). A difference should be noticeable if elk were having a biologically significant effect on bluebunch wheatgrass.

The maximum amount of green biomass seems dependent on weather. Elk took part of the first crop of leaves during some years, but by the end of the growing season those losses had been replaced. Severe winter grazing and moderate to light early spring (preflowering) grazing was not deleterious to the bluebunch wheatgrass or to the junegrass plants in the vicinity of the exclosure. This was indicated by the ability of the grass outside the exclosure to gain photosynthetic surface equal to that inside, together with the fact that the density and cover of bluebunch wheatgrass outside the exclosure did not differ from that inside.

Time of flowering of bluebunch wheatgrass was not advanced by the early spring of 1980 nor much retarded by the late spring of 1982. The consistency with which bluebunch wheatgrass flowered on the same date indicates likely photoperiod control. The dates reported here agree with earlier observations in the northern Rocky Mountains (Schmidt and Lotan 1980).

Timing of elk movement off the winter range did not seem related to elk numbers or to weather. Time of movements off the winter range was similar in 1981 and 1982 even though spring in 1982 was 20–25 days later than 1981 and only two-thirds as many animals were present in 1981. The number of elk migrating to the lower part of the winter range each winter is dependent on the severity of the winter and early spring weather (Houston 1982). Deep snow in the upper part of the range pushes the animals lower. Shallow snow allow more animals to remain higher.

The coincidence of elk movement and flowering of bluebunch wheatgrass described here could be entirely the vagaries of chance. There could also be, however, some causal mechanism. Spring migration of Rocky Mountain elk seems related to spring new growth of forage (Adams 1982). In the Selway River drainage of Idaho, spring elk migration began in late April and early May. This movement was attributed to the development (new growth) of herbaceous vegetation, although researchers did not specifically record the date of beginning new growth (Dalke et al. 1965). To obtain a definitive answer, one would have to document dates of new growth and of elk movements on the entire winter and summer ranges for 5 or more years.

Food quality may be a factor in the timing of elk leaving the winter range. Large ungulates have been shown to respond to nitrogen levels in their forage. Studies of migratory ungulates in East Africa (Maddock 1979) indicate that migration may be largely in response to changes in quality and abundance of food. On a landscape affected by drought, animals graze predominantly where rains have come and grasses are young and growing. As plants mature and nitrogen levels in the forage drop, the migratory ungulates move to areas where new growth is occurring.

Earlier studies of bluebunch wheatgrass have shown that nitrogen level drops sharply at the start of flowering (McIlvanie 1942) and that protein level during flowering is 35–41% of that during active growth (Stoddart 1946). Digestibility of bluebunch wheatgrass drops from about 52% during spring growth to about 35% just before flowering begins (Hickman 1975). Perhaps the elk are responding to nitrogen levels in bluebunch wheatgrass. In this instance they are moving to higher elevations where new grass is growing in areas more recently released from snow cover and where Idaho fescue is the dominant grass.

Another possible mechanism is the onset of calving. One study conducted near the northwestern corner of Yellowstone National Park suggested that the movement of cow and calf elk in spring was more related to calving period than plant development (Brazda 1953). Calving generally occurs during the same dates each year (Taber et al. 1982). Calves of the year were not seen with the elk groups during the counts until late May, but the cows may hide their calves for a week or two until the calves can keep up with the herd.

The slowness with which bluebunch wheatgrass recovers from clipping during flowering may be advantageous to its long-term survival. If the elk herd remained on the winter range during the critical flowering period in sufficient numbers to significantly affect the grass, food supplies for several subsequent winters would be considerably less—as much as 85% less—than normal (Mueggler 1975). Winter mortality could greatly reduce the elk population, relieving the grass from elk grazing pressure. Any mutation in the grass that resulted in earlier flowering would be quickly eliminated from the population. Such interactions are likely part of a complex feedback mechanism that maintains an elk–bluebunch wheatgrass equilibrium over time.

The migration of elk before the flowering of bluebunch wheatgrass occurs with regularity and is a possible explanation of why bluebunch wheatgrass is so abundant on the study area. More observations are needed in other areas where elk winter on bluebunch wheatgrass communities to determine the commonness of this pattern.

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Nutrient acquisition by clipped plants as a measure of competitive success: the effects of compensation

L. L. WALLACE and S. A. MACKO

Department of Botany and Microbiology
University of Oklahoma
Norman, Oklahoma 73019

and

Department of Environmental Sciences
University of Virginia
Charlottesville, Virginia 22903, USA

Summary

1. Few species from the tallgrass prairies exhibit compensation to herbivory while most species from the montane grasslands of Yellowstone National Park compensate for herbivory. This difference prompted the question whether plants which compensate may actually be competitively superior after herbivory.
2. Two grasses, *Andropogon gerardii* from the tallgrass prairie of Oklahoma and *Phleum pratense* from the montane grasslands of Yellowstone National Park, USA, were studied.
3. A labelled nitrogen fertilizer was applied to plants subjected to different clipping regimes. Procurement of labelled nitrogen from a distance equivalent to the species' competitive radius was equated to an active uptake rate of nitrogen. *Phleum pratense* showed significant uptake of labelled nitrogen when it was clipped while *Andropogon gerardii* showed uptake only when all of its surrounding neighbourhood was clipped, but it was left unclipped. Thus, species which compensate may be competitively superior following herbivory if the distance from which nitrogen is procured is an indication of the rate of uptake of nitrogen. A size-oriented hierarchy may be important for determining competitive dominance, although size was not significantly correlated with uptake of labelled nitrogen.
4. Knowledge of the mechanism of plant response to herbivory is necessary to make predictions of competitive interactions following grazing.

Key words: Andropogon gerardii, competition, grasslands, neighbourhoods, nitrogen uptake, Oklahoma, *Phleum pratense*, Yellowstone National Park

Introduction

Much theoretical work associated with plant competition has recognized that size is critical in determining plant success (e.g. el Moral, Clampitt & Wood 1985; Usmanov & Martynova 1989; Keddy & Shipley 1989; Gurevitch *et al.* 1990). Larger plants tend to procure a greater proportion of available nutrients and water from a given area than their smaller counterparts. Plants with large root systems are able to occupy a larger soil volume and hence could be superior competitors (Caldwell *et al.* 1987; Reichenberger & Pyke 1990), although root system structure is not highly dynamic in the short term (Coffin & Lauenroth 1990). Few studies have focused on the role of physiological activity of plants as a crucial component of competition (Austin 1982; Usmanov & Martynova 1988; Polley & Detling 1989). One way to do so would be to examine the competitive interactions of plants following grazing. After tissue loss to herbivores, some species have been found to compensate for that lost tissue by increases in photosynthetic rates, transpiration and nutrient uptake (McNaughton, Wallace & Coughenour 1983; Ruess 1984; Wallace, McNaughton & Coughenour 1984; Caldwell *et al.* 1987; Brown & Allen 1989). However, not all species are capable of these responses (Wallace 1987b, 1990).

Plant responses to simulated herbivory were examined by determining their abilities to procure stable isotopes of nitrogen from an NH_4SO_4 carrier placed some distance from the plant. Two disparate ecosystems were studied, the tallgrass prairie of Oklahoma and the mesic montane grasslands of Yellowstone National Park's northern range. The NH_4SO_4 carrier was chosen since the predominant form of nitrogen in many grasslands is ammonium (Clark 1977; Seagle, McNaughton & Ruess 1992). This is particularly true in the grasslands studied in Oklahoma (Smith & Rice 1983).

These two systems were chosen because of the different responses of their major plant species to grazing. In the tallgrass prairie, *Andropogon gerardii* Vitman (big bluestem) has been found not to compensate for herbivory (Wallace 1987a,b; Hartnett 1989). Thus, this species does not grow rapidly following tissue loss. In Yellowstone National Park, most of the dominant graminoids including an exotic grass, *Phleum pratense* (timothy), compensate for herbivory (Frank 1990; L. L. Wallace, submitted). Thus, following herbivory, *Andropogon gerardii* will not have enhanced growth rates and should, because of its reduced size, be a relatively poor competitor. The response of *Phleum pratense* should be enhanced rate of growth and nutrient uptake, thereby making it a superior competitor.

The hypotheses under consideration are:

1. After being grazed, plants which compensate for herbivory should be able to procure nitrogen located at the edge of their competitive radius (Tilman 1989) while plants which do not compensate will be unable to do so.
2. In situations when the majority of species do not compensate, smaller (grazed or clipped) plants should be less able to procure nitrogen from the edge of the competitive radius than large plants. Implicit within these hypotheses is the assumption that procurement of nitrogen placed some distance from the plant indicates that this individual is capable of rapid uptake of large quantities of nitrogen. This latter assumption was not tested in this study and is the subject of further work.

Materials and methods

To compare these two systems, the response of one of the dominant species in each was examined. *Andropogon gerardii* is a dominant matrix-forming species in the tallgrass prairie (Collins & Glenn 1991), while *Phleum pratense* is a highly invasive exotic species that has occupied large areas of Yellowstone's northern range (L. L. Wallace, personal observation) and has been found to be highly competitive in other studies (Taylor & Aarssen 1990). In order to determine how successful each of these species was in nutrient procurement, the size of the area from which each species procured nutrients, also termed its competitive radius (Tilman 1989), was determined. To do this, solutions of NH_4SO_4– ^{14}N 99.99% were placed in circles of different radii surrounding target plants of each species in their respective ecosystems. Note that this solution was depleted in the heavy isotope of nitrogen, ^{15}N. Hence, we measured and will discuss the procurement of ^{14}N throughout this report. The use of this type of label was a low-cost alternative to the use of ^{15}N-enhanced material. The radii. chosen were 110, 90, 70, 50 and 30 cm. Each radius was used around five replicate plants yielding a total sample of 30. Five control plants were also sampled, but no labelled fertilizer was added. Solutions were mixed and applied to yield a nitrogen concentration of 100 kg ha^{-1}. Morphological measurements were taken on the target plant prior to the addition of labelled fertilizer. These included leaf number, tiller number, basal circumference and height of the tallest live leaf. Plant volume was then calculated using basal circumference and height, assuming that the plant was a cylinder.

Plots were established at the same phenological stage in each ecosystem (late vegetative growth, early flowering). Three weeks following the establishment of each plot, samples (youngest leaf tissue) were harvested for ^{14}N analysis. All isotope analyses were done at the University of Virginia. Plant samples were dried and converted to CO_2, and N_2 for isotope analysis by the Dumas sealed-tube method as described by Macko *et al.* (1987). The dried sample powder was mixed with high-purity copper (Alpha Resources, Stevensville, Michigan, USA) and precombusted copper oxide in a quartz tube, which was then evacuated, sealed and combusted at 850° C for 1 h. The CO_2 and N_2 products were isolated cryogenically and analysed with a PRISM isotope ratio mass spectrometer (V. G. Isogas, Cheshire, UK). Uptake of the labelled fertilizer solution was indicated by enrichment of the light isotope in plant tissue relative to the level found in an atmospheric standard. Levels of ^{14}N enrichment in all plants in Yellowstone averaged –0.042% and 0.394% in Oklahoma. Significantly greater enrichment of ^{14}N was found in target plants with a 50-cm radius in Oklahoma (18.193%) and in target plants with a 30-cm radius in Yellowstone (0.384%). Calculations are outlined below. Therefore, the competitive radius of *Andropogon gerardii* was 50 cm while that of *Phleum pratense* was less than 30 cm. A 20-cm radius was chosen in the next experiment on *Phleum pratense* and a 50-cm radius for the experiments on *Andropogon gerardii.*

By using the competitive radius determined above as an indicator of the neighbourhood size in which a plant must compete, different clipping patterns were imposed within these neighbourhoods that could potentially lead to different competitive regimes. All plants had fertilizer solution deposited in either a 50- or a 20-cm radius around them (Fig. 1). Control plants (treatment C) were unclipped. In treatment T, the target plants (in the centre of the circle) were clipped to 10 cm above the ground. Treatment N plots had all neighbours within the 50- or 20-cm radius clipped 10 cm above the ground, but the target plant remained unclipped. Treatment TN had both target and neighbours clipped. Prior to clipping, morphological measurements were taken on the target plant as described above. Community structure data (per cent cover) were taken within the competitive radius. These treatments were imposed upon plants 6 weeks following the experiment described above.

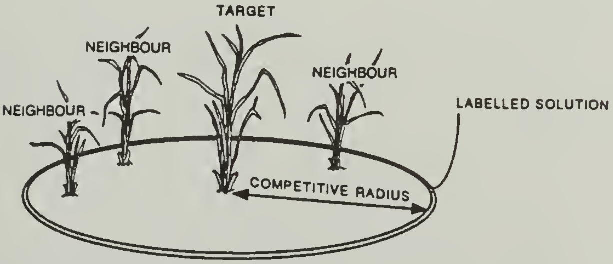

Fig. 1. Diagram of the placement of target and neighbour plants in relation to the labelled fertilizer solution.

Three weeks following the clipping treatments and fertilizer addition, tissue aliquots were taken from target plants and from a conspecific neighbour in the outer portion of the plot. This latter plant will be referred to as 'the neighbour'. Samples were analysed for ^{14}N as before.

All target plants were later harvested to determine biomass and biomass allocation. Following harvest, all plants were separated into the components of above-ground tissue, crowns and roots. These components were then oven dried at 60° C for 24 h and weighed.

Statistical analyses were performed using SAS. Proportional data were subjected to arcsine square root transformation prior to analysis. Raw signal data were transformed into per cent enrichment of ^{14}N using the formula,

$$\delta\,^{14}N = [R(\text{sample})/R(\text{standard}) - 1] \times 1000$$

where $R = {}^{15}N/{}^{14}N$ and solving for sample ^{14}N, assuming R(standard) = 0.366/99.634 (Coleman & Fry 1991). Atmospheric nitrogen was used as the standard. For comparisons of label acquisition between treatments, all sample values were standardized by subtracting the standard ^{14}N value from them, thus yielding a ^{14}N enrichment value relative to the standard. Data were examined using one-way Student's *t*-tests for comparison. Values which were significantly different from zero were deemed indicative of an acquisition of labelled nitrogen since the average values of untreated plants (–0.189 in Yellowstone and 0.164 in Oklahoma) were not significantly different from zero. Morphological, biomass and community structure data were compared between treatments using one-way ANOVA. Linear regressions were used to determine if there was any relationship between the acquisition of labelled fertilizer and plant size (total biomass).

Results

YELLOWSTONE ECOSYSTEM— *PHLEUM PRATENSE*

Comparisons of the cover values for the five most frequently occurring species yielded no significant differences between plots. Thus, neighbourhood structure was similar for all plants and was characterized by areas dominated by *Phleum pratense* (average 21.5% cover), followed in importance by *Poa pratense, Frageria virginiana. Geranium viscosissimum and Potentilia arguta* [nomenclature follows Hitchcock & Cronquist (1976)]. Also, no significant differences were found in plant morphology of the *Phleum pratense* targets prior to treatment (average leaf number, 26; tiller number, 7, circumference, 22.6 cm; height, 39.5 cm; volume, 909.2 cm^3).

The pattern of labelled fertilizer appearing in both target and neighbour plants did show significant differences among treatments (Fig. 2). The target plant in a clipped neighbourhood showed significant ^{14}N enrichment as did the neighbour plants in a completely clipped plot. In plots where the neighbours only were clipped, those neighbours also were enriched in ^{14}N. Clipping only the target yielded no significant differences from control values of ^{14}N.

Biomass allocation was not consistently affected by the treatments (Table 1). Although clipped biomass was not measured, it is estimated that approximately 20% of the total plant biomass was removed since the plants were clipped to 10 cm (estimate from V. Moorthy and L. L. Wallace, in preparation). In the treatments where the target was clipped, above-ground biomass was not significantly different from control values. This indicates that there was either a transfer of biomass from below-ground components or growth compensated for tissue loss due to clipping. Since the amount of biomass allocated to roots was not significantly different among treatments and the amount of biomass allocated to crowns was highest in these treatments, then compensatory growth did occur. Regression analysis of the per cent enrichment of ^{14}N in plant tissue with total biomass yielded no significant correlations. Thus, size was not a good predictor of whether or not the plant was able to procure nitrogen placed at the edge of its competitive radius over the time span of these treatments.

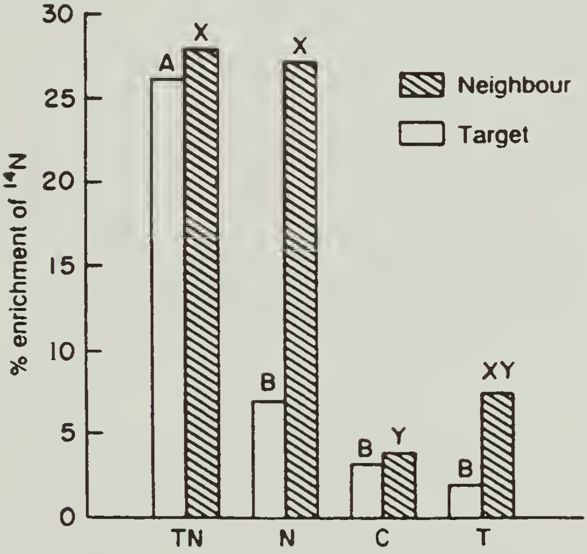

Fig. 2. Enrichment of sample ^{14}N content in both target plants and conspecific neighbours of *Phleum pratense* in Yellowstone National park. Values for: target plants (☐); neighbour plants (▧). Treatment codes: C, control, no clipping; T, target plant clipped; N, neighbouring plants clipped; TN, both target and neighbours clipped. The neighbourhood size was a circle with a radius of 20 cm. Means labelled with either a 'B' or 'Y' are not significantly different from zero.

OKLAHOMA ECOSYSTEM—*ANDROPOGON GERARDII*

Similar comparisons of the most frequently occurring species in this system also yielded no significant difference in community structure between plots. These plots were strongly dominated by *Andropogon gerardii* (average cover, 61%), followed in dominance by *Schizachyrium scoparium, Aster ericoides and Schrankia nuttallii* [nomenclature follows Correll & Johnston (1979)]. There were no significant differences between treatments in pretreatment target plant morphology (average leaf number, 6; tiller number, 2; circumference, 4.6 cm; height, 73.3 cm; volume, 328.2 cm^3).

The pattern of fertilizer acquisition was, however, quite different from the Yellowstone ecosystem (Fig. 3). The enrichment of ^{14}N in target plants was not significantly different from that in controls except where the neighbours were clipped. The per cent enrichment in the neighbours was also greatest where the neighbours were clipped.

Table 1. Allocation to different biomass components as affected by treatment

Site	Treatment			
Component	C	N	T	TN
YNP				
Above ground	0.236^{ab}	0.282^{a}	0.206^{ab}	0.152^{b}
Crown	0.499^{b}	0.575^{ab}	0.650^{a}	0.467^{b}
Roots	0.219^{a}	0.219^{a}	0.198^{a}	0.296^{a}
Total	20.6^{a}	14.5^{a}	11.0^{a}	20.6^{a}
OK				
Above ground	0.350^{a}	0.288^{a}	0.257^{a}	0.332^{a}
Crown	0.301^{b}	0.387^{ab}	0.488^{a}	0.364^{ab}
Roots	0.348^{a}	0.325^{a}	0.245^{a}	0.305^{a}
Total	7.3^{ab}	7.5^{ab}	11.2^{a}	3.2^{b}

Means followed by the same superscript letter within a row are not significantly ($P \leq 0.05$) different from one another, Duncan's Multiple Range Test. Treatment codes are: C, control; N, neighbouring plants only clipped; T, target plant only clipped; TN, target and neighbouring plants clipped. Total values are in g $plant^{-1}$.

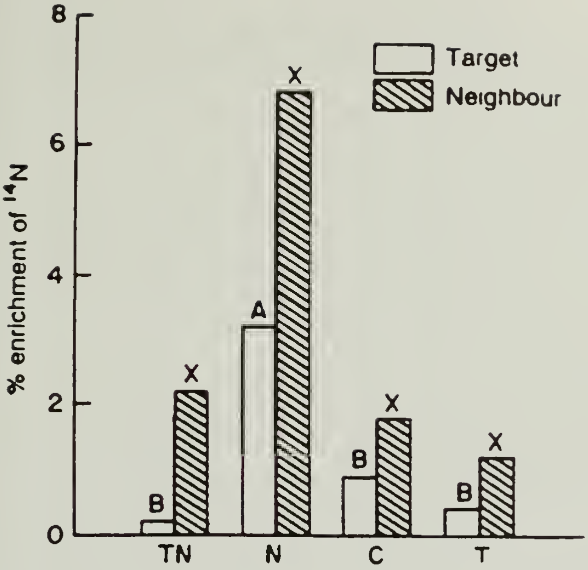

Fig. 3. Enrichment of sample ^{14}N content in both target plants and conspecific neighbours of *Andropogon gerardii* in Oklahoma. Treatment codes and labelling as in Fig. 2. The neighbourhood size was a circle with a radius of 50 cm.

Biomass allocation showed no consistent patterns, with no significant treatment effects on allocation to either roots or above-ground tissues (Table 1). There was a significant reduction in total biomass, however, in plants where both the target and neighbours were clipped. Since there was no significant reduction of biomass in the treatment where the target alone was clipped, it appears that this treatment compensated for herbivory while clipping the neighbours in addition caused an undercompensation. Regression analysis of target plant ^{14}N enrichment with biomass yielded no significant correlation, indicating that size was not a good predictor of short-term nitrogen uptake from the edge of the competitive radius of each plant.

Discussion

Given the large values of ^{14}N enrichment measured in the second series of experiments, the competitive radius of *Phleum pratense* appears to be 20 cm. The competitive radius of *Andropogon gerardii* was 50 cm. These radii are both smaller than the 70-cm radius reported by Tilman (1989) for *Schizachyrium scoparium* growing in sandy soils. As the soils in this study were well drained but clayey, the smaller radius may be because of this. Indeed, competitive radius is strongly influenced by soil texture and porosity (Whitehead and Bristow 1990), and the rooting morphology of the individual. Since root morphology was not directly determined in this study, the acquisition of labelled nutrients placed some distance from a target plant can yield an indirect measure of the competitive radius.

The two experiments occurred at slightly different phenological stages although the phenological stage was comparable for each experiment between ecosystems. In the first experiment (determination of competitive radius size), the phenological stage was late vegetative, early flowering. Growth rates are usually quite high at this stage in both ecosystems. However, due to the time period required for sample analysis, the second experiment examining the effects of clipping patterns on the spatial pattern of nitrogen procurement was not carried out until mid-flowering phenophase in both experiments. This may account for the lack of fertilizer acquisition by the control plants in both systems, since growth rate and presumably nitrogen uptake are both lower in this phenophase.

The two species responded quite differently to the clipping patterns used. Movement of ^{14}N in the Yellowstone system was highly dependent upon the clipping status of the individual plant. Even neighbours which were closest to the labelled nitrogen did not show significant acquisition of signal when they were unclipped. Therefore, it appears that an increase in nutrient uptake occurred with clipping. Plants which compensate for tissue loss with increased growth require increased nutrient uptake to support that growth (Ruess 1984; Caldwell *et al.* 1987; Usmanov and Martynova 1988); these clipped plants have apparently increased their uptake while unclipped plants have not. However, we can also see that clipping only one plant, the target, does not allow that plant, even though its uptake rate was increased, to become sufficiently competitive to procure labelled fertilizer in the midst of an unclipped neighbourhood.

In the tallgrass prairie, a different picture is presented by the response of *Andropogon gerardii*. Clipped neighbours do appear to be stronger competitors for labelled fertilizer than the target, even when the target is clipped. This is probably due to their closer proximity to the labelled nitrogen (Fig. 1). Indeed, clipping the target appears to put it at a competitive disadvantage since only the unclipped target in a clipped neighbourhood showed significant fertilizer acquisition. The cause of this response is unknown, but it appears that only clipped plants in the immediate proximity to labelled nitrogen are able to procure it. Clipping may reduce the size of the competitive radius of clipped plants in this ecosystem. Thus, it appears that clipping single plants of *Andropogon gerardii* puts them at a competitive disadvantage regardless of neighbourhood clipping status. Distance to the labelled fertilizer and a size-related competitive hierarchy may be important in this case (Grace 1985; Hartnett 1989).

The lack of ^{14}N acquisition suggests that plants which are clipped in isolation in the tallgrass prairie operate at a deficit following tissue loss. Analysis of the total biomass data (Table 1) alone does not lead to this conclusion since these plants had the highest total biomass. One interpretation of this is that ^{14}N was diluted by the large tissue mass of these plants. However, in Yellowstone, conclusions drawn on total biomass alone agree with the conclusions drawn on fertilized acquisition. Thus, the rapid growth of compensating plants was accompanied by a concomitant rapid rate of nutrient uptake and no dilution of ^{14}N is seen. This is supported by nitrogen mass studies which show an increase in the nitrogen content of grazed plants in this system (Coughenour 1991). This increase in the rate of nitrogen uptake means that grazed plants would have a lower R^* (*sensu* Tilman and Wedin 1991), and should be superior competitors. (R^* refers to the lowest level in the soil to which a species is able to drop a nutrient concentration. Therefore, species with low R^* values can draw soil nitrogen down further than species with higher values.)

Since most of the graminoid species in Yellowstone compensate for tissue loss (Frank 1990; L. L. Wallace, submitted for publication), then a size related hierarchy would not be critical in plant acquisition of limited nutrients immediately following herbivory. The relative sink strength of different plants based on plant uptake rates and regrowth would be more critical. The commonly stated assertion that grazing or mowing eliminates the competitive superiority of dominants (Parish et al. 1990) may not be entirely true if the dominant species compensate for herbivory. Since compensation is rare in the tallgrass prairie, a more classical size-related hierarchy would be important, with large plants (in this case presumably unclipped plants) able to procure nitrogen from the edge of their competitive radius when surrounded by smaller (clipped) plants. The distance of plants from one another and from the labelled nitrogen is also critical (Mack and Harper 1977). In this case the competitive superiority of the dominants would be eliminated by grazing as expected (Louda et al. 1990; Parish et al. 1990).

Although the ultimate result of herbivory in both systems would be the same (the maintenance of higher species diversity), the mechanisms whereby this result is achieved are very different. If one is to make predictions concerning species competitive interactions and community composition, mechanistic models that define the type of competitive responses are necessary (Tilman 1987). In systems with a high proportion of compensating species, herbivory may enhance diversity because of increasing the competitive status of the grazed plants. In systems without many compensating species, herbivory will decrease the competitive status of grazed plants, thereby allowing ungrazed plants to become competitively superior.

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Late Holocene Mammalian Fauna of Lamar Cave and its Implications for Ecosystem Dynamics in Yellowstone National Park, Wyoming

Elizabeth Hadly Barnosky

Department of Integrative Biology
University of California
Berkeley, California 94720

and

National Park Service
Division of Research
P.O. Box 168
Yellowstone National Park, Wyoming 82190

Abstract. Lamar Cave, a late Holocene paleontological site in Yellowstone National Park, Wyoming, has yielded 36 fossil mammal species from 10 stratigraphic units representing 1,700 years. Approximately 10,000 bones, including fish, amphibians, reptiles, birds, and mammals have been recovered and about 1,600 mammalian specimens have been identified at least to genus. Only the mammals are discussed. The fossil fauna is similar to the mammals in the park today and affords a unique opportunity to investigate paleocommunity and ecosystem dynamics through time. Environmental interpretations are based on the small mammal fauna found in the cave. Voles (*Microtus* sp.) dominate the small mammal assemblage of the oldest excavation levels—about 1695 B.P. 60 years. Sometime before 960 B.P. 60 years, vole percentages began to decline gradually relative to ground squirrel (*Spermophilus* sp.) percentages. This trend continues until ground squirrels dominate the small mammal assemblage by 960 B.P. 60 years. The occurrence of the prairie vole (*Microtus ochrogaster*) an extralimital species today, is limited to deposits in the cave older than 960 B.P. 60 years. The presence of this species and the trends in relative abundances of small mammals, particularly the inverse relations between voles and ground squirrels, are interpreted as evidence of declining grass cover near Lamar Cave between approximately 1,500 and 1,000 years ago. Support for this hypothesis is found in a pollen record from a nearby lake in northern Yellowstone National Park. Elk (*Cervus elaphus*) and wolf (*Canis lupus*) are both present in the Lamar Cave faunal record before 1,000 years ago, which provides evidence supporting the presence of these species before the influence of Europeans.

Key words: Climate, community, mammals, paleontology, vertebrates.

I describe a record of mammalian faunal changes over the past 1,700+ years in northern Yellowstone National Park, Wyoming. Faunal remains were excavated from Lamar Cave, a newly discovered paleontological site. Environmental interpretations are based on the site, which includes 10 stratigraphic levels and represents more than 3 m^3 of excavated cave fill. The Lamar Cave fauna is of interest because Holocene paleontological sites in the northern Rockies have received little study, and no Holocene faunal record has been described for Yellowstone National Park. Furthermore, the Lamar Cave faunal remains offer a unique opportunity to study the dynamics of a continuously functioning ecosystem during the past two millennia.

Reports of fossil vertebrates are rare from the northern Rocky Mountains, as are Holocene paleontological sites in general (Semken 1983). Species of particular interest are elk (*Cervus elaphus*), wolf (*Canis lupus*), and beaver (*Castor canadensis*), whose prehistoric occurrence and abundance in the Yellowstone area are a matter of debate (i.e., Frison 1978; Wright and Reeve 1981; Chase 1986; Despain et al. 1986; Kay 1987). I addressed specific questions referring to the presence or absence of these species.

Ecosystem perturbations can occur over both the short term (tens to hundreds of years) and long term (thousands to millions of years). Studies of relatively short-term changes may form a baseline for comparisons of modern ecosystem fluctuations: for example, evaluating the effect of human disturbances. Late Holocene studies also may provide a better understanding of the time frame and record completeness necessary to resolve and interpret evolutionary and ecological change.

My objectives in this study are to

1. document the mammalian species recovered from Lamar Cave;
2. interpret the significance of the faunal record for the modern Yellowstone ecosystem; and
3. evaluate the potential contribution of a late Holocene faunal assemblage to biology and paleontology.

Setting of Lamar Cave

Lamar Cave is located in northwestern Yellowstone National Park at 1,860 m. Elevation within 1 km of the cave varies from 1,830 to 1,950 m. The cave is shallow, with maximum dimensions of 6.2 m depth, 3.7 m width, and 2 m height; the entrance is 1.5 m high and 2.6 m wide. The cave is located on a south-facing slope along the Lamar River. Initial cave formation probably occurred with catastrophic flooding during deglaciation more recent than 14,000 B.P. (Hadly 1990).

A short gully (48 m long) immediately west of the cave focuses silty glacial till and rock fragments downslope into a small debris cone. The debris cone merges with talus from the cliff to form a slope in front of the cave rising 0.5 m above the interior floor. Episodic rainstorms channel fine-grained matrix from the gully into the cave. These deposits bury the exposed cave floor, thus providing clear stratigraphic markers between vertical units. The present cave floor is about 7 m above bank full river level.

Vegetation in the vicinity of Lamar Cave is a complex of microhabitats and ecotones. The predominant vegetation type is sagebrush–grassland that is dominated by sagebrush (*Artemisia tridentata*) and Idaho fescue (*Festuca idahoensis*) with isolated stands of Douglas-fir (*Pseudotsuga menziesii*). Douglas-fir is also present as both closed and open forest types. Mesic grasslands, aspen (*Populus tremuloides*) stands, limber pine (*Pinus flexilis*) in xeric habitats, and riparian areas with cottonwoods (*Populus* sp.), alder (*Alnus* sp.), and willow are all found within 2 km of the cave.

Methods

During summer 1987 and 1988, a single 1- × 2-m test pit in Lamar Cave was excavated with trowels to a depth of 170 cm. The alternating organic and inorganic layers were excavated as natural stratigraphic units. Inorganic layers were consolidated alluvial units that held smooth pit walls during excavation and allowed for clear distinction between levels. During excavation, no bioturbation was noted between organic levels separated by inorganic levels. Level numbers (1–10, top to bottom) were assigned to each unit.

All excavated material was washed through 1-mm mesh screen and dried in the field (except for level 1 and level 2, which were screened through 3-mm mesh). Fine matrix (between 1 and 3 mm) was sorted in the lab. Identifications of mammalian faunal remains were based on comparisons with museum collections at The Carnegie Museum of Natural History, Pittsburgh, and Museum of Northern Arizona, Flagstaff. Identification of all bones from large mammals was attempted, while only cranial material from small mammals was identified. A complete discussion of excavation techniques and identification criteria is found in Hadly (1990). All the Lamar Cave specimens, including mammals and yet-unidentified fish, amphibians, reptiles, and birds, will be reposited in the Yellowstone National Park Museum collections. Only the mammals are included in this analysis. Although the Lamar Cave test pit has been excavated to 170 cm, at least 1 m of fill was excavated during 1991–92.

Minimum number of individuals (MNI; Grayson 1973, 1978, 1979; Klein and Cruz-Uribe 1984) and species percentages were calculated for each level and used to appraise faunal change for the Lamar Cave deposits. Because the inorganic units are thought to represent instantaneous events and because they are relatively devoid of bone (MNI), level 2 and level 4 were lumped with level 3 and level 5, respectively, for percentage comparisons by level and interpretation based on the faunal remains (Hadly 1990). For taxa larger than members of Leporidae (rabbits and hares), any identifiable skeletal material was used to calculated MNI. For members of Cricetidae (murid rodents), Soricidae (shrews), Sciuridae (squirrels), Geomyidae (pocket gophers), Zapodidae (jumping mice), and Vespertilionidae (bats), MNI was based on identifiable dental material, particularly molars.

Results

Stratigraphy

Inorganic alluvial units, the majority of the Lamar Cave sediments, are predominantly silt and sand that were deposited rapidly from episodic, severe rainstorms washing material into the cave from the gully outside. These fine-grained, instantaneous gully deposits bury the organic remains, incorporating a few bones from the underlying organic unit. No evidence of erosion was found. Roof-fall is rare in these alluvial units.

The organic units are composed primarily of irregularly bedded duff, abundant roof-fall, and bones. Relative to the alluvial units, the organic units increase in thickness toward the rear of the cave, where the alluvial units are thin and sometimes discontinuous. The organic units are relatively thin at the front of the test pit. The cave floor is currently littered with roof-fall, wood, plant fragments, bone, feathers, hair, dung, shell, and conifer cones. This type of an accumulation, in varying degrees of preservation, is presumed to make up the bulk of the organic layers.

Taphonomy

Taphonomy refers to the sequence of events that occur to an animal's remains after death. Broadly speaking, this means everything that occurs to an animal from death to discovery (Olson 1980). Observations of woodrat (*Neotoma cinerea*) activity in the cave include sightings of the animals, presence of middens, and cemented urine deposits or amberat curtains. The similarity of the modern cave-floor accumulation to the fossil deposits strongly suggests that the main collection agents for bones have been woodrats, that take bone-laden scats of mammalian predators and raptors from a 100-m radius of the nest, as well as bones from decomposed carcasses, into their nests. This is corroborated by remains of woodrats found in every organic level of Lamar Cave.

The size and preservation of the small mammal bones indicate that most of the fossil material passed through the digestive tracts of diurnal and nocturnal raptors and mammalian carnivores (Mayhew 1977; Korth 1979; Hoffman 1988; Hadly 1990). This combination of taphonomic vectors is thought to yield a good representation of the small mammals in the vicinity of the accumulation (Korth 1979). Therefore, the spatial area sampled is, at most, the foraging area of the predators, presumed to be about 5–10 km (e.g., Newton 1979; Burn et al. 1982). Today within this radius of Lamar Cave are habitats suitable for all the animals found as fossils in the upper units of the deposit. No evidence of human use of the cave has been found.

Age of the Deposits

Three radiocarbon samples from Lamar Cave were submitted to Beta Analytic, Inc., for age determination by both conventional and Accelerator Mass Spectrometry (AMS) techniques. The radiocarbon age for a piece of wood from level 3 was 80 B.P. 110 years (Beta-24418; ETH-3675). Charcoal from level 5 and level 10 was dated at 960 B.P. 60 years (Beta-23031) and 1695 B.P. 60 years (Beta-30016; ETH-5044), respectively. These dates are consistent with the stratigraphic sequence and are expected for a late Holocene fauna from Yellowstone.

Description of Fauna

The mammalian faunal remains recovered from Lamar Cave span approximately 1,700 years and represent 6 orders, 14 families, 27 genera, and 36 species (Table). Of approximately 10,000 bones from 10 units, 1,600 mammalian bones consisted of mainly teeth (small mammals) and miscellaneous appendicular elements (large animals) which were identifiable to at least generic level. The Lamar Cave fossil record seems to adequately represent the local mammals for a variety of reasons. Discounting bats, 60% of the mammal species present in the entire park today are found as fossils in most levels of Lamar Cave. This percentage would be considerably higher if only species found within 5 km of the cave were counted, because virtually all of the species living in the vicinity of Lamar Cave are found as fossils in the deposits.

Except for the prairie vole (*Microtus ochrogaster*), no anomalous taxa (such as high-altitude mammals) are in the Lamar Cave assemblage, and the fossil fauna shows ratios of mammalian groups that are generally similar to the ratios of these groups in the living fauna. Small mammal remains in each level of Lamar Cave constitute 71–97% of the fossil fauna, herbivores 2–18%, and carnivores 0–12%. Other North American caves that are not natural traps have percentages of carnivores that range from 0–11% of the fossil fauna (White et al. 1984). These conditions

Table. Late Holocene Mammalian Species from Lamar Cave, Yellowstone National Park, Wyoming. Number of identified specimens (NISP) in parentheses.

Order INSECTIVORA Bowdich, 1821	
Family Soricidae Gray, 1821	
Genus *Sorex* Linnaeus, 1758	
Sorex cinereus Kerr, 1792	Masked shrew (1)
Sorex cf. *vagrans* Baird, 1858	Vagrant shrew (10)
Sorex palustris Richardson, 1828	Water shrew (2)
Sorex merriami Dobson, 1890	Merriam's shrew (1)
Sorex hoyi Baird, 1858	Pygmy shrew (5)
Sorex sp.	Long-tailed shrew (7)
Order CHIROPTERA Blumenbach, 1779	
Family Vespertilionidae Gray, 1821	
Genus *Myotis* Kaup, 1829	
Myotis sp.	Mouse-eared bat (2)
Order LAGOMORPHA Brant, 1855	
Family Leporidae Gray, 1821	
Genus *Sylvilagus* Gray, 1867	
Sylvilagus cf. *nuttallii* Bachman, 1837	Mountain cottontail (2)
Sylvilagus cf. *audubonii* Baird, 1857	Desert cottontail (1)
Sylvilagus sp.	Cottontail (1)
Genus *Lepus* Linneaus, 1758	
Lepus americanus Erxleben, 1777	Snowshoe hare (2)
Lepus townsendii Bachman, 1839	White-tailed jackrabbit (13)
Cf. *Lepus*	Jackrabbit (6)
Order RODENTIA Bowdich, 1821	
Family Sciuridae Gray, 1821	
Genus *Eutamias* Trouessart, 1880	
Eutamias sp.	Chipmunk (14)
Genus *Marmota* Blumenbach, 1779	
Marmota cf. *flaviventris* Audubon and Bachman, 1841	Yellow-bellied marmot (33)
Genus *Spermophilus* Cuvier, 1825	
Spermophilus richardsonii Sabine, 1822	Richardson's ground squirrel
or	
Spermophilus armatus Kennicott, 1863	Uinta ground squirrel (226)
Spermophilus sp.	Ground squirrel (4)
Genus *Tamiasciurus* Trouessart, 1880	
Tamiasciurus hudsonicus Erxleben, 1777	Red squirrel (11)
Family Geomyidae Gill, 1872	
Genus *Thomomys* Wied-Neuwied, 1839	
Thomomys talpoides Richardson, 1828	Northern pocket gopher (95)
Family Castoridae Gray, 1872	
Genus *Castor* Linnaeus, 1872	
Castor canadensis Kuhl, 1820	Beaver (1)
Family Cricetidae Rochbrune, 1883	
Subfamily Cricetinae Murray, 1866	
Genus *Peromyscus* Gloger, 1841	
Peromyscus cf. *maniculatus* Wagner, 1845	Deer mouse (144)
Genus *Neotoma* Say and Ord, 1825	
Neotoma cinerea Ord, 1815	Bushy-tailed woodrat (71)
Subfamily Microtinae Miller, 1896	
Genus *Clethrionomys* Tilesius, 1850	
Clethrionomys cf. *gapperi* Vigors, 1830	Red-backed vole (9)
Genus *Phenacomys* Merriam, 1889	
Phenacomys intermedius Merriam, 1889	Heather vole (30)
Genus *Microtus* Shank, 1798	
Microtus pennsylvanicus Ord, 1815	Meadow vole (48)

Table. *Continued.*

Microtus montanus Peale, 1848	Montane vole (87)
and/or	
Microtus longicaudus Merriam, 1888	Long-tailed vole
Microtus ochrogaster Wagner, 1842	Prairie vole (7)
Microtus sp.	Vole (313)
Genus *Ondatra* Link, 1795	
Ondatra zibethicus Linnaeus, 1766	Muskrat (14)
Family Zapodidae Coues, 1876	
Genus *Zapus* Coues, 1876	
Zapus cf. *princeps* J. A. Allen, 1893	Western jumping mouse (8)
Order CARNIVORA Bowdich, 1821	
Family Canidae Gray, 1821	
Genus *Canis* Linnaeus, 1758	
Canis latrans Say, 1823	Coyote (9)
Canis lupus Linnaeus, 175	Grey wolf (2)
Canis sp.	Coyote or wolf (1)
Genus *Vulpes* Bowdich, 1821	
Vulpes vulpes Linnaeus, 1758	Red fox (2)
Family Ursidae Gray, 1821	
Genus *Ursus* Linnaeus, 1758	
Ursus arctos Linnaeus, 1758	Grizzly bear (1)
Family Mustelidae Swainson, 1835	
Genus *Mustela* Linnaeus, 1758	
Mustela cf. *frenata* Lichtenstein, 1831	Long-tailed weasel (5)
Genus *Taxidea* Waterhouse, 1838	
Taxidea taxus Schreber, 1778	Badger (1)
Genus *Mephitis* E. Geoffroy Saint-Hilaire and G. Cuvier, 1795	
Mephitis mephitis Schreber, 1776	Striped skunk (1)
Order ARTIODACTYLA Owen, 1848	
Family Cervidae Gray, 1821	
Genus *Cervus* Linnaeus, 1758	
Cervus elaphus Linnaeus, 1758	Elk (28)
Family Antilocapridae Gray, 1866	
Genus *Antilocapra* Ord, 1818	
Antilocapra americana Ord, 1818	Pronghorn (4)
Family Bovidae Gray, 1821	
Genus *Bison* Hamilton-Smith, 1827	
Bison bison Linnaeus, 1758	Bison (2)
Genus *Ovis* Linnaeus, 1758	
Ovis canadensis Shaw, 1804	Bighorn sheep (6)

indicate whatever the taphonomic bias of Lamar Cave, it seems to have been consistent through time and allows meaningful level-by-level comparisons.

Discussion

Small Mammals

In a small mammal trapping survey, using both live and snap traps, Streubel (D. P. Streubel, Yellowstone National Park, Unpublished 1984 and 1985 reports on small mammals research) found that each of 11 microhabitats was associated with different percentages of chipmunks (*Eutamias* sp.), ground squirrels, deer mice (*Peromyscus maniculatus*), red-backed voles (*Clethrionomys gapperi*), heather voles (*Phenacomys intermedius*), voles (*Microtus* sp.), and jumping mice (*Zapus princeps*). In general, voles were associated with more mesic sites, including riparian–grass, aspen understory, and moist sagebrush–grassland. Vole percentages were lower in an alpine meadow, a mixed sagebrush–Douglas-fir–riparian association, and a dry sagebrush–grassland. Jumping mice dominated the small mammal assemblage in the alpine meadow but were present in small percentages in most mesic sites. Chipmunks and red-backed voles were associated with forested areas and the alpine meadow. The ground squirrel was found only in dry sagebrush–grasslands of northern Yellowstone National Park and a low elevation river bottom with a cottonwood canopy and dry sagebrush–grassland nearby. It is likely that small mammal trapping underrepresents ground squirrel percentages (D. P. Streubel, Yellowstone National Park, personal communication). Streubel's (D. P. Streubel, Yellowstone National Park, Unpublished 1984 and 1985 reports on small mammals research) trapping data are used as the interpretive framework for the Lamar Cave mammalian fauna.

Extralimital Species

The Lamar Cave mammalian record includes at least one species and perhaps two that are not present in Yellowstone National Park today. The prairie vole has not been found in the park, despite trapping efforts that should have located this species if it was present (D. P. Streubel, Yellowstone National Park, personal communication). The closest occurrence of the prairie vole is north of the park near Billings, Montana (Hoffman and Pattie 1968; Hall 1981). It prefers open grasslands without shrubs as codominants. In a study of small mammals in grassland ecosystems, the prairie vole was found only in tall and midgrass prairies (French et al. 1976). The presence of this species in the Lamar Cave fauna suggests the likelihood of an environment different than today's in the vicinity of the cave during the time represented by levels 9–10.

According to Hall (1981), the pygmy shrew (*Sorex hoyi*) is not found in the Yellowstone area today. The closest record of this species is north of the park along the Rocky Mountains; however, trapping attempts in this area for this species have been meager (K. Foresman, personal communication, 1989). Therefore, the presence of the pygmy shrew in the Lamar Cave fauna does not necessarily indicate environmental change.

Mammalian Species

Among small mammals in the Lamar Cave record, percentages of pocket gophers, deer mice, tree squirrels, chipmunks, and woodrats are relatively stable. There is little change among the carnivores and ungulates. Shrews are absent above level 6, which is probably the result of the size of the screen used in excavation rather than to environmental variables. A shift in dominance between voles and ground squirrels occurred in the Lamar Cave record sometime after 1700 B.P. and before 1000 B.P. (Figure). At level 9, voles dominated the small mammal assemblage, and ground squirrels are found in lesser percentages. Between level 9 and level 6, there is a subtle and gradual decline in vole percentages and a corresponding increase in ground squirrels. At levels 4 and 5, ground squirrels dominate the faunal assemblage, while voles are found in lower percentages. This change reverses by levels 2 and 3.

Two mesic grassland affiliates, the prairie vole and the jumping mouse, are present in only the lower levels—the prairie vole drops out at level 8; the jumping mouse drops out at level 7. Percentages of the woodrat, a mammal that is not particularly environmentally sensitive, remain constant throughout the Lamar Cave record. According to the evidence from Streubel (D. P. Streubel, Yellowstone National Park, Unpublished 1984 and 1985 reports on small mammals research) and others (French et al. 1976; Grant and Birney 1979; McGee 1982), the total Lamar Cave small mammal fauna represents a habitat with a dry sagebrush–grassland including some forest cover and probably a riparian zone with some moister grasslands nearby. This is in agreement with vegetation near the site today. Even with inherent biases in the small mammal trapping surveys, as well as potential taphonomic biases in the faunal collection from Lamar Cave, these two independent records are

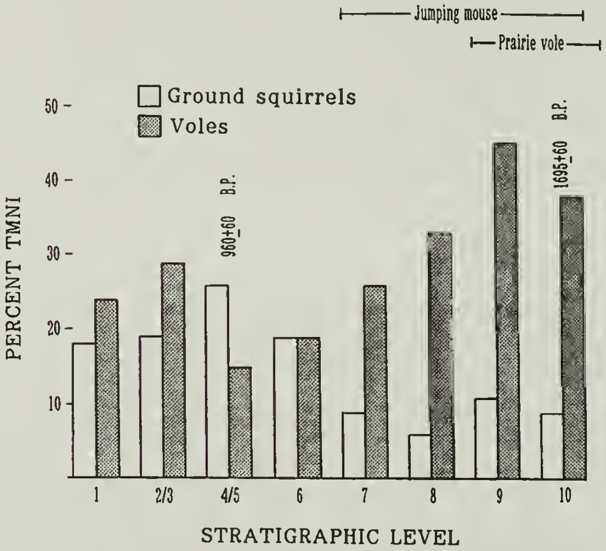

Figure. Relative abundance fluctuations of ground squirrels (*Spermophilus* sp.) and voles (*Microtus* sp.) as determined by percent TMNI by stratigraphic level (Top = 1; Bottom = 10), Lamar Cave, Yellowstone National Park, Wyoming.

in general agreement with regard to species' affinities to grasslands of differing moisture regimes.

Vegetation Change

Small mammal biomass and composition in grasslands of different moisture conditions today are found to vary significantly and to reflect differences in vegetational composition as grasslands grade from a mesic tallgrass prairie to xeric desert grassland (Grant and Birney 1979). This reflects a variance in small mammal habitat requirements, including cover, forage quality, and moisture availability. Belk et al. (1988) found that the red-backed vole (*Clethrionomys gapperi*) and the montane vole (*Microtus montanus*) preferred more canopy and herbaceous cover than did deer mice (*Peromyscus maniculatus*) and jumping mice (*Zapus princeps*), but the jumping mouse requires adequate grass and forb cover for nesting and as protection from predators (McGee 1982).

Evidence from mid-grass prairies of the Great Plains suggests that where mesic grassland is receding north, the herbivores (voles) are replaced by granivores and omnivores (squirrels and others; French et al. 1976). Experimental plot manipulation showed increasing voles when grassland was watered artificially and cover increased (French et al. 1976). Voles generally prefer habitats with increased grass cover, while squirrels do not require dense cover. This is supported by the small mammal trapping study done by Streubel (D. P. Streubel, Yellowstone National Park, Unpublished 1984 and 1985 reports on small mammals research) in Yellowstone. The faunal change in Lamar Cave is therefore interpreted to be a decline in grass density because of the observed abundance changes between these taxa. A decline in grass density may be the result of a variety of factors including climate, soil, fire frequency, topography, and population dynamics of the animals dependent on vegetation for food.

Climate

Climatic influences on vegetation include precipitation and temperature, both as long-term averages as well as minima and maxima over daily and seasonal time frames. Seasonality affects availability and production of vegetation, which is especially important for animals consuming the vegetation. Effective moisture and length of growing season are also important effects of climate. Density of vegetation (cover) depends primarily on mean annual precipitation (Grant and Birney 1979). Groundwater levels may ameliorate yearly fluctuations in effective moisture but may incorporate long-term climatic changes. Because groundwater is an important variable in maintaining water levels in small closed basins, the increase or decrease in water level in a kettle may influence the amount of sedges and grasses available on lakeshores.

In an experimental manipulation of a xeric grassland plot, the addition of water and fertilizer caused a change in vegetation structure, an increase in grass density, and an increase in voles (*Microtus* sp.) as the dominant member of a small mammal community (French et al. 1979). The effects of climate change on faunal populations, however, may not necessarily be expressed through the flora. Vegetation may lag 80–200 years behind climate change (Bryson et al. 1970). Snow depth, dry season moisture availability, and minimum winter temperatures may act in concert with vegetation to influence faunal populations; and in turn, faunal populations can influence the flora. For example, winter-killed elk in the 1988–89 season amounted to one-fourth the herd in northern Yellowstone and succumbed chiefly because of summer drought in 1988 combined with prolonged extremely cold temperatures in early 1989 (Singer et al. 1989).

The pollen record from Blacktail Pond, located 15 km west of Lamar Cave, suggests that climate change over a longer term time scale also affected the vegetation in northern Yellowstone (Gennett 1977). The data show an increase in grass about 1600 B.P., and Gennett (1977) postulates this was because of climatic cooling. After 1300 B.P., Gramineae declined, perhaps because of increasing temperatures or a decline in effective moisture. The Blacktail Pond pollen data support the evidence interpreted from the faunal changes in Lamar Cave over the past 1,700 years.

Soils

With the exception of rapid accumulation of organic matter in poorly drained areas, soils in Yellowstone National Park are very young and generally weakly developed because the park was glaciated before 14,000 B.P. (Richmond 1986). Soil development rates in northern Yellowstone National Park are low, and it is not likely that they have significantly influenced the flora during the past several thousand years.

Fire Frequency

While microsite and substrate may have a larger influence on extent of grasslands, burning inhibits isolated trees or shrubs, such as sagebrush, from colonizing open areas and may increase productivity of grasses (Kaufman et al. 1988). Burning conditions like fuel accumulation and ignition sources may vary on unknown time scales. In Yellowstone National Park, fire frequency may be on the order of 10–25 years in sagebrush–grasslands, as determined by fire-scar data (Houston 1982). In lodgepole pine (*Pinus contorta*) forests, fuel accumulation and fire activity probably fluctuates on the order of 300 years (Romme 1982; Romme and Despain 1989). Lightning strikes vary an unknown amount but occur every summer. Prehistoric humans may have purposefully or accidentally started fires in Yellowstone National Park, but this is not determinable. The ignition sources in Yellowstone National Park, however, are probably not as important as climatic conditions or fuel accumulation (Romme and Despain 1989).

The floor in Lamar Cave seems to have burned at least twice. Woodrat dung, twigs, and bones were burned in levels IV and V; neither burn resembles a hearth. Some bones in these levels show evidence of carnivore punctures and rodent gnawing before they were burned. Every organic level in the cave contains fragmentary pieces of charcoal, suggesting a relatively consistent fire frequency outside the cave.

Topography

Topographic changes influence the available moisture at a given site, but this has probably not varied in the past several thousand years around Lamar Cave. Landslides, fresh fault scarps, and newly exposed river terraces may increase the amount of mesic sites available in an area. The river terraces near the cave are probably older than 1,700 years, and no fault scarps or landslides are nearby. Local kettles and swales may be filling in with time, thus increasing or decreasing the surface area covered by mesic vegetation. Periodic drying of some kettles in the Lamar Cave area may also produce dry areas high in carbonate concentrations and poorly suited for lush plant growth.

Population Dynamics

It is possible that the changes observed in the Lamar Cave record are of a type inherent to the dynamics of the ecosystem and independent of a major external change. Faunal and floral population densities are a result of a variety of extrinsic and intrinsic factors. Changes in the structure of the plant communities at a given site may be the result of changes in the consumers of the vegetation. Population sizes of invertebrates, ungulates, or small mammals may fluctuate because of internal responses of the biota. Density and type of vegetation may also change as communities mature. Dynamic equilibrium means that constant, natural changes occur in the ecological distribution of the flora and fauna in a system. Some variables that influence numbers of taxa are dispersal, competition, disease and parasites, predation of fauna, self-defense mechanisms of plants, stress, and consumers of flora.

Any animal that consumes vegetation may influence it. Effects of insects are relatively unknown, but certain grasshopper infestations can decrease the availability of forage seasonally. Ungulate grazing and browsing are of present concern in northern Yellowstone National Park. Northern Yellowstone National Park is occupied by six species of large ungulates, and their interrelationships are under investigation (Singer 1989; Singer et al. 1989). Elk, pronghorn (*Antilocapra americana*), bison (*Bison bison*, and bighorn sheep (*Ovis canadensis*) have all been observed within 1 km of Lamar Cave and are all represented in the Lamar Cave fauna. Mule deer have also been observed on one occasion, and their absence in the fauna is unexpected. Moose (*Alces alces*) have not been observed within 5 km of the cave and are not represented in the cave fauna. Elk is the most abundant ungulate in the cave fauna. Although there are no appreciable changes in the Lamar Cave ungulates, ungulate population fluctuations may have influenced the local vegetation and indirectly, the small mammals. Population fluctuations of this order, however, probably occur over shorter time scales than is recorded in Lamar Cave.

The population fluctuation of small mammals on short-term (0–10 years) time scales is a matter of debate. Lidicker (1988) states that a variety of factors is responsible and that the mechanisms are relatively complex. Nevertheless, it is unlikely that these short-term population changes are responsible for the changes observed in the Lamar Cave record because each cave level represents at least 100 years of faunal accumulation.

Summary

Based on recent studies of small mammals in various environments, including Yellowstone National Park, small mammal taxa are found to be affiliated with certain microhabitats. These microhabitats are partially defined by grass density, which is found to be related to effective moisture. The Lamar Cave faunal assemblage shows changes in taxa that are sensitive to variations in grass density; therefore the faunal shifts in the Lamar Cave record seem to relate to declining grass cover and moisture.

Significance to Park Management

Elk is presently the most abundant ungulate in northern Yellowstone. Controversy has been generated by the management of this species in the park (Chase 1986; Despain et al. 1986; Kay 1987). Present park policy is based on the theory of natural regulation, meaning that floral and faunal resources ideally are not manipulated. This policy is an attempt to manage the park as a natural ecosystem, functioning much as it did before the presence of European man (Houston 1971).

A possible flaw in the basic assumptions supporting natural regulation in Yellowstone relates to the prehistoric presence of elk in the Yellowstone area. Some authors have stated that elk are rare in the prehistoric record of the Yellowstone area because they preferred plains habitats and therefore were not native to a mountainous environment (Frison 1978; Wright and Reeve 1981; Cassells 1983; Chase 1986). The argument has been based largely on evidence from archaeological sites and seems to be a simplistic interpretation of limited data. This argument is refuted by evidence from Lamar Cave. Elk occur in 7 of 10 levels from the cave, both above and below a level dated to 960 B.P. 60 years. Elk is also the most common ungulate in the Lamar Cave faunal assemblage. The occurrence of elk in the Lamar Cave fauna establishes its presence in the Yellowstone area before historic disturbances and is thus significant to park management and to the diachronic study of ecosystem dynamics. The elk remains from Lamar Cave are primarily juvenile, suggesting further that the area was used by elk in the past for calving much as it is today.

In a review of over 200 archaeological and paleontological sites reported from the northern Rockies, over one-third contained elk (E. A. Barnosky, unpublished data). From the late Holocene records of Wyoming, Montana, and Idaho, only 4 of 19 did not contain elk. Paleontological sites in this region are slightly more likely to contain elk remains than are archaeological sites, suggesting that either there may be a cultural bias reducing the representation of elk, or a bias in the reporting or identification of faunal remains from archaeological sites.

A related controversy exists over beaver populations in northern Yellowstone National Park (Chase 1986; Kay 1987; S. Consolo, The status of beaver in Yellowstone. Paper presented at the Second Annual Northern Range and Fire Ecology Symposium, 22–23 March 1989. Yellowstone National Park). Beaver prefer habitats with riparian zones along rivers and streams (Banfield 1974). Some authors (Chase 1986; Kay 1987) believe that beaver are affected negatively by competition with elk. According to this hypothesis, elk may compete with beaver by out-grazing them in riparian areas, causing habitat decline. Early studies of beaver abundance (Warren 1926; Jonas 1955) are cited as evidence of the recent expansion of elk and consequent decline of beaver. Historic photos (Houston 1982) document the decline of willows, a preferred beaver food, as a hypothesis of lower beaver numbers. It has also been suggested, however, that the historic reduction of carnivores and elimination of beaver trapping may have caused a temporary increase of beaver, followed by a population crash because of forage and habitat reduction (Warren 1926). Data from Lamar Cave are not conclusive regarding this controversy. Only one beaver has been recovered from the Lamar Cave excavation. Although the paucity of remains at the cave may be the result of low numbers of beaver in the area, it is more likely because of taphonomic bias.

Besides these controversies about the prehistoric presence of elk and beaver, the prehistoric presence of the wolf in the Yellowstone area is also a matter of popular debate. A newspaper article in the *Billings Gazette* (31 March 1989) quotes a historian as saying that wolves were not native to Yellowstone and, like elk, were inhabitants of lower elevations outside park boundaries. Much of this argument is based on the erroneous assumption that elk were absent, and wolves did not have ample prey for food. Wolf remains are present in level 6 of Lamar Cave, however, and the species was clearly present in Yellowstone National Park before the influence of Europeans.

Conclusions

The faunal remains at Lamar Cave are similar to the fauna observed in northern Yellowstone National Park today. Elk remains occur in the cave record both before and after the time of initial European influence, definitely establishing the prehistoric presence of elk in northern Yellowstone. The presence of wolf remains in Lamar Cave before 960 B.P. 60 years also shows that wolves were native to Yellowstone, another matter of popular debate. The occurrence of beaver in the Lamar Cave fauna is restricted to one individual from level 3; this evidence is inconclusive and probably relates to taphonomic bias.

The stratigraphy, depth of deposits, faunal diversity, and taphonomy of Lamar Cave provide a more detailed and time-constrained mammalian record than is available from other recorded late Holocene sites of Wyoming, Montana, and Idaho. The taphonomy includes collections by diurnal, nocturnal, and crepuscular avian and mammalian predators. Perhaps most importantly, woodrats have been a consistent member of the fauna throughout the cave record, and their collecting activities have undoubtedly been continuous as well. No evidence of human use of Lamar Cave has been found.

In addition to the variety of the faunal remains from the Lamar Cave deposits, the stratigraphic separation of discrete levels allows a comparison of faunal percentages through time. Depth of the cave deposits augments comparisons of species abundance by permitting fine-tuning of small mammal percentages, which may indicate environmental change on a time scale of 100–1,000 years. The Lamar Cave fauna seems to show a decline in the numbers of microtine rodents and a corresponding increase in sciurid rodents throughout most of the cave sequence. Also, a grassland prairie species, the prairie vole, is present only in the lowest units. Absence of this species, plus variation in the percentages of the other ecologically sensitive small mammal species are interpreted as a decline in grass cover culminating about 1000 B.P. The mechanism responsible for cover change is uncertain; hypotheses for the observed changes include effects of data collection methods, assemblage size, taphonomic change, and vegetation change. Because of factors discussed above and support from the pollen record of nearby Blacktail Pond, however, the most likely explanation relates to climate and particularly to effective moisture. Further excavation and analysis of the fauna at Lamar Cave should help to answer this question.

Modern ecosystem studies furnish data pertinent to understanding biological processes and interactions within such systems; however, these studies often lack the temporal component necessary to differentiate short-term fluctuations occurring in a dynamic equilibrium state from long term change toward a new, altered state. While paleontologic records yield insights into evolutionary biotic change, the nature of the fossil record frequently obscures biotic responses of communities, individuals, and species to environmental perturbations of relatively low amplitude. By assuming continuous operation of biological processes similar to those in the presently functioning ecosystem, the Lamar Cave record may be used to gain insights into 100–1,000-year ecological fluctuations.

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Tall-willow Communities on Yellowstone's Northern Range: A Test of the "Natural-Regulation" Paradigm

Steve W. Chadde
Charles E. Kay

Prior to 1968, Park Service personnel contended that an "unnaturally" large elk (*Cervus elaphus*) population which had built up in Yellowstone during the late 1800s and early 1900s had severely "damaged" the park's northern winter range, including willow (*Salix* spp.) communities (Skinner 1928; Rush 1932; Grimm 1939; Cahalane 1941, 1943; Kittams 1959; Pengelly 1963; Tyers 1981; Kay 1985, 1990; Chase 1986). Later biologists questioned the reality of any significant population buildup (Houston 1982:11–17) and hypothesized that the northern range population was "naturally regulated," its general level not having changed significantly in the 1800s and early 1900s except for short-term fluctuations associated with variations in winter weather (Cole 1971).

The "natural-regulation" hypothesis, first announced in 1967 as the "natural-control" management policy, has been difficult to test because there is no single succinct and comprehensive publication of the concept and its assumptions, supporting evidence, and implications. Except for brief discussion in Houston (1982:61–68), various aspects of the hypothesis have been presented by different authors in overview publications that make general reference to unpublished research reports, but do not explicitly cite scientific data from which generalizations are inferred (see Cole 1971, 1974,1983; Houston 1976; Despain et al. 1986). Hence any definition of the model's specifications, assumptions, hypotheses, predictions, and a priori criteria for acceptance is subject to interpretation. The account that follows is our understanding of the model based on careful consideration and synthesis of the above publications.

If human influence is removed from the system, elk populations in Yellowstone will "naturally regulate" their numbers through density-dependent reduction in recruitment and survivorship resulting from intraspecific competition for food, primarily winter forage (Cole 1971). There may be some density-independent mortality associated with winter

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Terms such as *over grazing*, *range damage*, and *unnatural* elk population were used in nearly all early government reports about the Northern Range. Since these terms are value laden, they are used here only in their historical context.

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weather of varying severity. Although predation was invoked in the "natural-control" version of the model under "natural-regulation" predation is considered to be an assisting but nonessential adjunct to the regulation of ungulate populations through density-dependent homeostatic mechanisms (Cole 1971; Houston 1976). If wolves or other predators were present, they would kill only animals slated to die of other causes, and hence would not limit or lower ungulate populations (see Cole 1971).

Although the elk population is essentially food limited, the park biologists reasoned on evolutionary grounds that the ungulates could not have "progressively reduced food sources that limit their own densities" (Cole 1971). Thus ungulate populations and vegetation must have been in rough equilibrium (Despain et at. 1986), and the vegetation conditions prevailing at the time of the park's formation must have reflected that equilibrium. Houston (1982:129) did observe that willows on the Northern Range may have declined by roughly 50% since the park was established, but that was attributed to primary succession, suppression of fire, and climate change, not to ungulate browsing.

In a 1971 American Association for the Advancement of Science symposium on research in national parks, Houston (1976) proposed a set of bases for rejecting the "natural-regulation" hypothesis. One was evidence that ungulates caused retrogressive plant succession. If willow communities had actually decked on the Northern Range because of ungulate browsing, this would be a basis for rejecting the hypothesis. Because the "natural-regulation" concept is based on an equilibrium model, grazing induced changes in vegetation stature (height) would also indicate that the herbivores were not in equilibrium with their food resources.

A second basis for rejection would be competitive exclusion of sympatric herbivores (Houston 1976). According to the "natural-regulation" hypothesis, sympatric herbivores in the park have been over time; and are in interspecific equilibrium through resource partitioning (Houston 1982:169–178; Despain et al. 1986). Any change in their abundance resulting from ungulate competition would question the existence of a "natural-regulation" equilibrium at the time of park formation.

The preceding is our interpretation of the "natural-regulation" model which was proposed in the early 1970s and is in essence held by park biologists up to the present (see Despain et al. 1986). This chapter examines historical changes in willow communities on the northern range and evaluates the factor or factors responsible for the evident, extensive changes which have occurred in the riparian habitats. It further considers evidence of change in sympatric herbivores and collectively presents this evidence as a test of the "natural-regulation" model based on the criteria for rejection proposed by Houston (1976).

METHODS

Study Area

The study area in this chapter encompasses the Northern Range of Yellowstone National Park, which is essentially the winter range of the northern elk herd (Despain et al. 1986). Houston (1982) provides a description of its climate, physiography, and vegetation.

In 1957 the Park Service constructed 2.1-ha ungulate-proof exclosures at Mammoth and Lamar–East that enclosed willow communities. Two additional 2.1-ha willow-containing exclosures at Lamar–West and Junction Butte were built in 1962. A fifth willow exclosure was erected at Tower Junction in 1957, but was removed in the early 1970s. Houston (1982:415–420) and Barmore (1981:453–459) provide background information on these exclosures.

Houston (1982) and Despain et al. (1986) should be consulted for Park Service interpretations regarding the northern Yellowstone elk herd. Chase (1986), Kay (1985, 1987, 1990), and Tyers (1981) provide alternative views.

Repeat Photography

Archival photographic collections at Yellowstone National Park, the Montana Historical Society, the University of Montana, Montana State University, the Museum of the Rockies, the University of Wyoming, the Colorado Historical Society, the Library of Congress, the National Archives, and the U.S. Geological Survey's Denver Photographic Library were searched for historical photos of willow communities on the northern range. Nearly fifty thousand images taken in the park were reviewed. However, only a small number were taken on the northern range and fewer still contained views of wetland communities. Other historical photographs were obtained from Warren (1926) and Jonas (1955). Seton (1909) provided several drawings of willow communities and beaver dams near Tower Junction in 1897.

The locations in these historical pictures were rephotographed during 1986–1989 to form sets of comparative photos, a process called repeat photography (Rogers, Malde, and Turner 1984). The photosets were visually evaluated to determine changes in the abundance and distribution of tall-willow communities (G. Rogers, personal communication 1987). Houston (1982) and Gruell (1980a, 1980b) also used comparative photography to study vegetation changes in the Greater Yellowstone Ecosystem.

Field Measurements

Willow communities and their environments were sampled and classified as part of a recent study of wetlands on the northern range (Chadde, Hansen, and Pfister 1988). Sample plots were located within relatively homogeneous stands of willows, based on species composition and dominance within the stand. The canopy-coverage (Daubenmire 1959) and height of all species occurring with 50-m^2 sample plots were estimated.

Soils were sampled and described using standard pedon description methods and terms (Soil Survey Staff 1975, Brichta 1987). Soils associated with willow communities were described to the family level. Water levels associated with representative willow stands were monitored from May to September of 1986 and 1987 using 1-m-long PVC tubes and a portable ceramic-tipped tensiometer. Other soil–water characteristics (conductivity, pH, dissolved-oxygen content) and physical features (elevation, aspect, topographic position) were recorded for each willow plot.

To develop a classification, sample plots were grouped into sets based on floristic similarities in both overstory and undergrowth layers (Chadde, Hansen, and Pfister 1988). Information on soil and site characteristics allowed the placement of community groupings along environmental and successional gradients. Associations or stable communities in equilibrium with environmental conditions were defined, as were seral community types. Grazing relationships for each community were inferred from field observations of browsing levels and from previously published studies on palatability and browsing response.

When the exclosures were constructed, the Park Service established one permanent willow belt transect inside and another outside each exclosure except at Lamar–West (Barmore 1981:453–459, Houston 1982:415–420, Singer 1987). At Lamar–West, a willow transect was established inside the exclosure but not outside. Instead, the agency used the Lamar–East outside willow belt as a control for both the Lamar–East and Lamar–West exclosures. Thus seven permanent willow belt transects are associated with these exclosures, three outside and four inside. The belt transects at Mammoth, Lamar–East, and Lamar–West are all 1.5 × 30.5m (5 × 100 ft.). Those at Junction Butte are 1.5 × 22.9 m (5 × 75 ft.).

Data on willow canopy-coverage, plant height, and number of individual plants have been collected by the Park Service at intervals since the exclosures were constructed (Singer 1987). They plotted each willow clump within the transect on graph paper and then determined canopy-coverage by using a grid method. However, these belt transects have inherent inadequacies limiting their usefulness in long-term willow trend studies. First, the single canopy-coverage value inside and outside each exclosure precludes statistical testing of mean differences. Second, the plotting technique is subject to a wide degree of observer variability and error. Third, each belt transect includes significant portions of nonwillow communities. Fourth, rare species and other undergrowth shrubs are underestimated or not recorded. Park Service counts of individual willow plants have also been highly variable.

For this study, a series of line intercepts (Hanley 1978) within the existing belt transects were established so that willow canopy-coverage within and outside each exclosure could be compared statistically. Each belt transect was subdivided into six 30.5-m line intercepts, except at Junction Butte, where there were six 22.9-m line intercepts. The length of each line intercepted by various willow species, as well as other shrub species, was recorded to the nearest centimeter. The maximum height of each plant was recorded. These transects were sampled in August 1988.

According to Hurlbert (1984), comparison inside and outside of a single exclosure represents pseudoreplication. However, the transects and the individual plants are not homogeneous and some measure of variance is necessary to evaluate the adequacy of sampling procedures. Statistical tests on data collected inside and outside one exclosure indicate only that the vegetation is different at that site. Statistical tests using each exclosure as a sample point are true replicates, and those results are more conclusive. Our statistical results should be viewed with these concepts in mind.

RESULTS

Historical Perspective

Forty-four repeat photosets were made of willow communities on Yellowstone's northern range. The earliest date from 1871. Some photosets contain four photographs, taken in 1893, 1921, 1954, and 1986–1988. Several contain three photos, taken in 1921, 1954, and 1986–1988. Forty-one out of forty-four comparative photosets show that tall willow communities have totally disappeared (figures 16.1–16.3). In the three other photosets, visual estimates indicate that only 5–10 percent of the original tall willows remain.

In 1871 Captains John W. Barlow and David P. Heap (1872:40) toured Yellowstone Park. On the northern range, they reported "thickets of willows along the river banks." Philetus W. Norris (1880:613), Yellowstone's second superintendent, noted that the park was "well supplied with rivulets *invariably* bordered with willows" (emphasis added). Norris (1880:617) further stated that there were "innumerable dense thickets of willow" in Yellowstone. Based on an analysis of pollen in the sediments from lakes and ponds on the northern range, Barnosky (1988) reported that willow pollen had declined since the early 1900s. All available evidence indicates that tall-willow communities were once common on the northern range but are now almost completely absent.

Four additional photosets were made of willow communities on Yellowstone's Gallatin winter range. Three contained four pictures, taken in 1924, 1949, 1961, and 1986, and the other photoset included 1937, 1961, and 1989 photos. Historically, the Gallatin has had an elk situation similar to that on the northern range (Packer 1963, Patten 1963, 1969; Streeter 1965; Peek, Lovaas, and Rouse 1967, Lovaas 1970). Patten (1968) reported that the vegetation along the Gallatin River changed rapidly from an area nearly devoid of willows near the park's boundary to extensive willow thickets a few kilometers upstream in the park. He noted, "between these areas lies a transition zone of stunted and dead willows." The area with the fewest willows had the largest concentrations of wintering elk (Peek, Lovaas, and Rouse 1967; Lovaas 1970). Where deep snow to the south or hunters north of the park limit elk use, tall willows occur.

Based on visual evaluation of the photographic evidence, tall willows decreased almost completely along this section of the Gallatin River and lower Daly Creek between 1924 and 1961. Since the 1970s, the Montana Department of Fish, Wildlife, and Parks has made a concentrated effort to reduce this elk herd when it migrates from Yellowstone Park. By instituting late-season hunts, the department has reduced the Gallatin elk population by at least 50% in recent years (L. Ellig, pers. comm. 1988). In apparent response to this decline in elk numbers, willows have increased in height and canopy-coverage, as shown in repeat photos from 1986 and 1989 (Kay 1990).

Willow Communities on the Northern Range

Willow communities on the northern range occur in a wide range of environments, elevations, and topographical settings. Brichta (1987) identified four general settings that support willow communities: (1) adjacent to stream and river channels, in overflow channels, and on floodplains; (2) in depressions and around kettle lakes formed by blocks of glacial ice; (3) adjacent to springs and seeps on foothill slopes; and (4) in abandoned beaver channels and ponds.

Eight unique willow associations and community types were identified on the northern range (Chadde, Hansen, and Pfister 1988), ranging from low-willow carrs (shrub-dominated wetlands on wet organic soils) to tall-willow types on seasonally dry mineral soils:

1. *Salix candida/Carex rostrata* association. These are infrequent at higher elevations of the northern range. They are restricted to anchored organic mats along pond and lake margins. In addition to *Salix candida* and *Carex rostrata, Carex aquatilis* and *Calamagrostis canadensis* may also be present. The low stature of *Salix candida* (maximum height of about 1 m) and its higher-elevation location preclude much ungulate winter use of this species. However, utilization during snow-free periods and the inability of this species to produce vigorous basal sprouts following repeated browsing may result in a conversion to dominance by *Carer rostrata.*
2. *Salix wolfii/Carex aquatilis* association. These common low-willow communities are found at mid-to-high elevations, where they occupy extensive areas of valley bottoms and basins. Soils are typically wet with organic surface horizons. Major species include *Salix wolfii, Salix planifolia, Potentilla fruticosa, Carex aquatilis, Carex rostrata*, and *Deschampsia cespitosa.* Ungulate use of these willows is typically heavy, with willows maintained at heights of 60 cm or less. A conversion to sedge-dominated communities is likely as willow dumps die and are not replaced.
3. *Salix wolfii/Deschampsia cespitosa* association. This low-willow association is a minor type of stream-side terraces and seeps. It typically occupies drier environments than the *Salix wolfii/Carex aquatilis* association. Major shrubs include *Salix wolfii, Salix planifolia*, and *Poten-*

Figure 16.1 a. Tall-willow communities in Yancy's Hole on Yellowstone's northern range. 1893 photo by F. Jay Haynes (H-3080) viewed east. Photo courtesy Haynes Foundation Collection, Montana Historical Society, Helena.

Figure 16.1 b. That same area in 1988. Note the disappearance of tall-willow communities, less than one hundred years later. Other photos of this area show that the tall willows had been heavily browsed and were declining by 1921. Tall willows were absent in 1954 photos. Photo by Charles E. Kay (no. 3051-12 and 3051-13), August 20.

Figure 16.2 a. Close-up of a tall-willow community in Yancy's Hole on Yellowstone's northern range. 1915 photo by Bailey (1930:57) viewed north. Note the dead willow in the right foreground and the hedged appearance of other willows due to "winter browsing by elk." Bailey (1930: 55–57) stated that in the early 1910s, "willows of many species are an abundant source of food supply along the streams and meadows. They are often trimmed to mere stumps during winter and in some places they are actually killed out by close browsing." From Vernon Bailey, *Animal Life of Yellowstone National Park* (1930); courtesy of Charles C. Thomas, Publisher, Springfield, Ill.

Figure 16.2 b. That same area in 1987; note the disappearance of tall willows since the 1915 photograph. Photo by Charles E. Kay (no. 2895-25), August 11.

tilla fruticosa. Important herbaceous plants include *Deschampsia cespitosa*, *Juncus balticus*, and *Poa pratensis.* Ungulates frequently graze these communities and browse on the short-statured willows.

4. *Salix lutea/Carex rostrata* association. These minor tall-willow communities are found on slopes adjacent to springs and seeps. Soils are wet and range from organic to mineral. *Salix lutea* and *Salix pseudomonticola* are often co-dominant. Other tall willows, such as *Salix bebbiana* and *S. geyeriana*, are common. Undergrowths are dominated by *Carex rostrata*, *C. aquatilis*, and *Poa palustris.* These communities could potentially form dense thickets 3–4 m tall. Current levels of ungulate browsing typically limit heights to l m or less. Canopy-coverages are also greatly reduced by repeated browsing.

Figure 16.3 a. A tall-willow community in the lower Soda Butte Valley on Yellowstone's northern range. Photo taken in 1896 or 1897 by A. E. Bradley; viewed northeast. Photo courtesy A. E. Bradley Collection (72-158), Mansfield Library, Univ. of Montana, Missoula.

Figure 16.3 b. That same area in 1988; note the disappearance of tall willows since the earlier photograph. Photo by Charles E. Kay (no. 2976-15A), June 21.

5. *Salix geyeriana/Carex rostrara* association. These widely distributed communities are found on fine-textured mineral soils of alluvial terraces, broad valley bottoms, and adjacent to former beaver ponds. Common tall-willow species include *Salix geyeriana*, *S. bebbiana*, *S. drummondiana*, and *S. planifolia*. Herbaceous species include *Carex rostrata*, *Calamagrostis canadensis*, and *Poa palustris*. Elk and moose use is high and results in willows of low stature and reduced canopy cover.
6. *Salix geyeriana/Deschampsia cespitosa* association. These common tall-willow communities occur on loamy soils adjacent to seeps and streams. *Salix geyeriana*, *S. boothii*, and *S. bebbiana* are the dominant willows. *Deschampsia cespitosa*, *Juncus balticus*, and *Poa pratensis* are common herbaceous species. These communities are potentially highly productive of both browse and forage. However, ungulate browsing maintains willows at heights of 1 m or less versus potential heights of 3–4 m.
7. *Salix bebbiana/Agrostis stolonifera* community type. This tall-willow community type occupies small areas adjacent to seeps and streams. Soils are mineral but may have surface organic matter accumulations. *Salix bebbiana, Rosa woodsii,* and *Betula occidentalis* are common. The introduced species *Agrostis stolonifera, Poa palustris, P. pratensis*, and *Phleum pratense* typically dominate undergrowths and probably are the result of repeated grazing. Browsing has produced open, short-statured stands, in contrast to potential growth of 3–4 m.
8. *Salix exigua/Agrostis stolonifera* community type. This tall-willow community type is typically restricted to low-elevation stream banks and cobble bars, often below high-water levels. *Rosa woodsii* is common. Other tall-growing willows may be present, indicating successional trends toward other willow types. Heavy browsing, however, often reduces or eliminates stands of this community type, leading to replacement by such herbaceous species as *Agrostis stolonifera* and *Poa palustris*.

In general, all willow stands are affected by ungulate browsing, higher-elevation stands being less affected than lower-elevation stands because of greater snow depths. Repeated browsing has resulted in sharp reductions in willow heights and canopy-coverage when contrasted with potential community structure.

Willow Exclosures

Willows inside exclosures are taller and have greater canopy-coverage than those outside (tables 16.1–16.3). Other less palatable shrubs, such as rose (*Rosa woodsii*) and river birch (*Betula occidentalis*) (Nelson and Leege 1982), exhibit this same pattern. When pooled, these differences are statistically significant across all exclosures (tables 16.4 and 16.5). Outside these exclosures, the mean height of all willow species was 34 cm whereas inside it was 274 cm. On average, willows had 10 percent canopy-coverage outside the exclosures, but 74 percent canopy-coverage where ungulates are excluded. However, all belt transects contained some nonwillow communities (table 16.6). When the nonwillow portions of the belt transects were excluded, willow canopy-coverage averaged 14 percent outside the exclosures and 95 percent inside, also a statistically

Table 16.1 Average canopy-cover and plant height of woody species inside and outside the Junction Butte exclosure on Yellowstone's northern range, August 1988.

	Canopy-Coverage (%)		Plant Height (cm)	
Species	*Outside*	*Inside*	*Outside*	*Inside*
Salix lutea	6.7	22.8*	27.5	167.0*
Salix bebbiana	6.7	55.8*	32.5	272.0
Salix geyeriana	1.5	2.0	43.5	192.2*
Rosa woodsii	1.0	10.7*	31.0	70.5*
Potentilla fruticosa	14.7	19.5	32.8	57.0*
Ribes spp.	0.3	2.3	38.2	113.0*
Populus tremuloides	1.8	—	30.8	—
Total willows	14.7	80.6*		
Total shrubs	32.5	112.8*		

*$p < .01$.

Table 16.2 Average canopy-coverage and plant height of woody species inside and outside the Lamar–West and Lamar–East exclosures on Yellowstone's northern range, August 1988

	Canopy-Coverage (%)			Plant Height (cm)		
Species	*Lamar–East Outside*	*Lamar–East Inside*	*Lamar–West Inside*	*Lamar–East Outside*	*Lamar–East Inside*	*Lamar–West Inside*
Salix bebbiana	3.0	40.3*	40.8*	49.5	357.0*	317.0*
Salix geyeriana	3.7	15.7*	—	40.8	330.5*	—
Salix boothii	—	4.0	36.2*	—	160.0	257.0
Rosa woodsii	3.2	2.8	0.7	29.0	71.0*	62.0*
Potentilla fruticosa	13.3	3.5	0.3	39.0	43.0	65.0
Ribes spp.	0.5	0.5	—	53.5	82.5	—
Populus tremuloides	—	3.2	2.8	—	161.0	375.8
Lonicera involucrata	2.0	4.2	—	34.0	91.8*	—
Symphoricarpos albus	—	—	T	—	—	37.5
Total willows	6.7	60.0*	77.0*			
Total shrubs	25.7	74.2*	81.2*			

*$p < .01$.

Table 16.3 Average canopy-coverage and plant height of woody species inside and outside the Mammoth exclosure on Yellowstone's northern range, August 1988.

	Canopy-Coverage (%)		Plant Height (cm)	
Species	*Outside*	*Inside*	*Outside*	*Inside*
Salix lutea	3.2	0.2	21.5	180.0*
Salix bebbiana	6.8	53.3*	23.8	403.2*
Salix geyeriana	—	12.0*	—	328.0
Salix boothii	—	13.2*	—	353.8
Betula occidentalis	4.7	5.0	82.5	481.8*
Rosa woodsii	0.8	12.0*	19.8	77.8*
Potentilla fruticosa	0.7	—	45.5	—
Total willows	10.0	78.7*		
Total shrubs	16.2	95.7*		

*$p < .01$.

significant difference (table 16.4). Thus willow canopy closure was nearly complete inside the exclosures.

When our line-intercept canopy-coverage data were compared with the Park Service's grid measurements, no significant difference existed for the transects outside the exclosures. However, the agency's method significantly underestimated the amount of willow canopy-coverage inside the exclosures (table 16.7). We believe our line-intercept data wore accurately represent the true conditions within the exclosures because aerial photos (Kay 1990) show nearly complete willow canopy closure.

At another willow exclosure on Slough Creek just north of the park, Chadde and Kay (1988) reported that willows increased in height and canopy-coverage when protected from ungulate browsing. At the Slough Creek exclosure, snow accumulation normally precludes that area's utilization as elk winter range, and winter use is generally limited to moose (*Alces alces*). Elk occasionally use the Slough Creek area in late fall and early spring or during winters of low snowfall.

Inside three exclosures in the Gallatin River drainage willows attained heights of 3–4 m with near-complete canopy closure, whereas unprotected plants were all less than 1 m tall (Kay 1990). In Rocky Mountain National Park, Gysel (1960) and Stevens (1980) noted that willows increased in canopy-

Table 16.4 Average willow canopy-coverage inside and outside Yellowstone exclosures. Entire belt transects compared with only the portion of those transects which contain willow communities, August 1988.

	Willow Canopy-Coverage (%)	
Exclosure	*Entire Belt Transect*	*Willow Type Only*
Mammoth		
Outside	10.0	12.3
Inside	78.5	109.2
Junction Butte		
Outside	14.7	21.0
Inside	80.7	93.2
Lamar–East		
Outside	6.7	9.7
Inside	60.0	86.5
Lamar–West		
Inside	77.0	92.0
Total		
Outside	10.5	14.3
Inside	74.0	95.2
t	9.20	10.77
p	<.01	<.01

Table 16.5 Average height of all willow species and rose inside and outside Yellowstone exclosure.

	Average Height (cm)	
Exclosure	*All Willow Species*	*Rosa woodsii*
Mammoth		
Outside	22	20
Inside	316	78
Junction Butte		
Outside	35	31
Inside	210	70
Lamar–East		
Outside	45	29
Inside	282	71
Lamar–West		
Inside	287	62
Total		
Outside	34	27
Inside	274	70
t	7.67	9.62
p	<.01	<.01

Table 16.6 Associations and community types found on permanent willow belt transects inside and outside exclosures on Yellowstone's northern range.

Exclosure/ Willow belt	*Year Established*	*Association or Community Type with Transect Percentage*
Junction Butte—In	1962	*Salix geyeriana/Carex rostrata* (87) *Potentilla fruticosa/Deschampsia cespitosa* (13)
Junction Butte—Out	1962	*Salix geyeriana/Deschampsia cespitosa* (80) *Populus tremuloides/Poa pratensis* (20)
Lamar–East—In	1957	*Salix geyeriana/Carex rostrata* (65) *Phleum pratense* (29) *Populus tremuloides/Phleum pratense* (6)
Lamar–West—In	1962	*Salix geyeriana/Carex rostrata* (85) *Carex rostrata* (15)
Lamar–East—Out	1957	*Salix geyeriana/Poa pratensis* (70) *Potentilla fruticosa/Poa pratensis* (30)
Mammoth—In	1957	*Salix geyeriana/Carex rostrata* (69) *Juncus balticus* (16) *Carex nebraskensis* (15)
Mammoth—Out	1957	*Salix bebbiana/Agrostis stolonifera* (80) *Poa pratensis* (20)

Note: Types follow Chadde et al. 1988.

Table 16.7 Willow canopy-coverage inside and outside exclosures on Yellowstone's northern range, 1958–1988.

	Willow Canopy-Coverage (%)							
							This Study	
	Park Service Measurements						Entire Transects	Willow Type Only
Exclosure-Transect	1958	1962	1965	1974	1981	1986	1988	1988
Junction Butte								
Outside	—	6.6	6.9	10.6	11.2	13.2	14.7	21.0
Inside	—	16.1	13.2	25.8	33.0	49.1	80.7	93.2
Lamar–East								
Outside	6.0	5.4	6.5	9.5	9.3	9.0	6.7	9.7
Inside	8.2	14.2	23.3	28.4	18.9	37.2	60.0	86.5
Lamar–West								
Inside	—	1.7	5.6	16.6	18.7	43.1	77.0	92.0
Mammoth								
Outside	7.5	8.6	6.2	9.3	8.8	12.9	10.0	12.3
Inside	4.5	10.3	25.2	31.2	26.9	31.2	78.5	109.2
Total								
Outside						11.7	10.5*	
Inside						40.2	74.0**	

Source: National Park Service data, 1958–1986, from Singer (1987).
*$t = 0.45$, ns.
**$t = 6.77, p < .01$.

coverage and height inside exclosures that excluded elk. On elk and moose winter range in Canada's Banff National Park, Trottier and Fehr (1982) reported that willows inside an exclosure were significantly taller than those exposed to ungulate browsing.

In addition to the measurements of plant height and cover that the Park Service has made over the years, they also photographed the willow belt transects each time they were sampled. Those photographs were repeated by Kay (1990) in 1987–1988. The resulting multiple-image photosets confirm that willows inside the exclosures have increased in height and canopy-coverage since they were protected, whereas willow communities outside the exclosures have not.

These comparative photos were also used to evaluate changes in willow communities observed in other repeat photosets because visual estimates from the exclosure photographs could be compared with actual plant measurements. This served to refine or calibrate the visual estimation technique used in this study. It also demonstrated that willows inside the exclosures now have the same stature as willows on the northern range did between 1870 and 1900. Thus the conditions inside the exclosures more closely approximate the level of ungulate use which existed when Yellowstone was created than do conditions in the park today.

WILLOW TRENDS

The observed decline in tall-willow communities has been attributed to: (1) normal plant succession, (2) climatic change, (3) fire suppression, and (4) ungulate browsing (Houston 1982; Despain et al. 1986). According to Houston (1982: 129–134), the willow decline may have been due in part to the lack of new substrates for willows to colonize. He presented a 1974 photo of a newly formed gravel bar in the Gardner River and a 1978 retake, which showed that willows had colonized that area.

Kay (1990) rephotographed that site in 1983, 1986, 1987, and 1988. Chadde, Hansen, and Pfister (1988) also established plots at that site as part of their riparian classification study. By 1983, willows were almost entirely absent from the gravel bar and had been replaced by grasses and other herbaceous plants. Thus this area changed from bare gravel to willows to grass in only nine years. Not only is this much faster than normal plant succession, but it is also contrary to expected successional directions. By the usual successional sequence, colonizing willows would have been replaced by other willow species and perhaps cottonwoods (*Populus* spp.) or eventually Engelmann spruce (*Picea engelmannii*), but not grasses, sedges, or forbs. Some willow communities on the northern range are seral, but on many sites willows normally form stable or climax communities (Chadde, Hansen, and Pfister 1988). In nearly all instances, willows are not seral to grasslands unless there has been a change in hydrology (Chadde, Hansen, and Pfister 1988). That has not occurred at this site along the Gardner River.

Houston (1982:276–277) also suggested that willow were seral to conifers. In some instances this is true, but not for most willow communities. Of the forty-eight repeat photosets of willow communities made for this study, only two show complete replacement by conifers (mainly Engelmann spruce). In three others, approximately 20 to 60 percent of the willow communities in the original photos have now been replaced by conifers. Thus only five of forty-eight photosets (10 percent) show conifer invasion of what were once willow communities. If beaver had not been virtually eliminated from the northern range due to interspecific competition with elk (see discussion below), they might have flooded several of these sites and thereby prevented conifer establishment.

As mentioned above, previous studies recorded the number of individual willow plants on the belt transects inside and outside the exclosures. Those data (Houston 1982:419; Singer 1987) generally show more plants outside the exclosures than inside and have been used to infer the relative ecological health of these communities, independent of plant height or canopy-coverage (Houston 1982:99).

Outside the exclosures, a few stems shorter than 1 m were counted as an individual plant, as was another small group of similar-sized stems a short distance from the first "individual." However, unless the roots are excavated or genetic tests performed, it is impossible to determine whether neighboring stems are really part of the same plant or different individuals. Some willow clumps may have been broken into "separate plants" by repeated browsing. Moreover, Park Service investigators contend that a plant outside an exclosure with a few short stems is equivalent to a plant inside the exclosure with several hundred 3-m-tall stems. In our opinion, the enumeration of supposed individual willow plants inside and outside exclosures is not an appropriate measure upon which to base ecological interpretations.

The decline of willows on the northern range has also been attributed to climatic change, especially the drought during the 1930s (Houston 1982:129–134). This suggestion is not supported by data from the exclosures, since the climate is the same on both sides of the fence. The microclimate inside the exclosures is certainly different today, but that is an incorporated variable caused by the plants' response to elimination of ungulate browsing, not the cause of the vegetation's response. Inside a small exclosure near Tower Junction, willows grew vigorously during and after the 1930s drought whereas those outside did not (see NPS photos 15078-4, 1935:51–21, 1951). Moreover, it is not climate that prevents the plants from growing to their full biological potential outside the exclosures. Measurements of subsurface water levels inside and outside the exclosures throughout the summer failed to show any less water available to the plants on the outside (Brichta 1987; Chadde, Hansen, and Pfister 1988).

The climate-change hypothesis is also not supported by photographic evidence or firsthand accounts. Willows started declining before the 1930s drought (figure 16.2; Kay 1990), and they have continued to decline in recent years. Willows in the western portion of Round Valley, for example, were severely hedged in 1949 but still alive. By 1988, a major decline had occurred in that community (figure 16.4) even though precipitation had been near normal during the 1949–1988 period (Houston 1982:104). Further, there still are abundant springs and seeps at the site (Kay 1990).

Yellowstone's Tower Junction willow exclosure was constructed in 1957, and by the late 1960s the protected willows had significantly increased in height and canopy-coverage (Singer 1987, Kay 1990). That exclosure was removed in the early 1970s and the protected plants exposed to ungulates. By the late 1970s and early 1980s those willows were extensively hedged and were reverting to lower-statured plants (Kay 1990). These changes certainly cannot be attributed to the 1930s drought. In addition, recent climatic variation appears to be unimportant since this area has abundant subsurface soil moisture (Brichta 1987; Chadde, Hansen, and Pfister 1988).

Houston (1982:101–107) noted that since the late 1890s the mean annual temperature on the northern range at Mammoth had increased 0.5–1.0° C, whereas the mean annual precipitation had declined 1–2 cm. However, to the best of our knowledge, no one has demonstrated that a climatic shift of that size will have any long-term impact on tall willows, especially since nearly all willow communities are subirrigated (Brichta 1987). Most perennial woody floras have so much biological or vegetational inertia that large-scale climatic changes of long duration are required before major shifts in plant species composition or stature occur (Cole 1985, Neilson 1986).

It has also been suggested that willow communities need to burn at frequent intervals if they are to persist on the northern range (Houston 1982) or grow beyond the reach of browsing ungulates. Based on a sample of fire-scarred trees, Houston (1973, 1982:107) calculated mean intervals of twenty to twenty-five years between fires on the northern range during the three to four centuries before Yellowstone Park was established and the agency began to suppress fires. Although a policy to let many lightning-caused fires burn has been in effect since the early 1970s, 1988 was the first year fires burned more than a small area on the northern range.

In spite of what were considered the worst burning conditions in the park's history, riparian communities were not overly susceptible to the 1988 fires. Some willow communities did burn, but the fires frequently skipped over them (Kay and Chadde, personal observation). Riparian areas and willows are generally too wet to burn. Furthermore, cottonwoods (*Populus trichocarpa* and *P. angustifolia*) have also declined and failed to regenerate successfully on the northern range (Chadde, Hansen, and Pfister 1988). These species are extremely susceptible to fire and are easily killed by even a light burn. Frequent fires certainly would not enhance cottonwood regeneration in the park. Finally, there is no evidence to support the idea, postulated by park personnel (D. Despain, pers. comm. 1988), that burning will cause resprouting willows to grow so fast or become so chemically

Figure 16.4 a. Heavily browsed willows along the west edge of Round Prairie, Pebble Creek Valley, Yellowstone National Park, in 1949. National Park Service photo no. 49-331.

Figure 16.4 b. That same area in 1988. Note the near-complete decline of willows that has occurred in the past four decades. Numerous springs and seeps still can be found in this area, which suggests that climatic change or lack of water is not primarily responsible for the observed change in plant communities. In all probability, the willows were killed by repeated ungulate browsing. Photo by Charles E. Kay (no. 2976-19A), June 21.

defended that they can grow beyond the reach of elk and reform tall-willow communities. Observations of experimental willow burns conducted by the Park Service on the northern range indicate that elk browsed all of the new sprouts; none were able to grow taller than 1 m except where physical barriers prevented elk use (Kay 1990).

Based on a process of elimination and the data we have presented, we conclude that frequent, repeated ungulate browsing is primarily responsible for the decline of tall-willow communities on the northern range. Browsing by elk and moose presently prevents the willows which do exist on the northern range from expressing their full biological height and canopy-coverage. From 1970 through 1978, willow utilization on the northern range averaged over 91 percent (Houston 1982:149) and has not decreased in recent years (Chadde, unpubl. data; F. Singer, pers. comm. 1989). Barmore (1981:358) likewise concluded that willows had declined on the northern range due to repeated ungulate browsing, not climatic change.

During the late 1950s and early 1960s, when the Park Service believed that an "unnaturally" high population of elk was causing "range damage" in Yellowstone, they reduced the herd by trapping, transplanting, and killing elk in the park. Barmore (1981:357) noted, "By the late 1960's, the growth form and condition of *Salix* spp. on most of the winter range began to more closely resemble the less heavily browsed conditions of the late 1800's and early 1900's. This change was associated with major reduction of the northern Yellowstone elk herd suggesting that the decline in the distribution and condition of *Salix* spp. from the 1920's to the early 1960's was at least partly due to heavy browsing by elk."

On the Gallatin River, willows have declined only where wintering elk concentrated most heavily (Patten 1968). The willows upstream and downstream from the main elk wintering area have not declined and commonly exceed 3 m. Thus, climatic or hydrologic conditions could not be primarily responsible for the decline near the park boundary since all sections of the river were subjected to the same physical factors. Patten (1968) found that willows farthest from the river had the highest grazing-induced mortality rates. He concluded that plants subjected to physiological stress were less able to withstand grazing pressure. However, it was ungulate browsing which actually caused most of the mortality and reduction in plant growth. Neilson (1986), who worked on a similar climatic change versus grazing problem, concluded that the vegetation would have persisted despite drought had the additional stress of grazing not completely altered the flora.

Houston (1982:131) argued that ungulates were not primarily responsible for the decline of willows on the northern range because willows had also declined outside Yellowstone, as well as on the park's summer range. Willows have in fact declined throughout the West since European settlement, but that has been primarily due to such agricultural practices as irrigation, dewatering, channelization, and livestock grazing, not climatic change (Meehan and Platts 1978; Dobyns 1981; Myers 1981; Marcuson 1983; Platts et al. 1983; U.S. General Accounting Office 1988). A recent study of 262 miles of streams in southwestern Wyoming found that since the 1850s 83 percent of the streams and their associated riparian areas had been severely altered by livestock grazing (Shute 1981). Furthermore, moose and elk also feed upon willows on the park's summer range (McMillan 1950, 1953). Until exclosures are built there, the impact of summer ungulate utilization on those communities cannot be determined.

Morgantini and Hudson (1989) reported that elk in western Canada shifted their diet to willows on summer ranges. In Rocky Mountain National Park, according to Stevens (1980:145), "willow forms a major part of the summer diet for elk, about 21%." Stevens (1980:139) also reported that on the park's summer range "53% of the elk were observed on willow types." Moreover, he found that elk grazing caused willows to decline on the park's summer range. "*Salix brachycarpa* decreased an average of 55% on three of the four transects, with an overall decline from 20% cover to 9%. *Salix planifolia* declined from 37% to 29% cover" (Stevens 1980:135). These declines occurred in only eight years as the elk herd built up in the park (Stevens 1980:136.

IMPACT ON OTHER SPECIES

Beaver. The decline of tall-willow communities on the northern range has in all probability had a negative impact on animals which are usually associated with that habitat, such as beaver. Houston (1982:182–183) implied that beaver were not widespread in Yellowstone until around 1900 and suggests that "ephemeral colonies may be characteristic of most of the park." However, in 1835, 1836, and 1837, Osborne Russell (1965) trapped beaver in Yellowstone Park, where he found a great many on the northern range. For instance, he and his companions trapped beaver from August 3 to 20, 1835, on the upper Gardner River. In 1836 Russell and his party spent several days trapping beaver on the streams which flow into Lamar Valley. The next year he and his associates spent nearly three weeks trapping beaver on Slough and Hellroaring creeks.

Norris (1880:613) reported that beaver were common in the park during the 1870s and 1880s. He stated that trappers took "hundreds, if not thousands" of beaver skins from the park each year during his tenure as superintendent. Seton (1909) found beaver abundant near Tower Junction on the northern range in 1897. Skinner (1927:176) noted that "beaver have always been quite common in Yellowstone National Park, and although fluctuations are noticed at times, the actual number present remains about the same throughout a course of years." Skinner added, "beaver occur in practically every stream and pond (where there is suitable food) in the park." He estimated that there were "about 10,000" beaver in the park.

Bailey (1930:112–114) observed, "beavers are found along almost every stream in Yellowstone Park." He also noted that "the extensive herds of elk" on the northern range kept down the growth of the beavers' food supply, young aspen and willows. Wright and Thompson (1935:72) concluded that beaver in Yellowstone were "endangered through the destruction of aspen and willow on the overbrowsed elk winter ranges." Thus, the available evidence strongly suggests that beaver were common in the Yellowstone area and on the northern range from before park establishment in 1872 through the early 1900s. Warren (1926:183) suggested that beaver had increased during the early 1900s, but he attributed it to "the protection from molestation by trappers" and the "killing of predatory animals" by the Park Service.

In the early 1920s, Warren (1926) conducted a detailed beaver study around Tower Junction on the northern range. He reported 232 beaver and extensive beaver dams. Jonas (1955) repeated Warren's study in the early 1950s and found no beaver or recent dams. Jonas (1955, 1956, 1959, pers. comm. 1987) attributed the decline in beaver to three factors: (1) lack of preferred food plants, (2) poor water conditions, and (3) the rapid silting in of beaver ponds. Jonas concluded that the beavers' "unfortunate food situation . . . was a result more from the overpopulation of elk than from any other single cause." He also concluded that the poor water conditions and the siltation of beaver ponds were caused by overgrazing. In 1986, Kay (1987, 1990) repeated Warren's and Jonas's surveys. He found no beaver and no indication of beaver activity since the 1950s (figure 16.5).

Beaver need tall willows or aspen—which have also declined in the park (Kay 1985, 1987, 1990)—as food and dam building materials. Aspen and willows cut by beaver normally resprout (Kindschy 1989) and in turn provide additional beaver food. However, once the mature aspen trees or tall willows are cut, the new suckers are entirely within reach of browsing elk (McMillan 1950). By preventing aspen and willows from growing into sizable plants, elk and moose eliminate beaver foods, and thus beaver. Flook (1964) reported that high elk numbers negatively affected beaver through interspecific competition for willows and aspen in Banff and Jasper National Parks. Bergerud and Manuel (1968) noted that high moose densities had a similar negative effect on beaver in Newfoundland. In South Dakota, heavy grazing by domestic livestock not only reduced woody vegetation, but also negatively impacted beaver populations (Smith and Flake 1983; Dieter 1987; Dieter and McCabe 1989). Though a few beaver persist in Yellowstone, for all practical purposes that species is ecologically absent from the northern range.

Recent studies by Bureau of Land Management and Forest Service researchers have shown that beaver create and maintain riparian areas which are critical to other wildlife. In fact, both agencies have transplanted beaver to restore livestock-damaged riparian areas (Munther 1981, 1983; Smith 1980, 1983a, 1983b). Moreover, other researchers have demonstrated that beaver is a keystone species that completely alters the hydrology, energy flow, and nutrient cycling of aquatic systems (Parker et al. 1985; Naiman, Melillo, and Hobbie 1986; Platts and Onishuk 1988).

Beaver dams impound water and trap sediments which raise the water table, increase the wetted perimeter, and allow the extension of riparian communities into what were once upland sites (Smith 1980; Apple 1983). In addition, beaver dams regulate stream flow by storing water, reducing peak or flood flow, and augmenting low flows during summer (Smith 1983b). During dry periods, 30–60 percent of the water in a stream system can be held in beaver ponds (Smith 1983a). By trapping silt over thousands of years, beaver dams created many of the West's fertile valley floors (Apple 1983).

Munther (1981, 1983) reported that a typical creek without beaver furnishes only about one to two hectares of riparian habitat per stream kilometer on the northern Rockies. With beaver activity, that area can be expanded to ten hectares per kilometer (Munther 1981, 1983). Hence, the elimination of beaver over most of the northern range may have significantly altered the ecology of areas that formerly supported the species.

According to the "natural-regulation" hypothesis, competitive exclusion of sympatric herbivores will not occur. Since elk and moose have apparently acted to competitively exclude beaver, this is another basis for rejecting the "natural-regulation" paradigm.

Figure 16.5 a. Beaver dam on the north fork of Elk Creek on Yellowstone's northern range near Tower Junction in 1921. Note aspen in upper left and willows to the right of the dam. Photo by Edward Warren (1926:84) courtesy College of Environmental Science and Forestry, State Univ. of New York, Syracuse. Photo no. 5145, August 10.

Figure 16.5 b. That same area in 1954. Note the decline of aspen and willows. The stream has downcut approximately 2 m through the old beaver dam. Photo courtesy Robert Jonas (1955:37), June 12.

Moreover, in the absence of beaver, several streams on the northern range have downcut 1–2 m (figure 16.5; Kay 1990), lowering the water table and reducing the wetted perimeter. In our opinion, the virtual elimination of beaver has had a greater long-term adverse effect on water resources available to willow communities than any drought or hypothesized climatic change. In all probability, many riparian communities on the northern range have become drier over the years due to the competitive exclusion of beaver by elk.

White-tailed Deer. A small population of white-tailed deer *(Odocoileus virginianus)* inhabited Yellowstone's northern range during the late 1800s and early 1900s (Skinner 1929). That population declined during the 1920s and was essentially extinct by 1930 (Houston 1982.182). These whitetails were associated with thickets of riparian vegetation (Skinner 1929:102), as is the case throughout their range north of the park. In recent years whitetail populations have increased outside the park, and a few have been observed in Yellowstone (Singer 1989). However, whitetails have not become reestablished in the park. In our opinion, the absence of tall-willow communities and other tall deciduous shrub habitats on the northern range due to repeated browsing makes it highly unlikely that whitetails will regain a permanent foothold in the park.

Other species. Judging from other studies (Page et al. 1978; Casey and Hein 1983; Marcuson 1983; Platts et al. 1983; Taylor 1986; Knopf, Sedgwick, and Cannon 1988; Putman et al. 1989), the decline of tall willow communities on Yellowstone's northern range may also adversely affect birds, small mammals, and even grizzly bears (*Ursus arctos*) (Kay 1990). The elimination of beaver and willow bank cover probably has also caused decreases in the distribution and numbers of native trout species (W. Platts, pers.

Figure 16.5 c. That same area in 1986. Note the continued absence of aspen and willows as well as the browse line on the conifers. Most of the area in the original photo has reverted to a dry grassland type. The stream has continued to downcut and is severely eroding its banks. Photo by Charles E. Kay (no. 3081-33), July 15.

numbers of native trout species (W. Platts, pers. comm. 1989). Entire plant and animal communities, not just tall willows, may have been altered by ungulate use in the park. Clearly, the physical stature of the vegetation is important in determining the composition of animal communities which use that habitat. The grazing-induced short-willow communities which presently exist in the park are not ecologically equivalent to the tall-willow communities that once occupied those same areas.

Our findings appear to reject the criteria proposed by Houston (in 1976) for evaluation of the "natural-regulation" hypothesis.

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Recent environmental changes inferred from the sediments of small lakes in Yellowstone's northern range

D.R. Engstrom[1], C. Whitlock[2], S.C. Fritz[1] & H.E. Wright, Jr.[1]

[1] *Limnological Research Center, University of Minnesota, Minneapolis, MN 55455, USA*
[2] *Division of Earth Changes, Carnegie Museum of Natural History, Pittsburgh, PA 15213; Current address: Department of Geography, University of Oregon, Eugene, OR 97403, USA*

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Abstract. Recent sediments of eight small lakes in the northern winter range of Yellowstone National Park were cored to examine stratigraphic records of past changes in limnology and local environment that might be attributed to grazing and other activities of elk, bison, and other large ungulates. Cores of undisturbed sediment were analyzed at close intervals to depths covering the last 100–150 years according to chronologies established by lead-210 dating. Pollen analyses were made to show changes in regional vegetation, and diatom and geochemical analyses were made to reveal possible limnological changes resulting from soil erosion and nutrient input from the lake catchments. Variations in sedimentary components prior to establishment of the park in 1872 indicate some natural variability in environmental factors e.g. erosional inputs in landslide areas west of Gardiner. All lakes had abundant nutrient inputs.

After the park was founded, fire suppression may have been responsible for small increases in pollen percentages of various conifers and *Artemisia tridentata* (big sagebrush) at different times in different lakes. Perceptible decreases in pollen of willow, aspen, alder, and birch at different times may reflect local ungulate browsing, although drier climatic conditions may have been a factor as well.

The most striking manifestation of accelerated erosion in a catchment was found at a lake located beside a road constructed in the 1930s. In contrast to changes at this site, the record of erosion at other lakes is hardly perceptible. Changes in sediment-accumulation rates seen at most sites result from redistribution of sediment within the lake after initial deposition.

In the century following park establishment, the abundance of planktonic diatoms relative to benthic taxa varies among lakes and may reflect differential nutrient inputs or changes in lake level. Four of the five lakes analyzed for diatoms show in the last few decades an increase in planktonic relative to benthic species, implying elevated nutrient inputs. The recent flora, however, is similar to that in pre-park levels which suggests that these lakes have not been perturbed outside their normal range. Increased nutrient supply in recent decades for at least two of the lakes is supported by the geochemical data, which show an increase in biogenic silica and in organic matter.

As a whole, our investigation of the sedimentary record does not support the hypothesis that ungulate grazing has had a strong direct or indirect effect on the vegetation and soil stability in the lake catchments or on the water quality of the lakes.

Key words: diatom stratigraphy, elk populations, erosion rates, lead-210 dating, paleoecology, paleolimnology, pollen analysis, range management, sediment geochemistry, ungulates, Yellowstone National park.

Introduction

The northern range of Yellowstone National Park (Fig. 1) is so named because in the winter the principal ungulates in the park—elk, bison, antelope, and deer—move out of the higher-elevation forested regions down to the valleys of the Lamar and Gardner rivers, where snow cover is less deep and forage is more accessible. It has been suggested that an increase in the winter population of ungulates, particularly in the last 20 years, has resulted in deterioration of the range because of over-utilization of food resources and increased erosion (Chase, 1986; Kay, 1984). Evidence cited to support this hypothesis is the decline of aspen, willow, and other browse and increased turbidity in the Yellowstone River downstream from the park.

The controversy surrounding management of the northern range centers on the question of whether Yellowstone Park is an intact ecosystem in which ungulate populations are regulated by the carrying capacity of the winter range, or whether substantial human manipulation of these populations is required because key elements of the pristine ecosystem (predators, Indians, contiguous range outside the park) are permanently missing. Early park management (1886–1930) encouraged the expansion of ungulate herds through winter feeding and the elimination of predators and hunting. However, concern for the long-term viability of winter rangelands led eventually to direct reduction of elk populations by trapping and shooting from 1935 to 1968 (Houston, 1982). Because of increasing political and scientific criticism, elk removals were curtailed in 1969, and the current policy of 'natural regulation' (whereby animal populations are allowed to fluctuate according to environmental conditions) began.

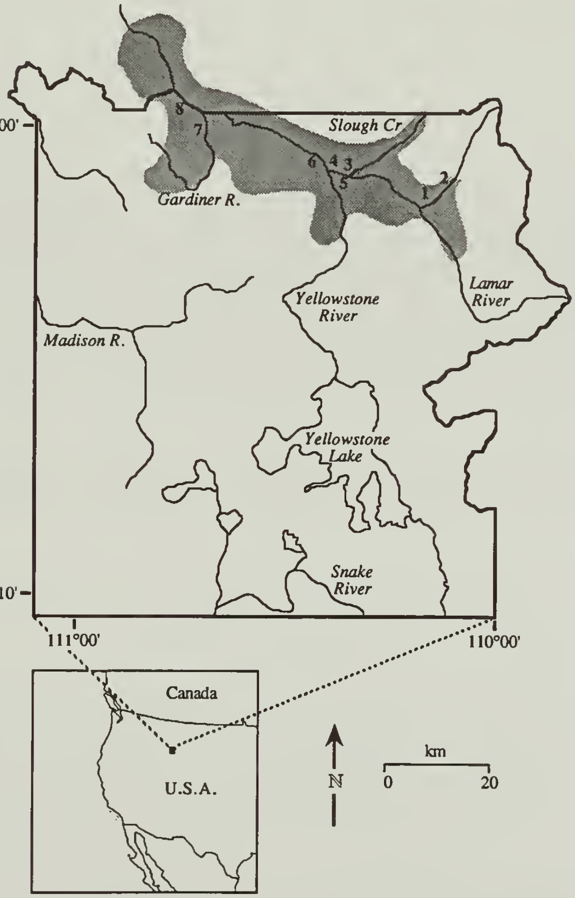

Fig. 1. Map of Yellowstone National Park and the northern winter range (shaded); after Houston (1982). Study lakes are marked by number: (1) Foster, (2) Buck, (3) Slough Creek, (4) Buffalo Ford, (5) Big Trumpeter, (6) Floating Island, (7) Big Slide, (8) Middle Rainbow.

The dramatic rise in elk and bison populations since the late 1960s (Fig. 2) has again raised concerns about overgrazing and the question of whether such numbers of ungulates are indeed a natural component of the northern range. If large ungulate herds predate park establishment, conditions today would seem to fall within the limits of natural environmental variability. If not, then the potential for permanent degradation of vegetation and soils would appear quite real. In the words of one protagonist in this debate (Chase, 1986): 'The key to the future of Yellowstone, therefore, 'lies' in its past.' Unfortunately, the observations of early explorers and park mangers in the late 1800s are inconclusive on this matter, and an understanding of Yellowstone's past must come instead from the sedimentary record.

The objective of the present study is to examine the landscape history recorded in sediments of small lakes in the northern range in order to unravel the environmental perturbations of the last 150 years. Of particular interest are changes that took place after the park was established in 1872. A simple model that isolates elk as the sole agent of environmental change in the northern range would predict the following: Overpopulation of elk should be recorded in lake sediments by (1) an increase in silt derived from eroded hillslopes or from trampled lake margins; (2) a decrease in the pollen of aspen, willow, alder, and birch; (3) an increase in the pollen of weedy plants associated with soil disturbance, including ragweed and various chenopods; (4) an increase in indicators of eutrophic conditions in the lake, caused by increased manuring near the lake shore.

In reality the model is by no means so simple. During the 117-year history of the park other environmental changes have occurred in addition to fluctuations in ungulate numbers, and any landscape

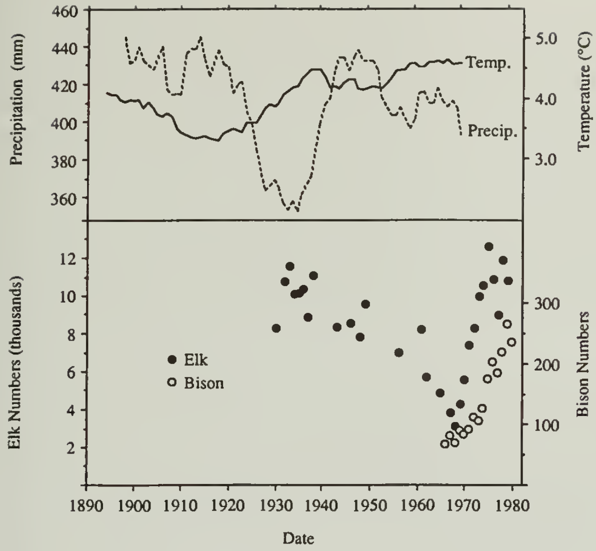

Fig. 2. Historical records of climate change and ungulate populations in the Northern Range (from Houston 1982). Mean annual precipitation and temperature trends from Mammoth Hot Springs are shown as 15-yr running averages.

history of the northern range must consider the synergistic effect of all these factors. For example, climate has changed throughout the period in question (Fig. 2). Droughts occurred in the park in the 1880s, 1897–1905, 1922–1924, 1930–1937, 1952–1957, 1966, and 1973–1974 (Dirks & Manner, 1982). On the other hand, some early years of the park (1889–91) were wetter than average, as was the period from 1910 to 1917. Climate change could be an external force controlling erosion and sedimentation patterns, vegetation, animal populations, and their interactions.

Another factor in shaping the landscape of the northern range is the notable absence of fire. The natural recurrence interval of fires in the northern part of the park is estimated at 20–25 years on the basis of fire-scars on Douglas-fir (Houston, 1973). However, under climatic conditions of the last 117 years and a policy of fire suppression most of the northern range has not burned. The fires of 1988 reached one of the study sites, and even then burned it only partially. The effects of fire suppression and climate are obvious when photographs taken 80 to 100 years ago are compared with the modern landscape. The character of the steppe has changed towards more sagebrush, and forests have become more closed (Houston, 1982).

Animals other than ungulates have also left their imprint on lakes in the region. Beavers were active on the northern range until about 1950 (Warren, 1926; Jonas, 1955); today they are rare. Their demise has been ascribed to climate changes, overgrazing of riparian vegetation by elk, and consequent loss of their habitat and food source, all of which should be evident in the sedimentary record.

Finally man and his activities have changed the northern range in ways that should be preserved in lake sediments. Evidence of agriculture, ranching, and road construction dating back to the 1860s can be found in both fossil and chemical records.

In order to reconstruct a landscape history of the last 150 years, we examined the sedimentary record of eight small lakes in the northern range (Table 1). Sediment chronology was determined by lead-210 analysis, and concentrations of major metals and nutrient elements were studied to determine shifts in sediment input and nutrient enrichment. Pollen was examined to determine changes in the local and regional vegetation, and diatoms were analyzed at five sites to identify changes in lake trophic-state related to water depth and nutrient input. Study lakes were chosen that (1) were in largely unforested areas known to receive heavy winter use by elk bison, and antelope; (2) were small and had small catchments; (3) were unlikely to have dried in the last 150 years; (4) had a minimal fringe of littoral vegetation, which might screen out sediment washed in from hillslopes; and

Table 1. Location and certain morphometric and chemical characteristics of the lakes investigated. Water chemistry data for Foster, Buck, and Big Trumpeter lakes from Jones *et al.* (1978) and Sharpe & Arnold (1966).

Lake	Latitude	Longitude	Elevation (m)	Area (ha) Lake	Land[1]	Depth max	mean	Volume $(10^3\ m^3)$	Cond. (µS/cm)	Major ions	total-P (ppb)
Foster	44° 52′	110° 10′	2018	3.2	90	5.8	2.2	70	390	$Mg(Ca):HCO_3^-$	36
Buck	44° 54′	110° 08′	2118	2.3	40	11.3	4.7	108	250		
Slough Creek	44° 56′	110° 21′	1884	2.1	100	8.0	4.0	84	480	$Mg(Ca):HCO_3^-$	34
Buffalo Creek	44° 58′	110° 23′	1917	4.3	300	5.4	3.4	144			
Big Trumpeter	44° 55′	110° 22′	1873	12.3	80	3.0	1.6	194	850	$NaMg:HCO_3^-$	52
Floating Is.	44° 57′	110° 27′	1996	3.2	60	3.0	1.4	46	600	$Mg(Na):HCO_3^-$	13
Big Slide	45° 00′	110° 42′	1728	3.0	330	4.5	2.8	84	270	$Ca(Mg):HCO_3^-$	143
M. Rainbow	45° 02′	110° 44′	1792	2.3	210	2.6	1.4	32	210	$Na(Ca):HCO_3^-$	86

[1] Area of catchment excluding lake.

(5) were located far enough from a road (with one exception) so that erosion during road construction would not be a significant constituent of the sediment.

Modern vegetation

The vegetation of the northern range has been described by Houston (1982) and Despain *et al.* (1986); see Table 2 for common and scientific names used in the text. Forty-one percent of the range is forested by conifers, 2% is covered by aspen, 27% is grassland, and the remainder is a mixture of vegetation types along with barren ground (Despain *et al.*, 1986). The upland grassland is dominated by Idaho fescue, bearded wheatgrass, and bluebunch wheatgrass at its highest elevations, northern slopes, and ridgetops. Steppe dominated by big sage and bluebunch wheatgrass grows

Table 2. Common and scientific names used in text; nomenclature follows Despain (1975).

Common Name	Scientific Name
Alder, mountain	*Alnus incana*
Aspen	*Populus tremuloides*
Birch, water	*Betula occidentalis*
Bitterbrush	*Purshia tridentata*
Bulrush	*Scirpus*
Cattail	*Typha latifolia*
Chenopod/amaranth families	Chenopodiineae
Clematis	*Clematis*
Composite family	Compositae, including Tubuliflorae
Douglas-fir	*Pseudotsuga menziesii*
Duckweed	*Lemna*
Fescue, Idaho	*Festuca idahoensis*
Fir, subalpine	*Abies lasiocarpa*
Gooseberry	*Ribes*
Greasewood	*Sarcobatus*
Hairgrass	*Deschampsia*
Honeysuckle	*Lonicera*
Juniper, common	*Juniperus communis*
Juniper, Rocky Mountain	*Juniperus scopulorum*
Oregon grape	*Mahonia*
Pahute weed	*Suaeda*
Pine, limber	*Pinus flexilis* (Haploxylon-type)
Pine, lodgepole	*Pinus contorta* (Diploxylon-type)
Pine, whitebark	*Pinus albicaulis* (Haploxylon-type)
Pond lily, Indian	*Nuphar polysepalum*
Pondweed	*Potamogeton*
Poplar, narrow-leaved	*Populus angustifolia* (*balsamifera*-type)
Rabbit-brush	*Chrysothamnus*
Ragweed	*Ambrosia*
Rose, Wood's	*Rosa woodsii*
Sage, sagebrush	*Artemisia*
Big	*Artemisia tridentata*
Silver	*Artemisia cana*
Saltbush	*Atriplex*
Sedge	*Carex*
Sedge family	Cyperaceae
Snowberry	*Symphoricarpos*
Spirea	*Spiraea*
Spruce, Engelmann	*Picea engelmannii*
Wheatgrass, bearded	*Agropron cristatum*
Wheatgrass, bluebunch	*Agropyron spicatum*
Sumac, smooth	*Rhus trilobata*
Water-milfoil	*Myriophyllum spicatum*
Water smartwood	*Polygonum amphibium*
Willow	*Salix*

on the alluvial soils of valley floors and west, south, and east slopes between 1800 and 2500 m. Deep alluvial valleys support wet meadows of hairgrass and sedge, as well as riparian shrubs such as willow, birch, and alder. The forest from 1500 to 2100 m is composed of Douglas-fir and, to a lesser extent, lodgepole pine. In cold-air drainages and at higher elevations Engelmann spruce and subalpine fir are common, and whitebark pine occurs on northern slopes above 2700 m. Aspen occurs as small groves along forest–grassland boundaries, flood plains, and stream banks. At lower elevations in the Gardner and Lamar valleys, Rocky Mountain juniper and limber pine grow along streams, as do narrow-leaved poplar and water birch. The slopes are sparsely vegetated on the shale substrates at lower elevations, and greasewood and saltbush are common on alkaline soils.

Modern limnology

The limnological of the eight study sites are summarized in Table 1, with morphometry and core-site locations illustrated in Fig. 3. The lake basins represent small glacial kettles or landslide depressions of 2–12 ha in surface area at 1728–2118 m in elevation. Most of the lakes are fairly shallow, with mean depths less than 5 m and maximum depths under 8 m (except one site at 11 m). Limited water-chemistry data indicate that the lakes are moderately high in dissolved solids with Mg^{2+}, Na^{+}, and HCO_3^- the dominant ions in most cases. Total phosphorus values are generally above 30 ppb, implying that these lakes are presently mesotrophic to eutrophic (Jones *et al.* 1978, and results from this study).

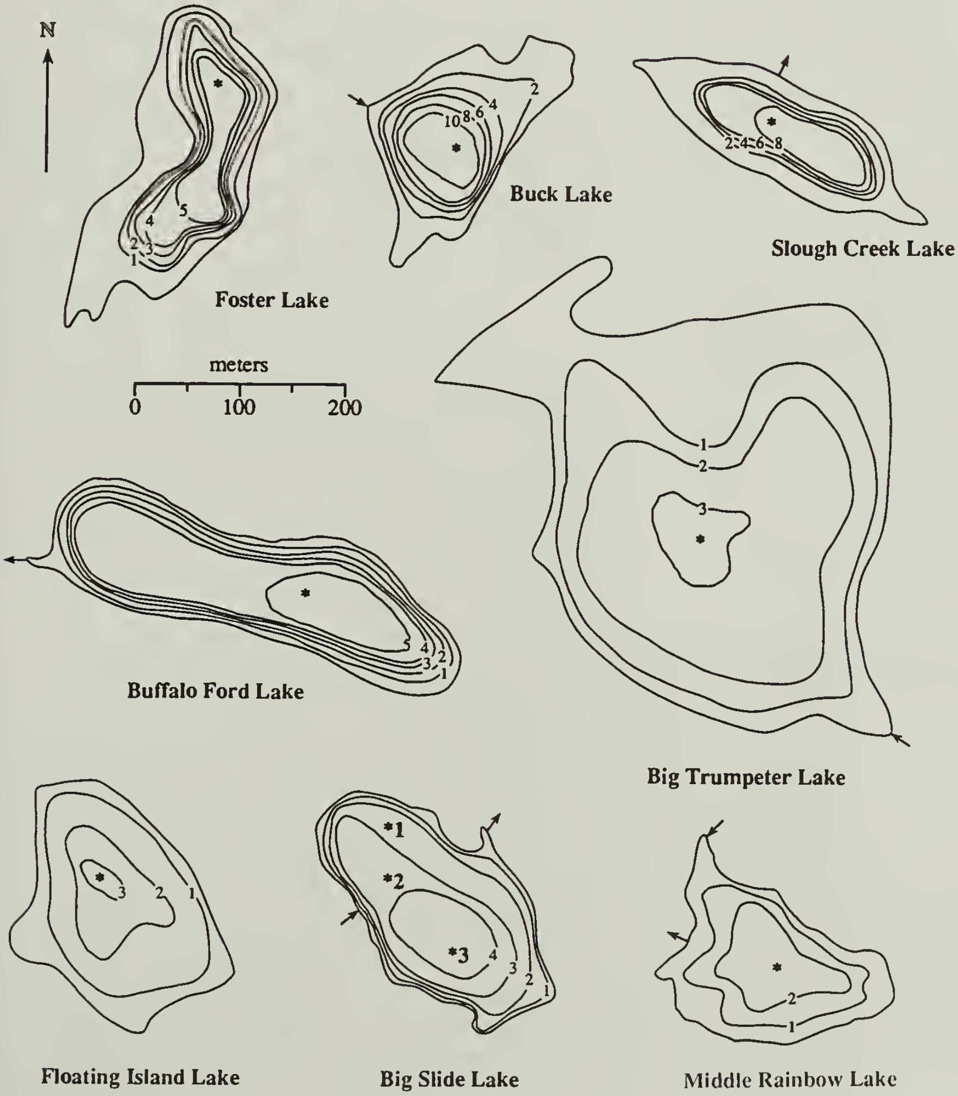

Fig. 3. Bathymetric maps of the lakes investigated, showing location of coring sites; depth contours in metres. Bathymetry for Big Trumpeter and Middle Rainbow lakes from Jones *et al.* (1978) and Dean *et al.* (1974).

Methods

Coring

Cores about one meter long were taken from the deepest part of each lake by means of a 5-cm diameter polycarbonate tube fitted with a piston and operated from the lake surface by rigid drive-rods. This device recovers even the very loose uncompacted sediment surface without disturbance. Cores were extruded vertically from the top of the tube at intervals of 0.5–2.0 cm. The samples were stored in polypropylene containers and refrigerated until subsampled for various analyses.

Pollen

Pollen samples were prepared according to procedures described by Faegri & Iversen (1975). A known quantity of a *Eucalyptus* pollen was added to each sample as a tracer to permit calculation of pollen concentration. Residues were mounted in silicon oil, and pollen was identified under magnifications of 400× and 1000×. At least 400 terrestrial pollen grains were counted for each level.

Diatoms

Samples for diatom analysis were oxidized in nitric acid and potassium dichromate and then washed repeatedly with distilled water to remove excess acid. Diatom samples were mounted in Naphrax and counted at magnifications of 1425×. A minimum of 500 valves was counted at each level.

Lead-210 Dating

Sediment cores were analyzed at 12–19 depth intervals for ^{210}Pb to determine age and sediment-accumulation rates for the past 100–150 years. Lead-210 was measured through its granddaughter product ^{210}Po, with ^{208}Po added as an internal yield tracer. The polonium isotopes were distilled from 0.2–4.0 g dry sediment at 550° C following pretreatment with concentrated HCL and were plated directly (without HNO_3 oxidation) onto silver planchettes from a 0.5 N Hcl solution (modified from Eakins & Morrison, 1978). Activity was measured for $1–5 \times 10^5$ s with Si-depleted surface barrier detectors and an Ortec Adcam^{TM} alpha-spectroscopy system. Unsupported ^{210}Pb was calculated by subtracting supported ^{210}Pb (estimated from constant activity at depth) from total activity at each level. Dates and sedimentation rates were determined according to the c.r.s. (constant rate of supply) model (Appleby & Oldfield, 1978), with confidence intervals calculated by first-order error analysis of counting uncertainty (Binford, 1990).

Geochemistry

A step-wise procedure for selective dissolution of lake sediments modified from Engstrom & Wright (1984) and Engstrom & Swain (1986) was used to separate authigenic components from allogenic materials, with a separate extraction for biogenic silica. In this procedure, 0.1 g dried sediment was first oxidized with 30% hydrogen peroxide, followed by treatment with 1 M hydroxylamine hydrochloride in 25% acetic acid to dissolve carbonates, oxyhydroxides, and organically bound metals (the authigenic fraction). The remaining mineral residue (the allogenic fraction) was fused with lithium metaborate to complete the digestion. Biogenic silica was selectively dissolved from a separate 0.1 g aliquot of sediment in 0.2 M NaOH, and allogenic silica was determined by the difference between the borate fusion and the hydroxide extract. The elemental composition of each fraction was measured with a Spectraspan III^{TM} DC plasma spectrometer. Sediment composition was also estimated by loss-on-ignition techniques, whereby organic matter and carbonate content were calculated from loss of mass at 550° C and 1000° C, respectively (Dean, 1974).

Geochemical interpretation

Interpretation of geochemical stratigraphy generally follows a review of this subject by Engstrom & Wright (1984). The authigenic component is here represented by concentration curves (mg/g dry sediment) or simple ratios of P, Fe, Mn, and Ca, and the allogenic fraction is illustrated by profiles for K_2O and SiO_2. The ratio between K_2O and SiO_2 provides an index for variations in clastic composition that might indicate changes in the source of erosion. In practice these fractions are operationally defined by the extraction protocol and thus only approximate the true provenance of the sediments.

The chemical stratigraphy or radiometric dating of a single sediment core, if viewed independently, can prove deceptive in reconstructing environmental change on a lake-wide basis. Paleolimnological interpretations usually require an understanding of basinwide changes in deposition, but chemical composition alone does not reveal changes in flux, and sediment accumulation at a single core-site may not be a reliable index of lake-wide events. The difficulty in reconstructing input changes from profiles of chemical composition arises from the numerical interdependence of concentration data; it is difficult to know if the flux of one component is increasing or if the flux of another is decreasing. Changes in an accumulation profile may reflect shifts in the pattern of sediment deposition within the basin, as opposed to changes in material input to the lake. The possibility that sediment focusing underlies an increase in sedimentation at a single core-site is not always recognized in the paleoecological literature (see Battarbee, 1978; Dearing, 1983; Engstrom & Swain, 1986).

It is possible however, to distinguish between shifts in sediment accumulation within a lake and changes in sediment input to its basin by examining the sedimentary components of a single core. Major changes in material input to a lake (nutrients, clastics, etc.) should be evidenced by stratigraphic changes in sediment-accumulation rates and in chemical composition. On the other hand, if pronounced changes in sediment accumulation are not coincident with a shift in sediment composition, then sediment redistribution within the basement is suggested. In order for sediment accumulation to accelerate (or decelerate) without corresponding changes in chemical composition, the inputs of all sedimentary components must increase (or decrease) in constant proportion to one another—a highly unlikely event. Instead, a shift in sediment deposition pattern within the lake basin, which could move more material to a core-site without changing its composition, is much more probable.

Results

Lead-210 dating

A summary of ^{210}Pb parameters in Table 3 reveals considerable variation in sedimentary conditions among the study sites. Values for cumulative unsupported activity range from 7 to 17 pCi/cm^2 (excluding Buck Lake with 32 pCi/cm^2). The ^{210}Pb flux equivalent to these residuals is 0.21– 1.0 pCi cm^{-2} yr^{-1}, which is comparable to the estimated mean annual deposition rate (ca. 0.2–1.0 pCi cm^{-2} yr^{-1}) for atmospheric fallout (Krishnaswamy & Lal, 1978). The high ^{210}Pb flux at Buck Lake probably results from more intense focusing of fine-grained sediments (with which ^{210}Pb is associated) in this deep steep-sided basin. The effect of sediment focusing on ^{210}Pb flux is also shown by the relationship between water depth and ^{210}Pb residuals in the three cores from Slide Lake. Core 1, located in the deepest part of the basin (4.20 m) has nearly twice the cumulative unsupported activity as cores 2 and 3 (taken respectively in 3.10 and 2.25 m water depth). Such spatial differences in ^{210}Pb flux are typical of many lakes (Oldfield & Appleby, 1984) and will not compromise dating accuracy so long as the pattern of ^{210}Pb deposition remains constant over time.

Unsupported ^{210}Pb concentrations in the surface sediment of most of the sites are about 10 pCi/g. However, surface activities are almost twice this high in Slough Creek Lake (17.7 pCi/g) and less than half this value in Big Slide and Middle Rainbow lakes (3–5 pCi/g). High sediment inputs to Big Slide and Middle Rainbow lakes (0.08–0.18 g cm^{-2} yr^{-1} are mean rates since 1872) severely dilute the atmospheric flux of ^{210}Pb, while low sediment loading to Slough Creek Lake (0.013 g cm^{-2} yr^{-1}) has the opposite effect. An inverse relationship between sedimentation rates and mass-specific lead-210 activity is predicted by the c.r.s. dating model (Appleby & Oldfield, 1983). Supported ^{210}Pb activities at depth in these cores ranges from 0.3 to 1.3 pCi/g.

Plots of ^{210}Pb concentration versus cumulative dry mass (Fig. 4) are, for the most part, non-exponential and

Table 3. ^{210}Pb parameters and sediment-accumulation rates for cores from the Northern Yellowstone Range.

Coring Site	Cumulative unsup. ^{210}Pb (pCi/cm)	Unsup. ^{210}Pb conc. at surface (pCi/g)	Supported ^{210}Pb (pCi/g)	Number of supported samples	Mean sed. rate since 1872 (g cm^{-2}y^{-1})	Mean ^{210}Pb flux (pCi cm^{-2}y^{-1})
Foster	9.52	10.14	0.32	4	0.028	0.30
Buck	31.97	11.54	1.26	2	0.041	1.00
Slough Creek	11.70	17.72	0.26	5	0.013	0.37
Buffalo Ford	13.94	9.47	1.12	3	0.031	0.44
Big Trumpeter	9.96	10.24	0.34	2	0.038	0.31
Floating Island	6.71	11.63	0.40	6	0.014	0.21
Big Slide						
Core #1	17.48	4.13	0.85	4	0.080	0.55
Core #2	8.85	4.81	0.59	6	0.064	0.28
Core #3	8.14	4.64	0.51	3	0.175	0.26
Middle Rainbow	13.37	3.11	0.67	2	0.099	0.42

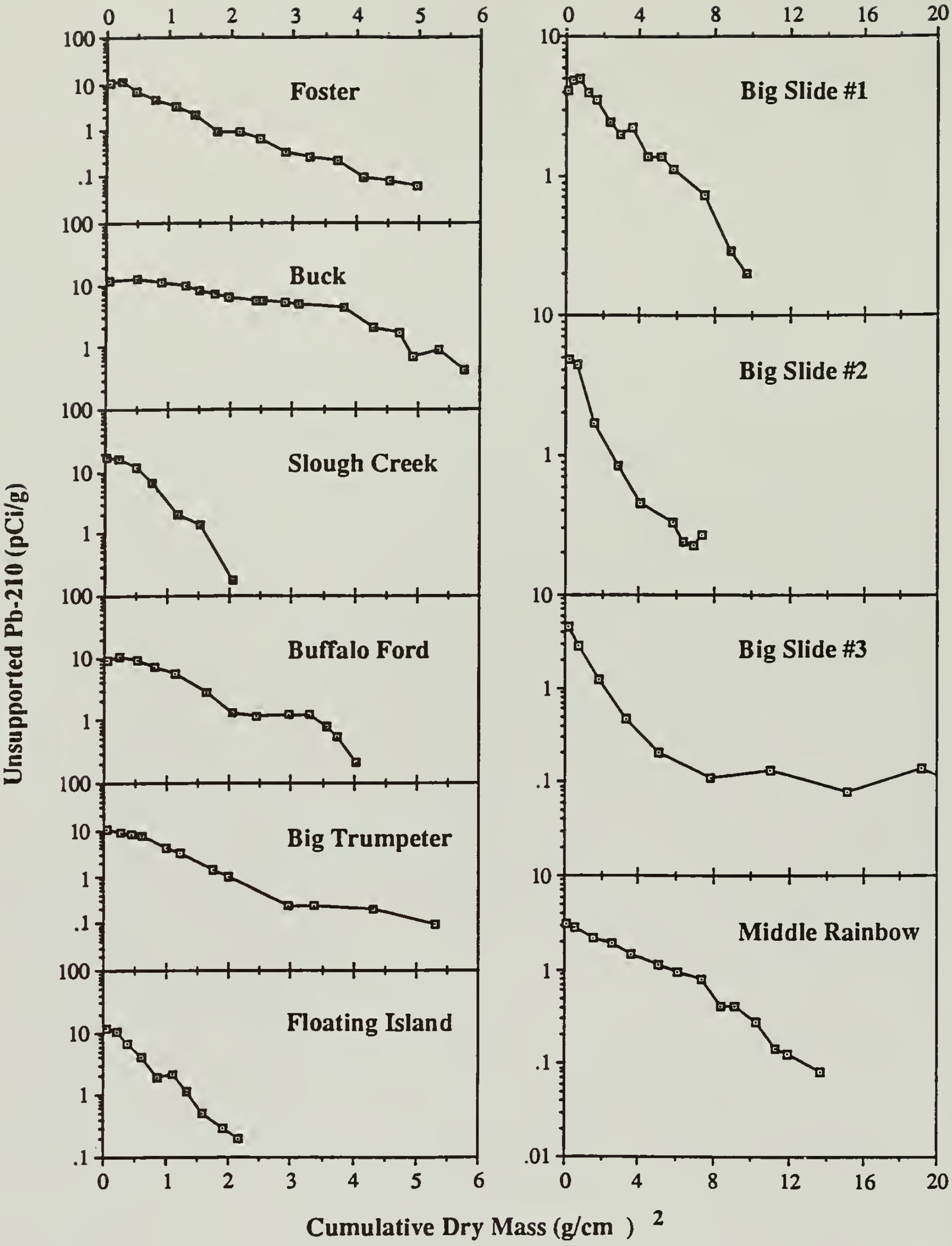

Fig. 4. Plots of unsupported lead-210 vs. cumulative dry mass. Counting errors are generally smaller than the plotted symbols and are not shown.

in some cases non-monotonic. In these curves changes of slope, particularly flat spots and kinks, represent major shifts in sediment accumulation that can only be fully explored by the c.r.s. dating model. Age–depth relationships derived from c.r.s. calculations are shown in Fig. 5, and sedimentation rates are illustrated in Fig. 6. The error bars shown in these graphs represent one standard deviation propagated from counting errors and are minimal estimates of dating uncertainty. The error terms become notably large for dates greater than 100–120 years old (about five ^{210}Pb half-lives) such that pre-park sedimentation rates are poorly known. The dating of older sediments from Big Slide and Middle Rainbow lakes is particularly imprecise, in large measure because of low unsupported ^{210}Pb concentrations caused by high sediment loading.

Foster Lake

Setting

Foster Lake lies at 2018 m elevation near the lower forest/steppe ecotone in the Lamar Valley. The lake is 3.2 ha in surface area and has a maximum depth of 5.8 m. Its waters are rich in Mg^{2+} (Ca^{2+}) and HCO_3^- (conductivity = 390 µS/cm), and mesotrophic with respect to

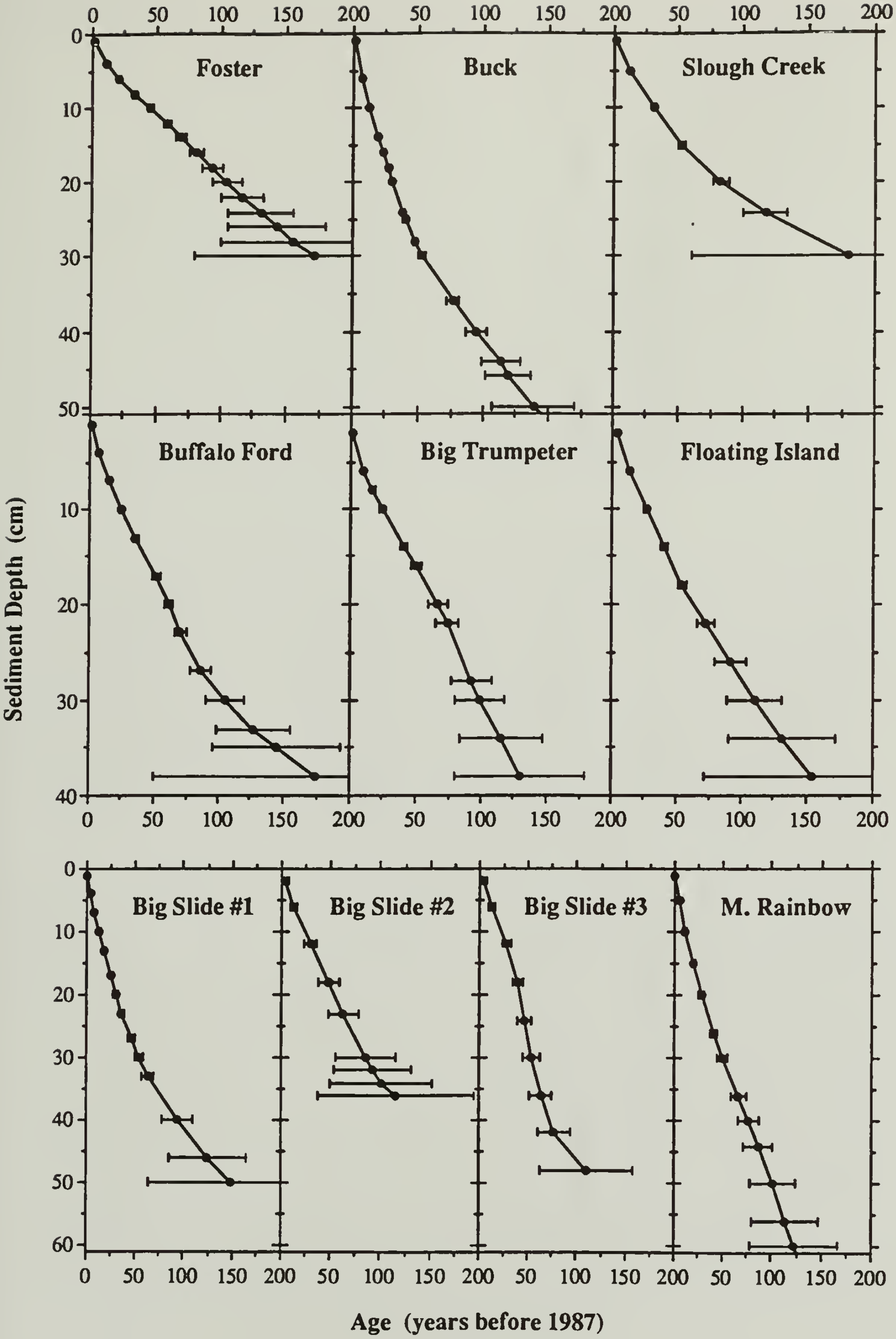

Fig. 5. Plots of age vs. sediment depth. Error bars represent 1 s.d. propagated from counting uncertainty.

phosphorus content (36 ppb). Secchi depth readings and phytoplankton collections suggest low phytoplankton production (Jones *et al.* 1978).

Surrounding the lake are stands of Douglas-fir, Engelmann spruce, and lodgepole pine. Common juniper, buffaloberry, Wood's rose, small aspen, gooseberry, snowberry, honeysuckle, and Oregon grape grow in the understory, as well as a diversity of herbs. Big sagebrush, bluebunch wheatgrass, and Idaho fescue are major elements of the steppe vegetation. Along the lake shore are willows, most of which show evidence of browsing. Water-milfoil, water smartweed, and pondweed are among the aquatic macrophytes.

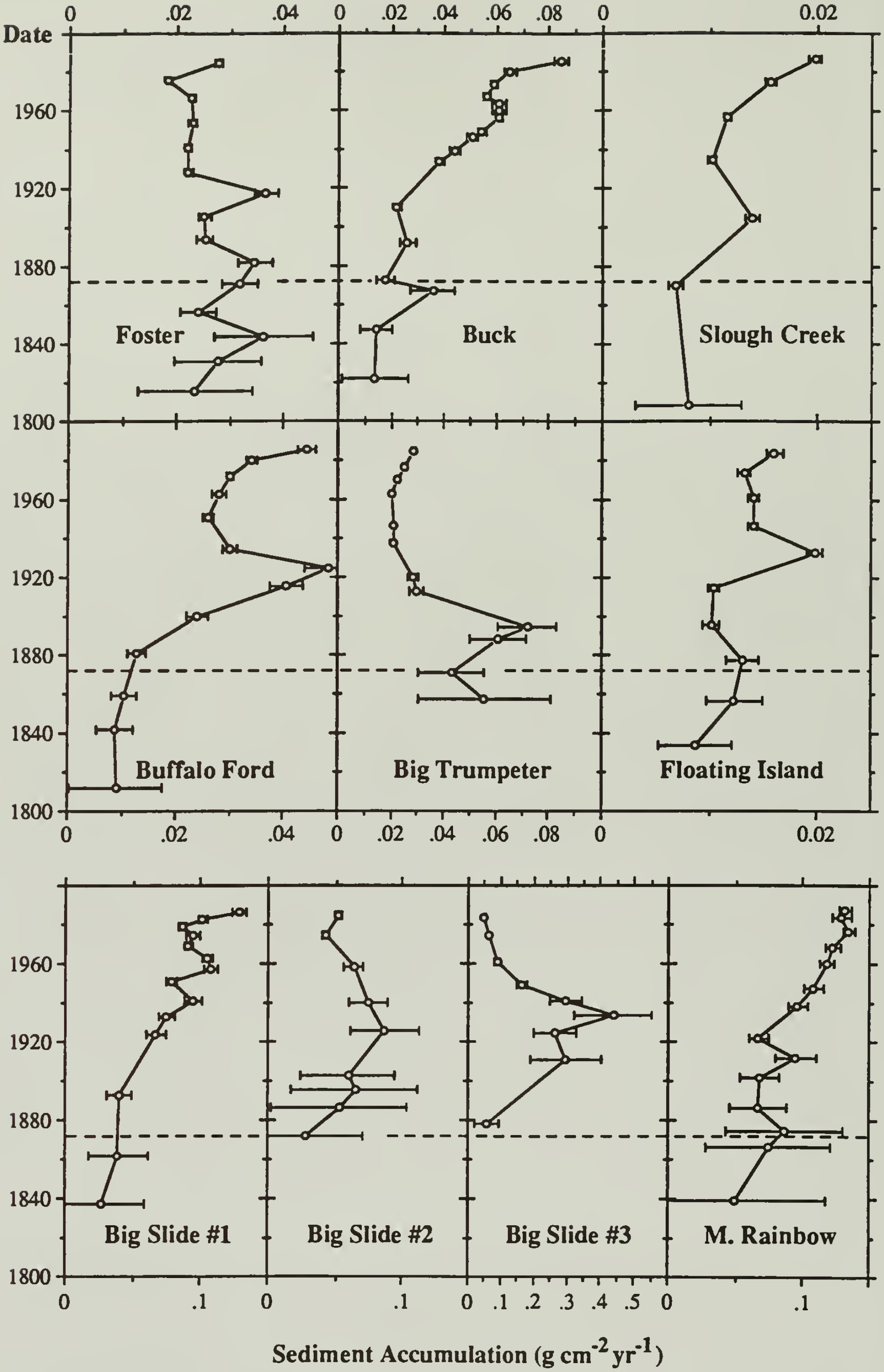

Fig. 6. Plots of sediment-accumulation rate vs. age. Error bars represent 1 s.d. propagated from counting uncertainty. Dashed line represents the date of park establishment, 1872.

Foster Lake is located in an active landslide region. A core taken in 1988 recovered only 1.75 m of lake sediment above gravel. The absence of Mazama ash in the core suggests that Foster Lake is younger than 6700 yr B.P. The lake has two inlets: a small stream on the north end, which drains a nearby meadow, and a spring on the northwest shore (Jones *et al.* 1978). The outlet at the southwest end was not active in 1986 or 1988.

Pollen

The pollen record (Fig. 7) is dominated by *Pinus*, most of which is Diploxylon-type and attributed to

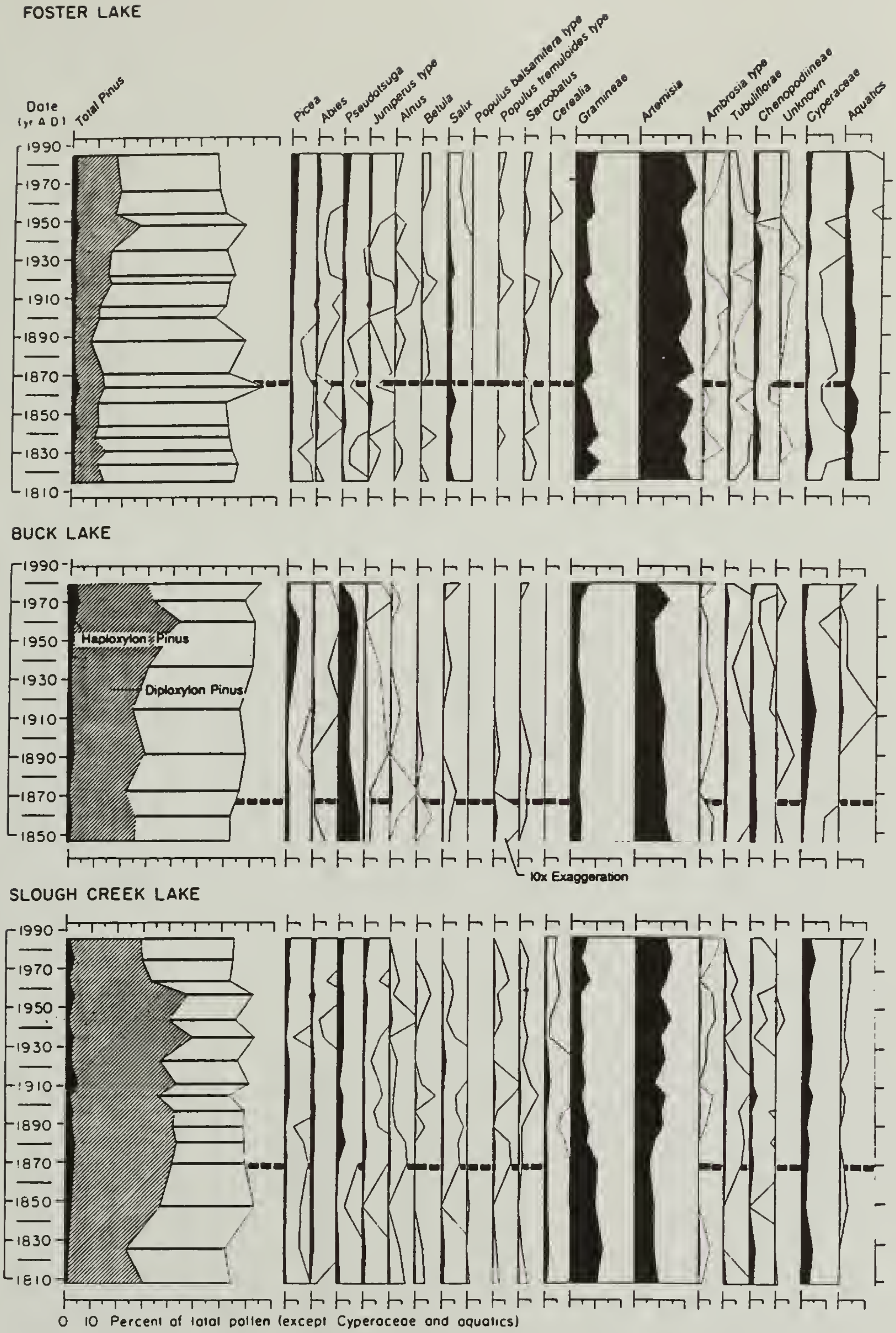

Fig. 7. Pollen diagrams for Foster, Buck, and Slough Creek lakes. Dates below 1850 are extrapolated from the base of the ^{210}Pb profile. Dashed line indicates the date of park establishment, 1872.

lodgepole pine. Diploxylon-type pine pollen is more abundant from 1895 to the present than before, but total *Pinus* does not increase during this period. Percentages of *Picea* and *Pseudotsuga* pollen increase slightly from 1900 to the present. *Abies* values also rise from 1900 to the present, although they decrease slightly from 1920 to 1950. *Salix* percentages decline after 1920. *Populus tremuloides*-type pollen is present both in park and pre-park levels in trace amounts. Cereal grasses are recorded after 1920; their source is probably ranches adjacent to the park. *Artemisia* and *Gramineae* are both well represented and show no trends through the record.

Geochemistry

The sediment core from Foster Lake (Fig. 10) is composed of roughly 24% organic matter, 32%

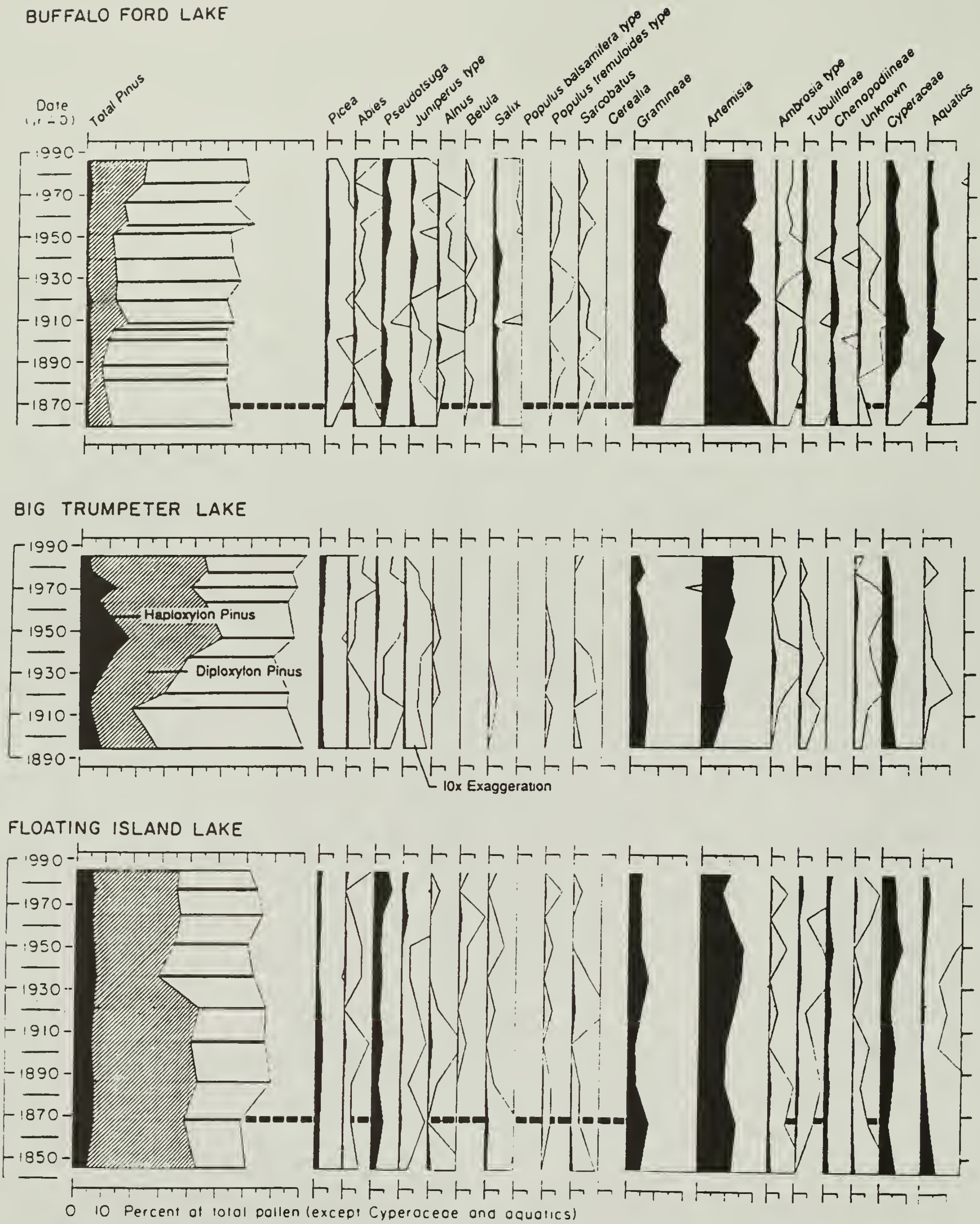

Fig. 8. Pollen diagrams for Buffalo Ford, Big Trumpeter, and Floating Island lakes. See Fig. 7 legend for further explanation.

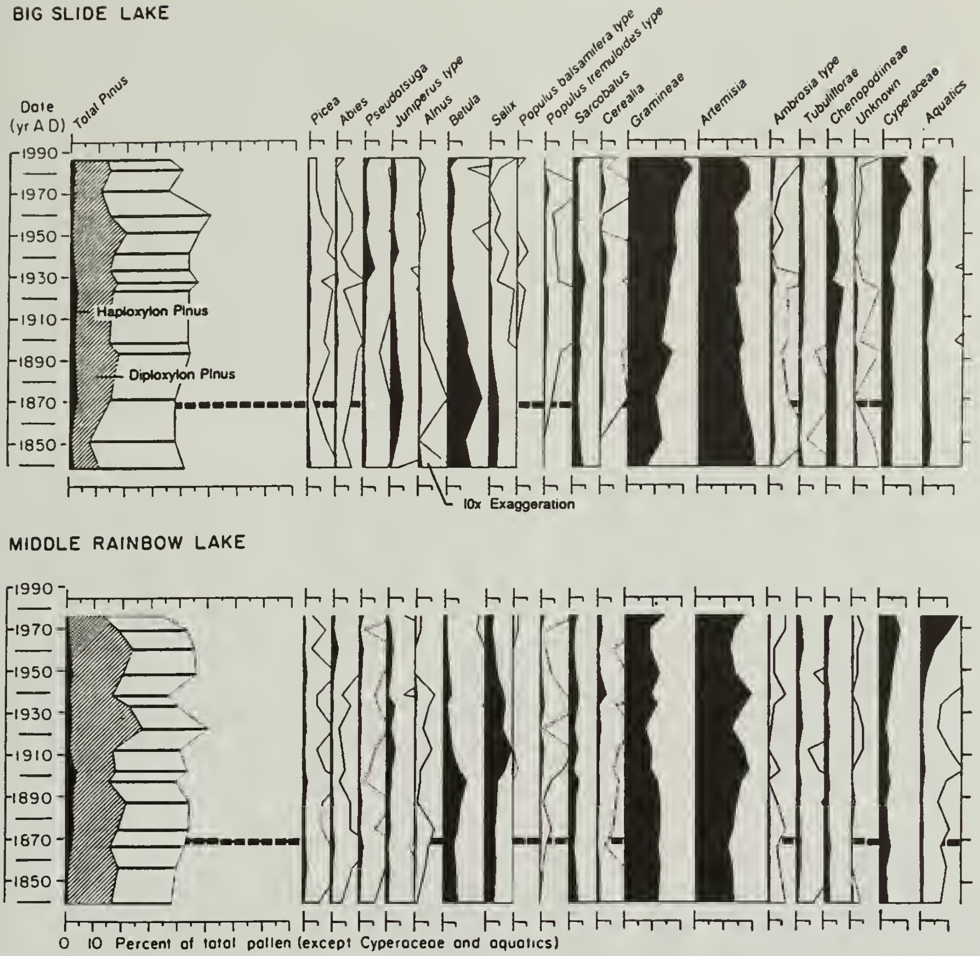

Fig. 9. Pollen diagrams for Big Slide and Middle Rainbow lakes. See Fig. 7 legend for further explanation.

carbonate (as $CaCO_3$), and 44% other inorganic materials (average dry-mass basis). The carbonate content of these sediments, which is high by comparison to the other lakes in this study, is manifest in a mean Ca content of 140 mg/g. Clastic silicates comprise the major share of the inorganic fraction, as shown by the large proportion of allogenic SiO_2 (220 mg/g) and the small contributions of non-clastic materials: biogenic SiO_2 = 30 mg/g (low by comparison to the other study sites), authigenic Fe = 10 mg/g, and authigenic P = 1 mg/g (Fe and P content are generally similar among all sites). The sediment accumulation rate for this core ranges between 0.02 and 0.03 g cm^{-2} yr^{-1}, with no obvious trends over time (Fig. 6).

The major stratigraphic changes in the Foster Lake core begin with a small pre-park increase in clastic content (allogenic SiO_2, K_2O, %-inorganic) and a corresponding decrease in biogenic SiO_2 and carbonates between 1800 and 1850. Around 1900–1920 clastic components again increase, the ratio of allogenic K_2O:SiO_2 rises, and carbonate and Ca decline by one-fourth. Because a small peak in sediment accumulation occurs at this time, an increase in clastic inputs from erosion is implied. This trend is reversed after 1930, when sediment accumulation declines and carbonates increase at the expense of clastics. Peaks in phosphorus, iron, and biogenic silica are present at the top of the core, but post-depositional mobilization or incomplete disgenesis of recent sediments rather than historical changes in deposition are probably responsible for these features.

Diatoms

The diatom stratigraphy of Foster Lake (Fig. 13) shows distinct changes in the last 150 years. The base of the analyzed sediments (ca. 1845) is dominated by the planktonic taxa *Stephanodiscus parvus* Stoerm, H. & K., *S. minutulus* (Kütz) Cl. & Möll., and *Cyclotella stelligera* Cleve & Grun. Several benthic and epiphytic species are also abundant, including *Amphora ovalis* v. *pediculus* (Kütz) V.H., *Gomphonema dichotomum* Kütz., *Cocconeis placentula* v. *lineata* (Ehr.) Cleve, *Fragilaria pinnata* Ehr., *F. brevistriata* Grun., *Navicula cryptocephala*

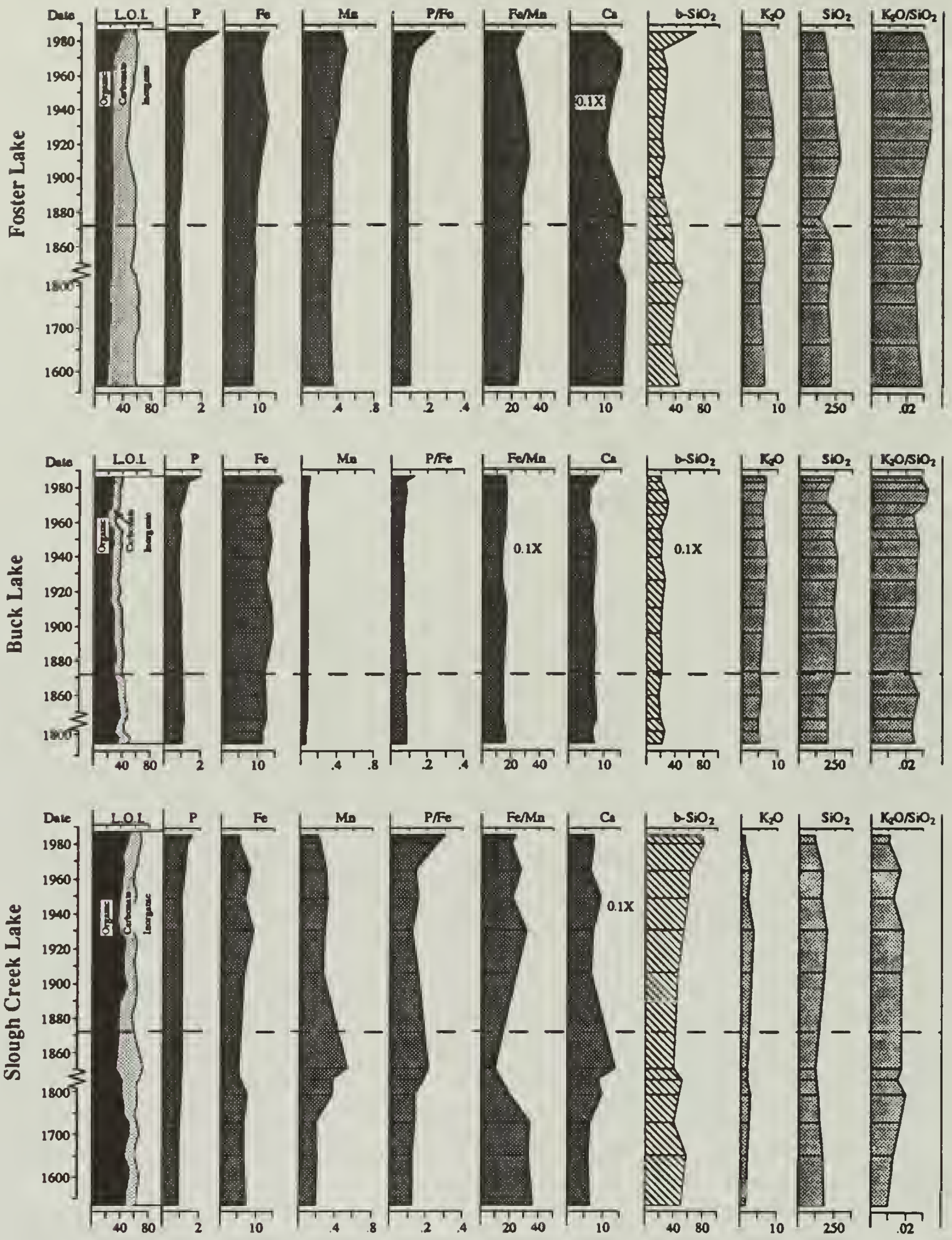

Fig. 10. Geochemical profiles for Foster, Buck, and Slough Creek lakes. Dates below 1850 are extrapolated from the base of the ^{210}Pb profile; note break in scale. Dashed line indicates the date of park establishment, 1872. L.O.I = % composition of dry sediment as determined from loss-on-ignition methods. P, Fe, Mn and Ca represent authigenic components, b-SiO$_2$ = biogenic silica, and K$_2$O and SiO$_2$ represent allogenic components. Elemental concentrations in mg/g dry sediment or as simple ratios. Profiles marked as 0.1 are scaled to 1/10th actual value.

Kütz, *N. trivialis* Lange-B, and *N. tripunctata* (O.F. Müll) Bory, with smaller percentages of *Achnanthes* spp. and *Cymbella* spp. The combination of *Stephanodiscus* spp. and *Cyclotella stelligera* suggests that Foster Lake was moderately rich in algal nutrients (mesotrophic) early in the 19th century. The great diversity of benthic taxa, however, suggests that water transparency was still quite high, permitting light penetration to the sediment surface sufficient for algal photosynthesis.

Beginning late in the 19th century (after 1875) the diatom plankton decreases. The mesotrophic/eutrophic *Stephanodiscus* spp. are first to decline, followed by the cosmopolitan *Cyclotella stelligera*, with correlative increases in the relative abundance of a variety of benthic species. This shift in dominance from planktonic to benthic diatom taxa may indicate higher water transparency and lowered phosphorus or nitrogen concentrations or alternatively silica limitation of diatom plankton. The increased proportions of chrysophycean stomatocysts indicate an expansion of chrysophytes, which may be competitively superior to diatoms during periods of low nutrient concentrations (Smol, 1985).

A pulse in the mid-1950s of *Cyclostephanos invisitatus* (Hohn & Hell.) Ther., Stoerm., Håk., a

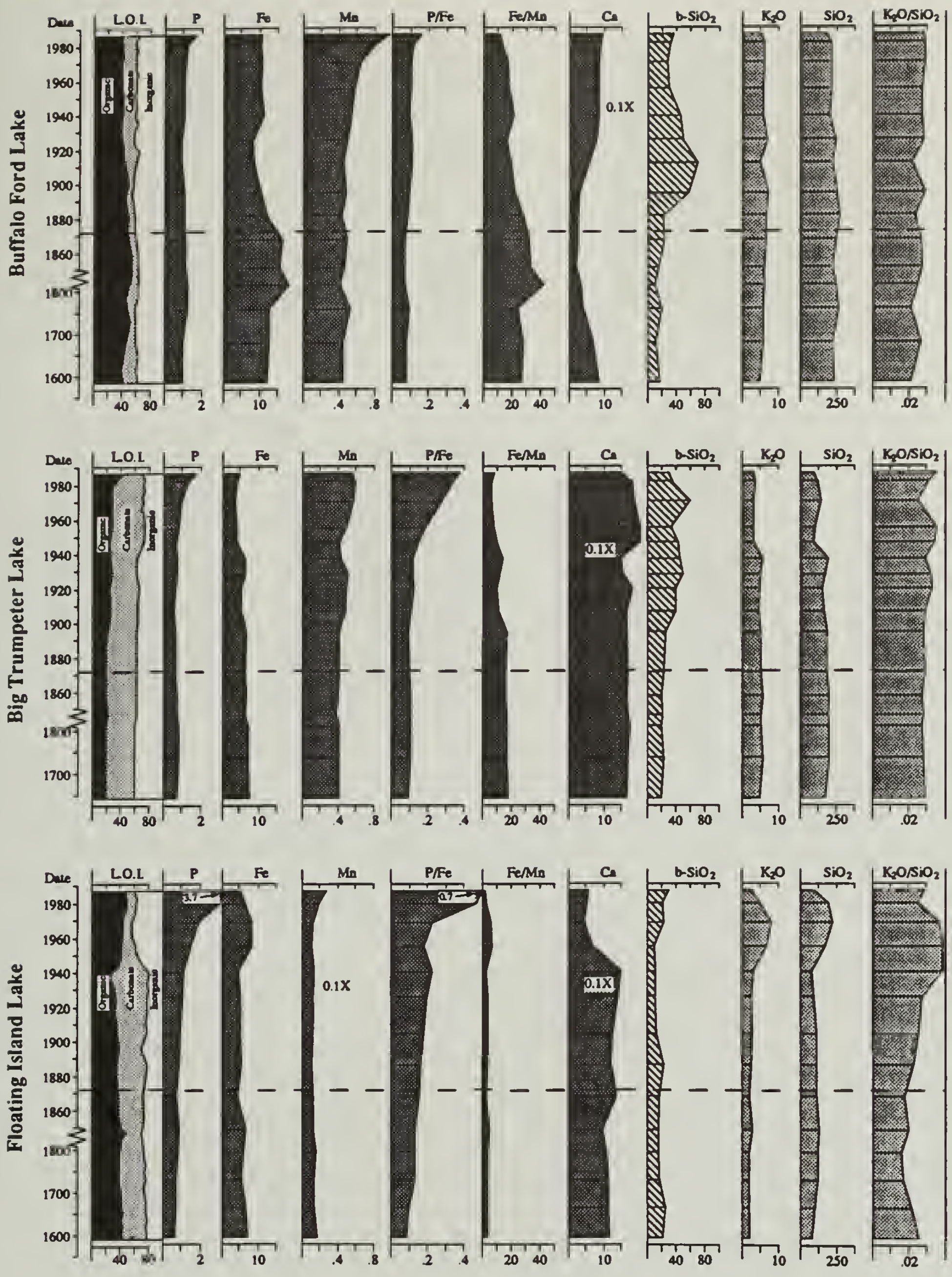

Fig. 11. Geochemical profiles for Buffalo Ford, Big Trumpeter, and Floating Island lakes. See Fig. 10 legend for further explanation.

eutrophic taxon common during periods of low dissolved silica (H. Håkansson, pers. comm.), coincident with a decline in the relative abundance of chrysophycean stomatocysts, suggests a brief return to higher nutrient levels. After the 1960s, however, planktonic diatoms are a negligible part of the diatom community.

By the mid-1960s *Fragilaria* spp. (*F. brevistriata, F. pinnata, F. construens* v. *venter* (Ehr.) Grun.), which grow on the sediment surface and as epiphytes, attain nearly total dominance, suggesting oligotrophic conditions and high water transparency (Brugam, 1980). This conclusion is corroborated by phytoplankton samples from the late 1970s, which show very low plankton densities (Jones *et al.*, 1978).

Both diatoms and chrysophytes require silica for cellular metabolism. Benthic diatoms can obtain silica from the sediments, whereas planktonic diatoms and chrysophytes must depend on dissolved silica in the water column. The decline of planktonic diatoms and chrysophytes in Foster Lake may therefore reflect lowered availability of dissolved silica. Another possibility is that lowered concentrations of nutrients required by all algal groups (particularly phosphorus)

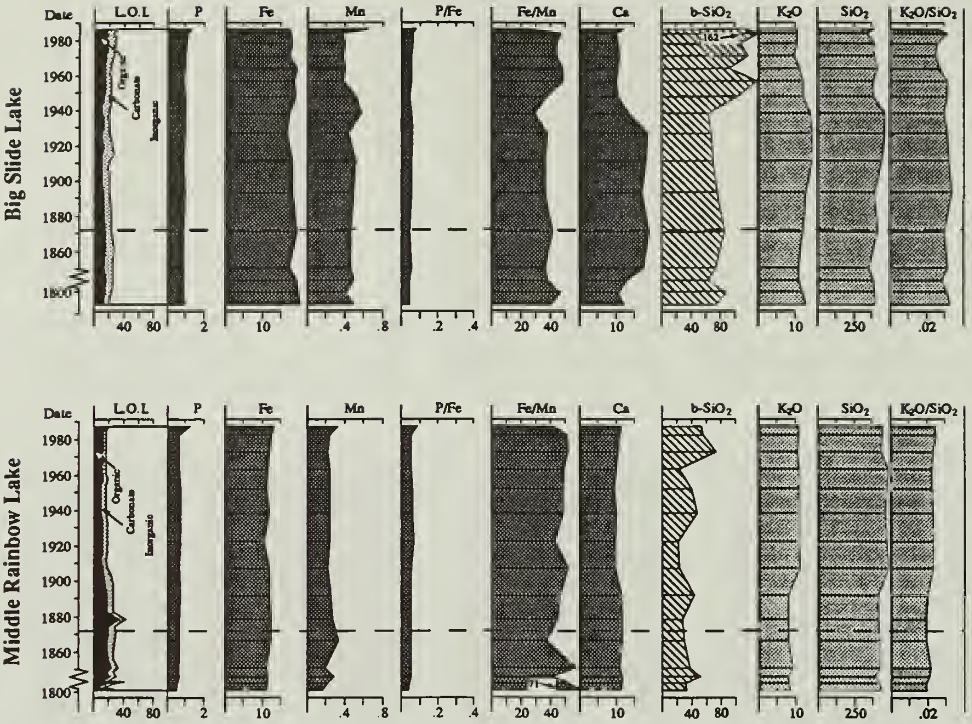

Fig. 12. Geochemical profiles for Big Slide and Middle Rainbow lakes. See Fig. 10 legend for further explanation.

may have affected all planktonic algae. With the available data we have no means of determining whether the plankton decline included only silica-requiring algae or all algal groups.

Buck Lake

Setting

Buck Lake lies at 2118 m elevation in a small deep basin (2.3 ha surface area, 11.3 m maximum depth) with steep forested slopes. Water chemistry data are unavailable for this site. A small stream flows into the lake from Shrimp Lake, but no permanent outflow stream exists. The slopes are covered by Douglas-fir, Engelmann spruce, and lodgepole pine. Whitebark pine and subalpine fir occur in small numbers. Forest shrubs include common juniper, snowberry, honeysuckle, Wood's rose, clematis, buffaloberry, and spirea. Duckweed, water smartweed, water-milfoil, and pondweed are part of the aquatic flora.

Buck Lake is located within a large landslide complex on the south side of Mount Hornaday. The lake was once renowned for its cutthroat trout, and records show that as late as 1931 it was heavily stocked. Few fish have been caught from the lake since 1965, because the lake has limited spawning habitat (Sharpe & Arnold 1966). In 1910 a federal fish hatchery in Bozeman began collecting eggs from nearby Trout Lake, and a hatchery was active at the lake from 1922 to 1945. An old road to Trout Lake runs by Buck Lake. It may have been built as early as 1910 after egg collecting began there, or it may have been built in 1922 during hatchery construction.

Pollen

The pollen record (Fig. 7) shows an increase in *Pinus* percentages from 1850 to the present. Diploxylon-type pine pollen increases from 1915 to 1960, and Haploxylon-type pollen increases between 1940 and 1980. *Picea* increases between 1890 and 1960. *Abies* and *Juniperus* percentages show little change from 1845 to the present. *Pseudotsuga* pollen is present in values between 4 and 8% for most of the record, but the 1980 level drops to 2%. *Betula* pollen is present before 1890, but not afterwards, and percentages of *Alnus, Populus tremuloides*-type, and *Sarcobatus* show similar decreases. *Artemisia* pollen is more abundant than that of *Gramineae*, except at the 1980 level where they are equally represented. Percentages of Chenopodiineae other than *Sarcobatus* decrease after about 1915 but increase at the 1980 level. Cyperaceae pollen is most abundant around 1915.

Geochemistry

The sediments from Buck Lake (Fig. 10) are similar in organic content to those of Foster Lake (28%

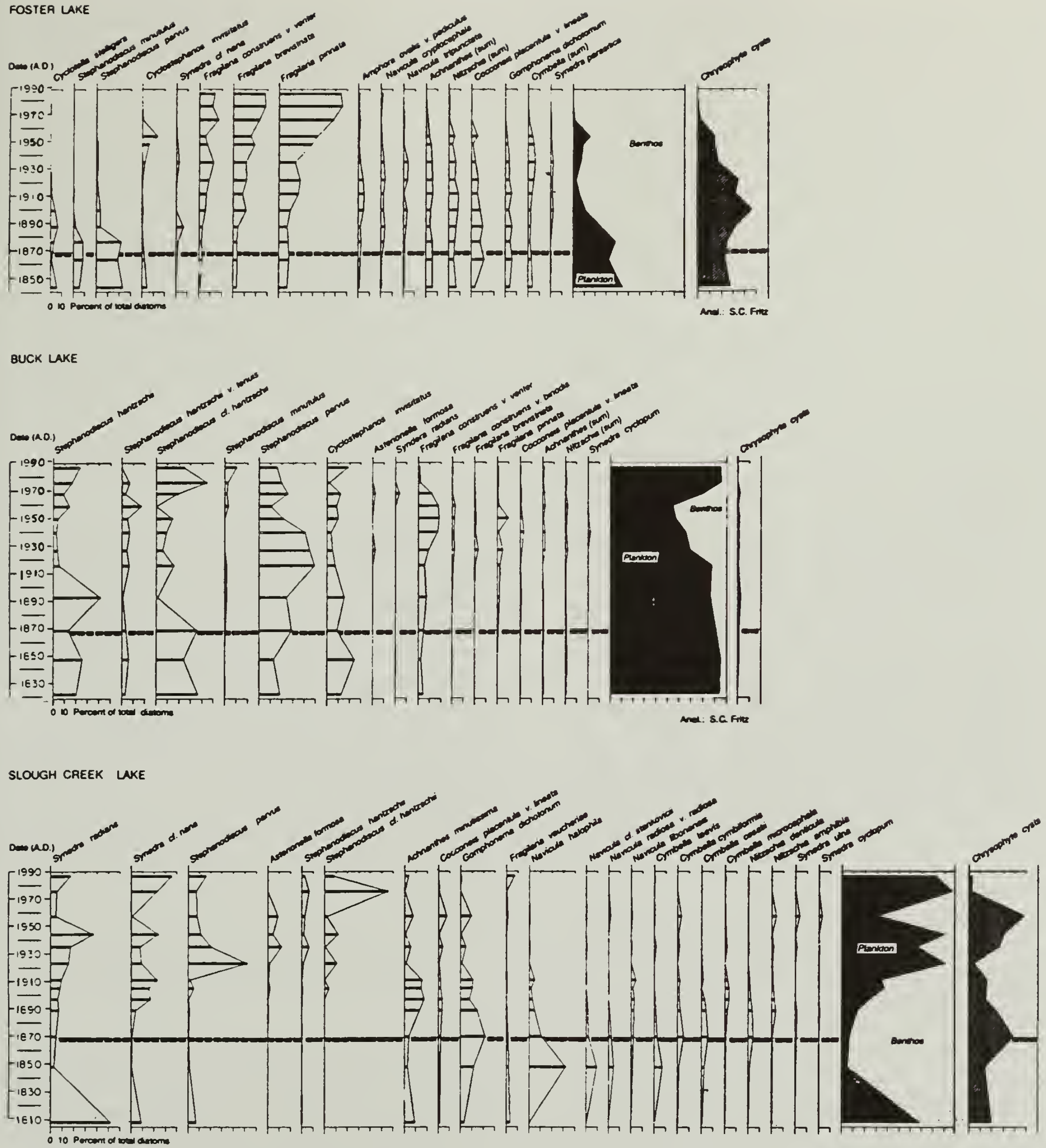

Fig. 13. Diatom diagrams for Foster, Buck, and Slough Creek lakes. Dates below 1850 are extrapolated from the base of the ^{210}Pb profile. Dashed line indicates the date of park establishment, 1872.

of dry mass) but are much lower in carbonates (only 11%). The non-carbonate inorganic fraction, which is higher than most sites (61%), is composed of biogenic silica and clastic silicates in roughly equal proportion. The very large fraction of biogenic SiO_2, in this core (an average 230 mg/g) implies high diatom production. Sediment accumulation is of the same order of magnitude as Foster Lake (0.02–0.08 g cm^{-2} yr^{-1}), but shows a general increase after 1920.

Among minor sedimentary components, authigenic Mn is unusually low compared to the other study lakes (0.09 mg/g), and the Fe:Mn ratio is correspondingly high. This contrast in redox-sensitive elements probably results from hypolimnetic anoxia and resulting mobilization of Mn (II) from the Buck Lake core site. Buck Lake is relatively deep and well protected from wind-stress by a steep catchment, so that seasonal stratification of the water column and hypolimnetic anoxia are likely to occur. This conjecture is supported by our field observations of faint laminations and abundant gas bubbles (probably methane) in the Buck Lake core. The low carbonate content of the core may also reflect seasonal anoxia and dissolution of endogenic calcite as it descends into hypolimnetic waters with high p-CO_2.

The lowest stratigraphic change in the Buck Lake core (ca. 1860–70), an increase in inorganic matter (principally clastics), a decrease in organic content, and a small peak in sediment accumulation may signal an increase in erosion just prior to park establishment. Sediment composition then remains constant until about 1960, despite a 3-fold increase in sediment accumulation after 1920. This change in accumulation unaccompanied by changes in composition almost certainly reflects a shift in sediment deposition pattern within the lake; external changes in erosion rate or lake productivity are unlikely (see above). After 1960 biogenic silica increases by 25% and other major components decrease (allogenic SiO_2, organics, carbonates). Sediment accumulation increases shortly thereafter, implying increased diatom production and enhanced eutrophication in recent times.

Diatoms

The diatom data from Buck Lake (Fig. 13) suggest a more stable diatom flora over the last two centuries in comparison with Foster Lake. Sedimentary assemblages are overwhelmingly dominated by small *Stephanodiscus* species (*S. hantzschii* Grun., *S. hantzschii* v. *tenuis* (Hust.) Håk. & Stoerm., *S. parvus* Stoerm. & Håk., and *S. minutulus*) and *Cyclostephanos invisitatus,* taxa characteristic of eutrophic waters. Their high relative abundance throughout the analyzed sediments (53–92%) indicates that the lake has been nutrient rich for at least 170 years. This implies that eutrophication preceded management of the landscape and is a result of natural environmental processes.

The only clear stratigraphic change at Buck Lake is an increase from the mid-1920s to mid-1960s in the proportion of benthic and epiphytic diatoms relative to planktonic *Stephanodiscus* spp., involving primarily an expansion of *Fragilaria* spp. This increased representation of non-planktonic diatom taxa in the sediments could result from a decrease in lake level and the consequent increase in littoral area for both benthic diatoms and for macrophytes, or alternatively could result from decreased phosphorus, nitrogen, or silica availability for planktonic populations. Lowered nutrient availability can affect the proportion of benthic to planktonic diatoms in several ways: (1) low silica concentrations may encourage algal plankton other than diatoms and hence decrease the accumulation of planktonic diatoms in the sediments, (2) increased phosphorus loading may cause silica limitation of diatom plankton, or (3) decreased total plankton biomass may increase light penetration to the sediment surface and enhance the growth of benthic algae.

Slough Creek Lake (informal name)

Setting

Slough Creek Lake (No. 1033-61 in the park list) lies in a kettle-hole depression at 1884 m elevation just north of the junction of the Lamar River and Slough Creek. The basin is steep sided with a maximum depth of 8 m and surface area of 2.1 ha. Its waters, like those of Foster Lake, are dominated by Mg^{2+} (Ca^{2+}) and HCO_3^- and are moderately rich in total-P (34 ppb). The site is located in steppe vegetation of bluebunch wheatgrass, Idaho fescue, big sage, and silver sage. Stands of aspen on the northwest side shows signs of 'high-lining'-browsing by ungulates up to head height. Isolated large Douglas-fir trees grow near the shore as outliers of a predominantly Douglas-fir forest at elevations just above. The lake is surrounded by a margin of cattail, bulrush, and sedge. The charophyte *Nitella* and water-milfoil were noted in the aquatic vegetation.

Pollen

The pollen record (Fig. 7) shows little change in *Pinus* and *Abies* percentages during the last 150 years. *Picea* and *Pseudotsuga* values increase steadily after 1872. *Juniperus* percentages also increase after 1872 but drop slowly between 1900 and 1935. *Betula, Salix,* and *Populus tremuloides*-type pollen are present in pre-park and park levels in trace amounts. *Populus* pollen is present more consistently after 1872 than before. Cereal-type pollen is noted throughout but is most abundant from 1820 to 1925. Its occurrence as early as 1810 has no obvious explanation, for it predates settlement of the Yellowstone Valley by at least 50 years. *Artemisia* increases steadily after 1890, while Gramineae pollen declines. *Ambrosia* and other

Tubuliflorae are present consistently from 1880 to the present.

Geochemistry

Sediments in this core (Fig. 10) are highly organic (ca. 48% dry mass) and relatively low in carbonates (17%) and other inorganic components (35%). Because overall sediment accumulation is low (0.01–0.02 g cm^{-2} yr^{-1}), this composition probably results from a low influx of clastic materials and modest carbonate precipitation, rather than a high flux of organic carbon. Eroded materials may have been prevented from entering the lake by the extensive mat of littoral vegetation that rims the shoreline today.

The most noticeable stratigraphic change in the Slough Creek core occurs ca. 1800–1850 when carbonates (and the associated curve for Ca) peak at the expense of clastics (allogenic SiO_2, K_2O), organic matter, and most other components. A parallel increase in Mn implies that $MnCO_3$, (rhodochrosite) may be present in these sediments as well. A small peak in sediment accumulation associated with a 10% rise in organic content occurs ca. 1900–1920, suggesting a possible increase in lake productivity. After 1960 sediment accumulation doubles, organic content again increases along with biogenic SiO_2, and clastics decline. Although a gradual rise in biogenic SiO_2 implies that this change may have begun several decades earlier, these signals represent the strongest geochemical evidence for increased productivity among any of the study sites.

Diatoms

The diatom flora of Slough Creek Lake (Fig. 13) differs considerably from that of Foster, Buck, Slide, and Rainbow lakes in both the assemblage of planktonic species present in the sediments and the persistently low abundance of littoral *Fragilaria* spp. The basal sediments (ca. 1810) are dominated by *Synedra radians* Kütz., with moderate percentages of *Synedra* cf. *nana* Meister and *Stephanodiscus parvus*, an assemblage indicative of moderate nutrient levels (mesotrophy). Subsequently these planktonic taxa decline to very low percentages, and from the mid-19th century to ca. 1910 the sediments are dominated by a variety of benthic and epiphytic taxa, particularly *Achnanthes minutissima* Kütz., *Gomphonema dichotomum,* and *Navicula halophila* (Grun.) Cleve, an assemblage suggesting clear water and low nutrient concentrations.

From the mid-1920s to the present. the sediments are again dominated by planktonic taxa (except for a brief period in the mid-1950s), indicating a return to higher nutrient concentrations. The alterations in dominance among the major planktonic taxa during this period suggest fluctuating nutrient availability. Culture experiments show that *Asterionella formosa* Hass. and *Synedra* species grow efficiently when phosphorus concentrations are low (high Si/P), whereas *Stephanodiscus* spp. do poorly under such conditions (Tilman *et al.,* 1982; Lovstad, 1984). On the basis of these culture data, the diatom succession suggests that phosphorus concentrations rose to a peak in the mid-1920s, declined through the mid-1950s, and then rose again to intermediate levels from the 1960s through the present. The relative abundance of chrysophyte cysts in the Slough Creek Lake sediments is highest when diatom plankton are low, which also suggests fluctuating nutrient levels.

Buffalo Ford Lake (informal name)

Setting

Buffalo Ford Lake (No. 1033-52 in the park list) is located at 1917 m elevation on the north side of the Lamar River near Tower Junction. The lake has a surface area of 4.3 ha and a mean depth of 5.4 m; its water chemistry is unknown. The northern, eastern, and western slopes of the catchment are covered by sagebrush/grass steppe, and the higher slopes by Douglas-fir forest and aspen groves. Douglas-fir forest with some Engelmann spruce, fir, and lodgepole pine grows on the southern slope close to the lake margin. A wet meadow along the southern margin contains willow as well as various grasses, sedges, and wetland herbs. Along the lake margin is a discontinuous fringe of cattail, bulrush, and sedge.

Pollen

The pollen record (Fig. 8) indicates that Diploxylon-type pine is more abundant after 1910 and particularly since 1950, but because total *Pinus* percentages do not increase this trend is attributed to better pollen preservation towards the top of the core, permitting differentiation of pine pollen types. *Picea* and *Abies* show little stratigraphic change. *Pseudotsuga* pollen is slightly less abundant between 1910 and 1940 than before or afterwards. Pollen of *Alnus, Betula, Salix,* and *Populus tremuloides*-type is present in pre-park and park intervals. *Salix* percentages decline slightly after 1940, and *Populus tremuloides*-type pollen is less abundant after 1965.

The aquatic pollen, dominated by *Nuphar* and *Myriophyllum,* is abundant in levels from 1860 to 1900; above that Cyperaceae is more common.

Geochemistry

The sediments from the Buffalo Ford core (Fig. 11) are compositionally very similar to those from Slough Creek Lake; organic content is high (44% of dry mass), whereas carbonates (17%) and other inorganic components (39%) are low. This lake also possesses an extensive mat of littoral vegetation and peat that could intercept clastic inputs. Sediment accumulation ranges from 0.01 to 0.05 g cm^{-2} yr^{-1}.

The earliest stratigraphic signal in this core begins several hundred years before park establishment. From ca. 1600 to 1850 the sediments become more organic (increasing from 40% to 50%) and poorer in carbonate (20% to 10%). The trend is reversed beginning around 1900, eventually restoring the organic/carbonate balance of earlier centuries.. This oscillation in sediment lithology is clearly evident in the profile for authigenic Ca, but its environmental significance is uncertain. The 20th century rise in carbonate content generally corresponds to a 3-fold increase in sediment accumulation. Thus, increased carbonate precipitation, possibly induced by greater phytoplankton production, may be responsible for periods of high carbonate content. A major increase in biogenic silica between ca. 1890 and 1920 is coincident with the rise in sediment accumulation, supporting the contention of higher production during this interval. However, a subsequent oscillation in sediment accumulation from 1930 to the present is unaccompanied by any change in sediment composition and may be more related to changes in deposition patterns within the lake.

Major trends in Fe and Fe/Mn are closely correlated with changes in loss-on-ignition, implying that variations in organic content, rather than the redox environment at the lake bottom, control these profiles. Similar correlations between Fe and organic content are also evident in the cores from Big Trumpeter and Floating Island Lakes.

Big Trumpeter Lake

Setting

The Trumpeter lakes lie in the stagnant-ice terrain of the Lamar Valley in the sagebrush/grass steppe. These lakes are shallow (maximum depth of Big Trumpeter = 3.0 m) and, their water level fluctuates considerably. The waters of Big Trumpeter are rich in dissolved solids (conductivity = 850 µS/cm), primarily Na^+, Mg^{2+}, and HCO_3^-, and are moderately productive (total-P = 52 ppb; Jones *et al.*, 1978).

Pollen

The pollen record (Fig. 8) from Big Trumpeter Lake during the 1930s and 1950s shows little evidence to suggest major vegetational changes during periods of drought. Haploxylon-type *Pinus* percentages reach highest values between 1935 and 1940. *Juniperus, Sarcobatus,* and *Ambrosia* and other Tubuliflorae are slightly more abundant at the 1920 and 1935 levels than before or after. *Populus* pollen is absent after 1945 but present in trace amounts between 1915 and 1935. Gramineae percentages generally decrease, whereas those of *Artemisia* increase from 1895 to the present.

Geochemistry

Sediments from this site (Fig. 11) are carbonate-rich (41% of dry mass) and moderately organic (26%); the remaining inorganic component (33%) is composed primarily of clastic silicates. The high Ca content (170 mg/g) reflects the abundance of carbonate. Sediment accumulation rates are similar in magnitude to those for Buffalo Ford Lake (0.02–0.06 g cm^{-2} yr^{-1}), but they apparently decrease after establishment of the park, unlike all the other sites.

The interpretation of this core is more problematic than that for the other sites, because of evidence for significant shallowing or intermittent drying of the lake sometime in the recent past. Sediments below about 25–30 cm (ca. 1900) have a blocky soil-like texture and a much lower water content (<80%) than mud at similar depth in the other cores. These are characteristic features of a dry lake bed and thus have serious implications for ^{210}Pb dating. Therefore, a major decrease in sediment accumulation after 1900 must be viewed with some suspicion, particularly since it is accompanied by only minor changes in sediment composition. Organic content and biogenic SiO_2 increase slightly around 1920, but otherwise sediment lithology is relatively constant until about 1945. At this time clastic components (SiO_2 and K_2O) decrease substantially while carbonates, Ca, and P/Fe increase. Sediment accumulation increases from 0.02 to 0.03 g cm^{-2} yr^{-1} shortly thereafter, implying a possible increase in lake productivity.

Floating Island Lake

Setting

Floating Island Lake lies at 1996 m elevation in a shallow glacial depression (3.0 m maximum depth) on the northeast side of Crescent Hill. Its waters are rich in Mg^{2+}, HCO_3^-, and a surprising concentration of Cl^- (59 ppm), but are relatively low in total phosphorus (13 ppb). It is surrounded by a discontinuous margin of bulrush, cattail, and grass. The southern slope is forested by Douglas-fir, Engelmann spruce, and subalpine fir. Aspen grows just south of the lake. Studies by Jonas (1955) on the Yellowstone beaver include a pair of photographs from the south end of Floating Island Lake. A photograph taken in 1923 (by E.R. Warren, in Jonas, 1955) shows a stand of young aspen along the shore, whereas 32 years later these aspen are dead and the sagebrush in the foreground is heavily browsed. Jonas (1955) points to Floating Island Lake as a good example of how overbrowsing by elk led to starvation of beaver. A beaver lodge apparently occupied the island in 1923, and aspen around the shore provided food and constructional material as late as 1937. Warren (1926) noted that beaver activity in the 1920s was confined to a distance of 100 ft from the lake. By 1954 the activity had ceased and the banks were dry and supported sagebrush. By 1953 the large lodge was gone (Jonas, 1955).

This site was studied to determine the sedimentological signature produced by construction of a road near the site. The magnitude of this signal in the sediments provides a means of estimating stratigraphic disturbances in other lakes caused by nonhuman activity. The paved road that runs along the north side of Floating Island Lake was constructed between 1932 and 1934. In subsequent years the road was oiled to keep down dust (T. Manns, National Park Service, pers. comm.).

Pollen

The pollen record (Fig. 8) shows no change in *Populus tremuloides*-type pollen, despite the photographic evidence that aspen trees along the shore have died. *Alnus* pollen is present before 1920 but not after, and *Betula* percentages increase after 1905. As at Big Trumpeter Lake, *Sarcobatus* and some of the Tubuliflorae are slightly better represented in the 1920s and 1930s levels, which may signify an increase during drought. There is no significant stratigraphic change in percentages of *Pinus*, *Picea*, and *Abies* pollen at this site. *Pseudotsuga* and *Juniperus* increase after 1960.

Geochemistry

Sediments from this site (Fig. 11) are high in both organic matter (40%) and carbonates (33%) and correspondingly low in other inorganic materials (27%). The low values for the inorganic component probably reflect the interception of clastics by littoral vegetation (as at Slough Creek and Buffalo Ford) coupled with active deposition of carbonates (mollusc shells are abundant throughout the core). Sediment accumulation is generally low by comparison with the other sites (0.01–0.02 g cm^{-2} yr^{-1}), implying only moderate organic production.

The most striking stratigraphic features in the Floating Island core are the marked increase in clastic content (allogenic SiO_2 and K_2O) and organic matter, and the equivalent decline in carbonate content (and authigenic Ca) at ca. 1940. This change is nearly concurrent with a sharp peak in sediment accumulation, thus providing strong evidence for an increase in catchment erosion. Moreover, a clear increase in K_2O/SiO_2 after 1930 implies a change in provenance for the eroded silicates. To the present day sediment accumulation remains elevated above pre-park values, and the sediments remain richer in clastics. However, the increase in sediment accumulation does not fully offset the carbonate decline (ca. 40% to 10%), nor does an increase in erosion explain the rise in organic matter. It appears that, in addition to greater erosion, carbonate deposition decreased and organic production may have increased sometime around 1940. Increased productivity may also be manifest in higher values for phosphorus and biogenic silica in the upper part of the core.

Big Slide Lake

Setting

Big Slide Lake is located at 1728 m elevation in the active landslide area at the base of Sepulcher Mountain. It has a surface area of 3.0 ha and a maximum depth of 4.5 m and is chemically dominated by Ca^{2+} (Mg^{2+}) and HCO_3^- ions. It is a highly productive lake, with a total-P content of 143 ppb. The inlet stream comes from a small lake 0.5 km to the southwest that flows into little Slide Lake, which in turn drains into Big Slide Lake. A stream exits Big Slide Lake on the north side and drops down the canyon to the Gardner River. The Old Gardiner Road was built in late 1879 or early 1880 (T. Manns, National Park Service, pers. comm.). The old road has been maintained ever since that time, probably because of the continual problems with keeping the main canyon road open through the slide area. Beaver have populated the Slide Lake region for many years but never in large numbers. Jonas (1955) noted that around Big Slide Lake all woody species but juniper were heavily browsed. The dense growth of water birch at the site, however, suggested to him that browsing pressure was less intense than at other places, and he was puzzled as to why beaver had taken sagebrush when birch and cottonwood were available.

The drainage into Big Slide Lake is forested with Douglas-fir, lodgepole pine, limber pine, and Rocky Mountain juniper. Water birch, mountain alder, narrow-leaved poplar, smooth sumac, and willow grow near the lake margin and along the stream course. The upland slopes are sparsely vegetated with saltbush, greasewood, bitter-brush, sagebrush, grasses, and scattered trees of Rocky Mountain juniper, and limber pine. The margin of bulrush, cattail, sedge, and grass surrounds the lake. Water-milfoil and pondweed were common aquatic macrophytes.

Pollen

The pollen record (Fig. 9) shows a decline in *Pinus* pollen after 1960, particularly Diploxylon-type. *Picea and Abies* percentages show little change in the last 150 years. *Pseudotsuga* pollen is more abundant after about 1930. *Betula* percentages decrease steadily after 1872, and *Salix* values after about 1900. *Populus balsamifera*-type and *P. tremuloides*-type are present in the pollen record in the park intervals after 1890, but not before then. Gramineae pollen increase after 1872, and Cyperaceae pollen is most abundant after 1930. The pollen profiles for *Sarcobatus, Artemisia, Ambrosia*-type, Tubuliflorae, and other Chenopodiineae show little stratigraphic change.

Geochemistry

The chemical stratigraphy of Big Slide Lake (Fig. 12) is interpreted from the analysis of one of three cores collected from the basin (core I). The cores were taken in different parts of the lake (Fig. 3) at roughly 1-m intervals of water depth (core I = 4.2 m, core 2 = 3.1 m, and core 3 = 2.2 m) in order to better characterize sedimentation rates for the lake as a whole. Lake muds from this site are rich in silicates (inorganic matter = 76%, allogenic SiO_2 = 400 mg/g) and poor in carbonates and organic matter (15% and 9%, respectively). The loss-on-ignition profiles from cores 2 and 3 (not shown) indicate a similar lithology for other parts of the basin. The accumulation of sediments in the lake is very rapid, although sedimentation rates are both temporally and spatially variable. Sediment accumulation in cores I and 2 ranges from 0.03 to 0.1 g cm^{-2} yr^{-1} but is considerably higher in core 3 (0.05–0.4 g cm^{-2} yr^{-1}). These rates and a clastic-rich composition indicate high erosion, presumably from the soft Eocene sedimentary rocks in the catchment. The content of biogenic SiO_2, although only about 10% of the dry sediment in core I, represents very high diatom production, given the fast sedimentation rates for this lake.

A major increase in sediment accumulation begins in all three cores around the time of park establishment and continues until about 1940. Pre-park accumulation rates are unknown for cores 2 and 3 (because of low ^{210}Pb activity, see dating section) but are probably similar to those at ca. 1880, based on complacent accumulation rates for this period in core I. Allogenic components (SiO_2 and K_2O) increase concurrently with the rise in sediment accumulation, although the change is subtle because clastics comprise such a large sediment fraction before 1880. This change in composition together with increasing sediment accumulation at all core sites represents strong evidence for higher erosion in the Big Slide basin during the early history of the park than before or afterwards.

The trend toward increasingly inorganic sediments ends around 1940 when curves for allogenic SiO_2 and K_2O decline and organic content and biogenic silica rise. A concurrent decline in authigenic Ca is not expressed in lower carbonate content, so it must signify a change in some other phase of calcium. Sediment accumulation decreases after ca. 1940 in cores 2 and 3 but remains elevated and nearly constant in core I except for a small increase in the topmost level. The lithologic change in core I implies reduced erosion, which is consistent with the decrease in sediment accumulation seen in cores 2 and 3. The fact that accumulation in core I does not respond in the same manner as in cores from shallower water can be attributed to a greater focusing of sediments into deeper parts of the basin following the reduction in sediment loading (Murchie, 1985; Engstrom and Swain, 1986). The particularly strong increase in biogenic SiO_2 concentration after 1940 may signify greater diatom production as well as a reduction in eroded clastics.

Diatoms

The diatom flora of Big Slide Lake (Fig. 14) is broadly similar to that of Buck Lake, having been dominated by the eutrophic *Cyclostephanos invisitatus* and *Stephanodiscus* spp. (particularly *S. parvus* and *S. hantzschii*) throughout the last 200 years. Increased proportions of benthic and epiphytic diatoms relative to plankton from the mid-19th century through the first

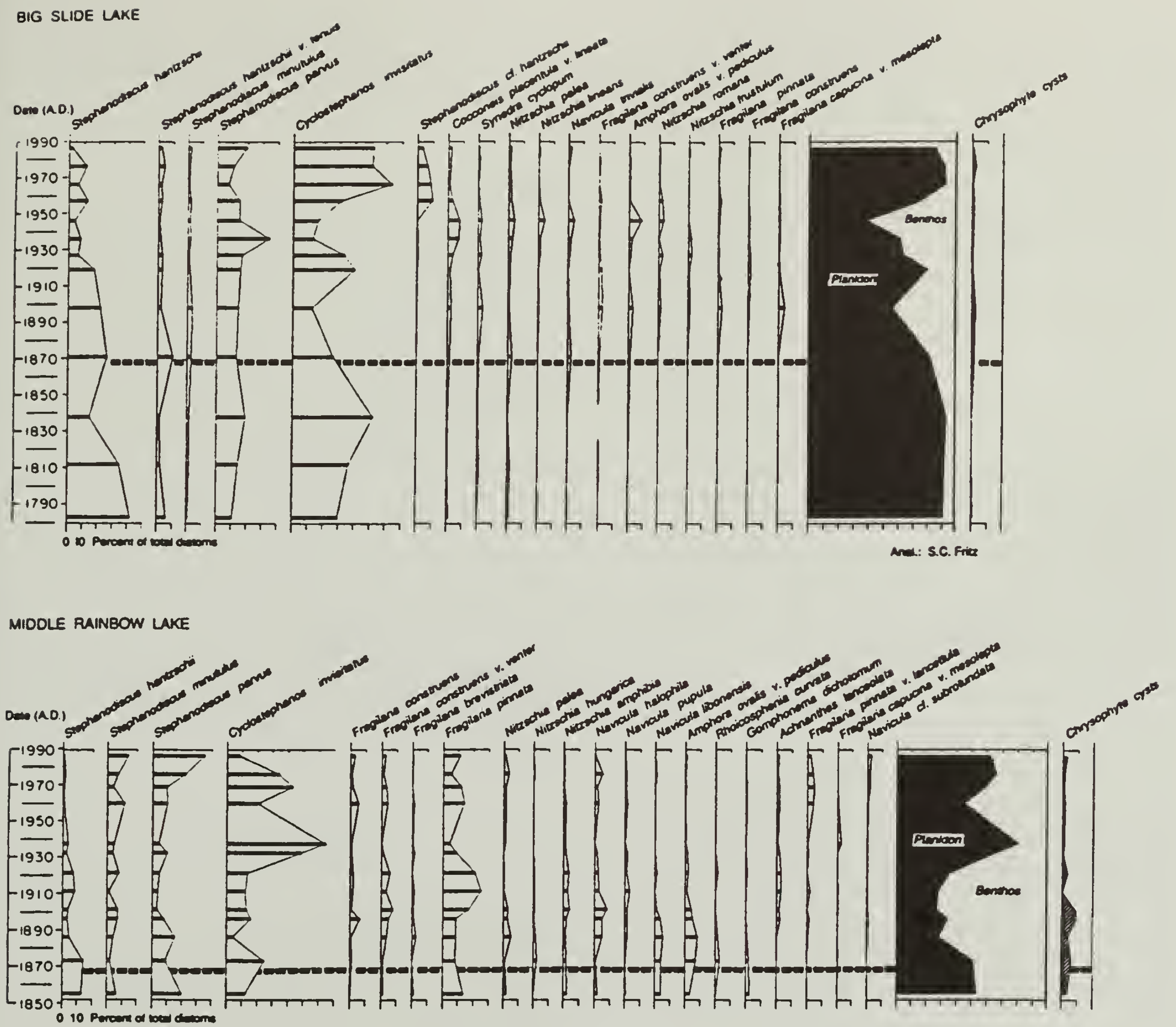

Fig. 14. Diatom diagrams for Big Slide and Middle Rainbow lakes. See Fig. 13. legend for further explanation.

decade of the 20th century, and again from the late 1920s through ca. 1950, suggest periods of either slightly lowered nutrient availability or lowered water level. This diatom response is reflected in a variety of attached diatom taxa, including *Cocconeis placentula* v. *lineata, Amphora ovalis* v. *pediculus, Fragilaria construens* (Ehr.) Grun. and v. *venter, F. pinnata, Navicula trivialis,* and several *Nitzschia* spp.

Middle Rainbow Lake

Setting

The three basins comprising the Rainbow Lakes lie in an area of active landslides on the north side of Sepulcher Mountain. The largest of the lakes, Middle Rainbow, has a surface area of 2.3 ha and a maximum depth of 2.6 m. Its waters are rich in total-P (86 ppb) and are dominated by Na+ (Ca2+) and HCO_3^-. The lake is surrounded by sparsely vegetated grassland that includes bluebunch wheatgrass, sagebrush, rabbitbrush, greasewood, and saltbush, with gooseberry in the forest understory. Douglas-fir and Rocky Mountain juniper are scattered on the landscape, and at higher elevations are forests of pine, spruce, and fir. At the margin of the pond grow cattail, sedge, and bulrush. Pondweed and Indian pond lily form a mat over much of the water surface. Willow and a few aspen were found within the local catchment as well.

Middle Rainbow Lake lies at the edge of the 1872 boundary of the park. A Crow wickiup has been reported near the site, as well as a cabin (T. Manns, pers. comm.). Beaver have also been active in the area. An old road extends from the Stevens Creek Road to the lake, and apparently the Rainbow Lakes were a popular tourist spot at one time. The Yellowstone Valley was first settled by placer miners in the 1860s, and the region around Gardiner was settled in the 1870s. The northern boundary was used by local ranchers prior to its acquisition by the park in 1932 (T. Manns, pers. comm.).

Pollen

The pollen record (Fig. 9) shows little change in the abundance of conifers. *Betula* decreases after a peak in 1900; *Salix* percentages reach a maximum in 1910 and decline thereafter. *Populus* pollen is present in the park levels but not in the pre-park levels. *Artemisia* is slightly higher in park levels than before. Pollen of *Potamogeton*, *Sparganium*, *Myriophyllum*, and *Typha* all increase in the last 25 years, suggesting a general shallowing and stabilization of the lake margin.

Geochemistry

The lithology of sediments from this site (Fig. 12) is very similar to that from nearby Big Slide Lake; clastic materials predominate (LOI inorganic = 78%, allogenic SiO_2 = 400 mg/g), while organic matter and carbonates are small components (15% and 7%, respectively). Easily eroded Eocene sediments are also present in the catchment and responsible for the high rates of sediment accumulation (0.05–0.13 g cm^{-2} yr^{-1}).

The Rainbow Lake core becomes more inorganic shortly after park establishment as shown by increasing concentrations of allogenic SiO_2 and K_2O between ca. 1880 and 1900. No significant change in sediment accumulation occurs during this period. However, dating precision, particularly before 1900, is very poor (in large measure because high inputs of clastic sediments have severely diluted ^{210}Pb activities), and sedimentation rates are in effect unknown. Thus, there is still a good possibility that erosion into Rainbow Lake increased during the early history of the park, as suggested by the 1880 rise in clastic content. A notable increase in sediment accumulation does occur after 1940, but in this case no change in sediment composition is evident until the 1960s when biogenic SiO_2 doubles. This increase in accumulation rate probably signifies a shift in sediment deposition pattern within the basin, although enhanced diatom production after 1960 may also be indicated.

Diatoms

Middle Rainbow Lake (Fig. 14) is dominated in the mid-19th century by eutrophic diatoms, including *Stephanodiscus hantzschii, S. minutulus, S. parvus*, and *Cyclostephanos invisitatus,* yet the moderate percentages of benthic species, such as *Fragilaria pinnata*, *Amphora ovalis* v. *pediculus*, and *Navicula libonensis* Schoeman, suggest that water transparency was still quite high. Benthic diatoms, including *Nitzschia palea* (Kütz) W. Smith, *N. amphibia* Grun., *Achnanthes lanceolata* Bréb., *Navicula pupula* Kütz., *N. halophila*, *Fragilaria pinnate*, and *F. construens* v. *venter* increase in Middle Rainbow Lake in relative abundance beginning in the late 1870s and continuing through the 1920s. *Stephanodiscus* spp. and *Cyclostephanos invisitatus* then increase to percentages slightly higher than those in pre-20th century levels. Planktonic diatoms dominate throughout the rest of the 20th century except for a brief period in the late 1950s.

Discussion

Our pollen, diatom, geochemical, and ^{210}Pb stratigraphies reveal a complex picture of environmental change in the northern range of Yellowstone. Major stratigraphic events and their interpretation are summarized in Figs 15 and 16 and are annotated according to the confidence placed on the interpretation.

Vegetational change

Stasis is the major signal in the pollen record of all eight sites, inasmuch as the changes noted are modest in comparison with the overall complacency of the record. In addition, there is no synchroneity in the timing of pollen changes that might suggest a regional vegetational response to a widespread environmental perturbation. All the pollen records are dominated by *Pinus,* and, where differentiated, Diploxylon-type pine (attributed to lodgepole pine) is more abundant than Haploxylon-type pine (referred to either whitebark pine or limber pine). Spruce, fir, Douglas-fir, and

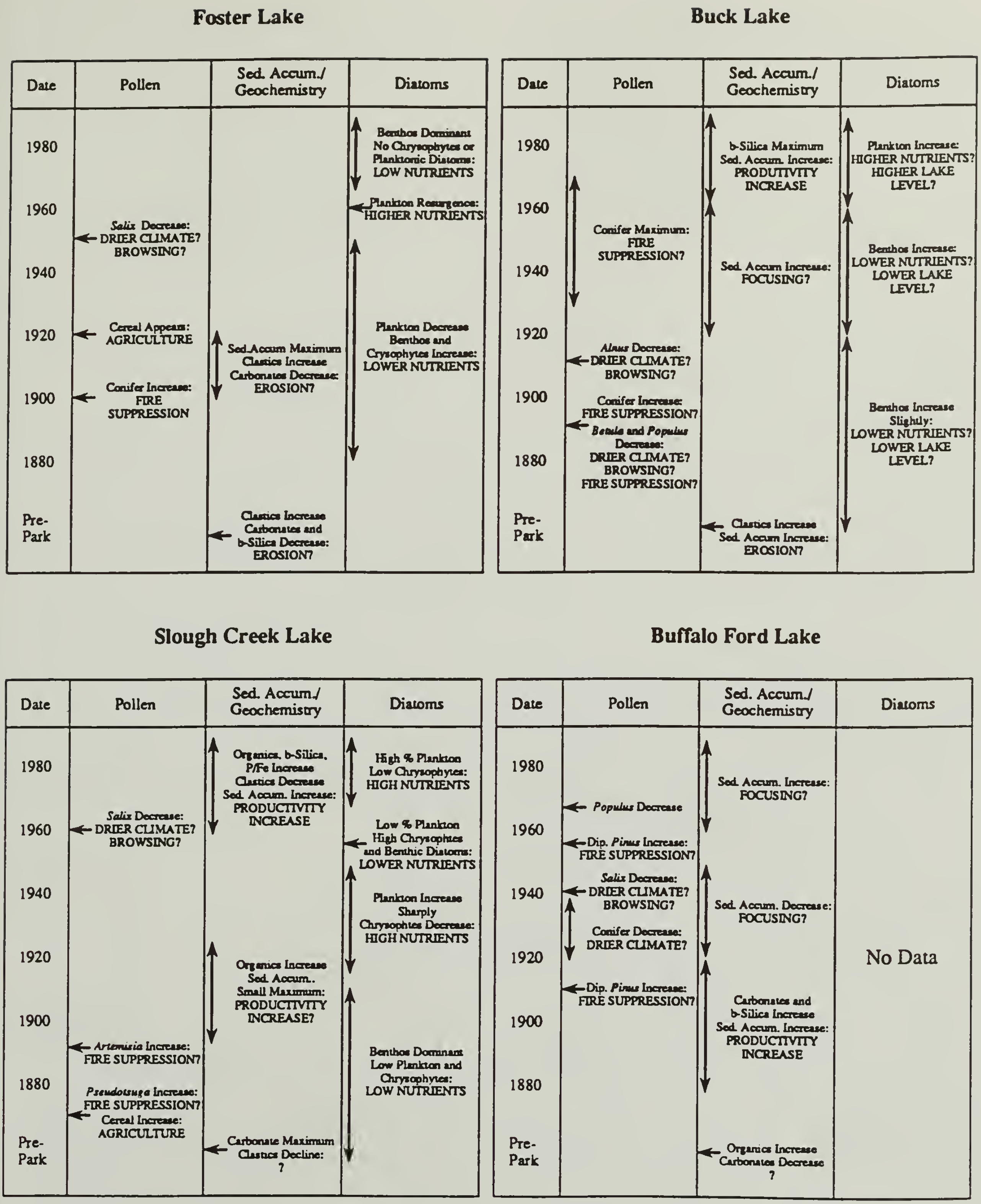

Fig. 15. Major stratigraphic changes at Foster, Buck, Slough Creek, and Buffalo Ford lakes, with tentative interpretations.

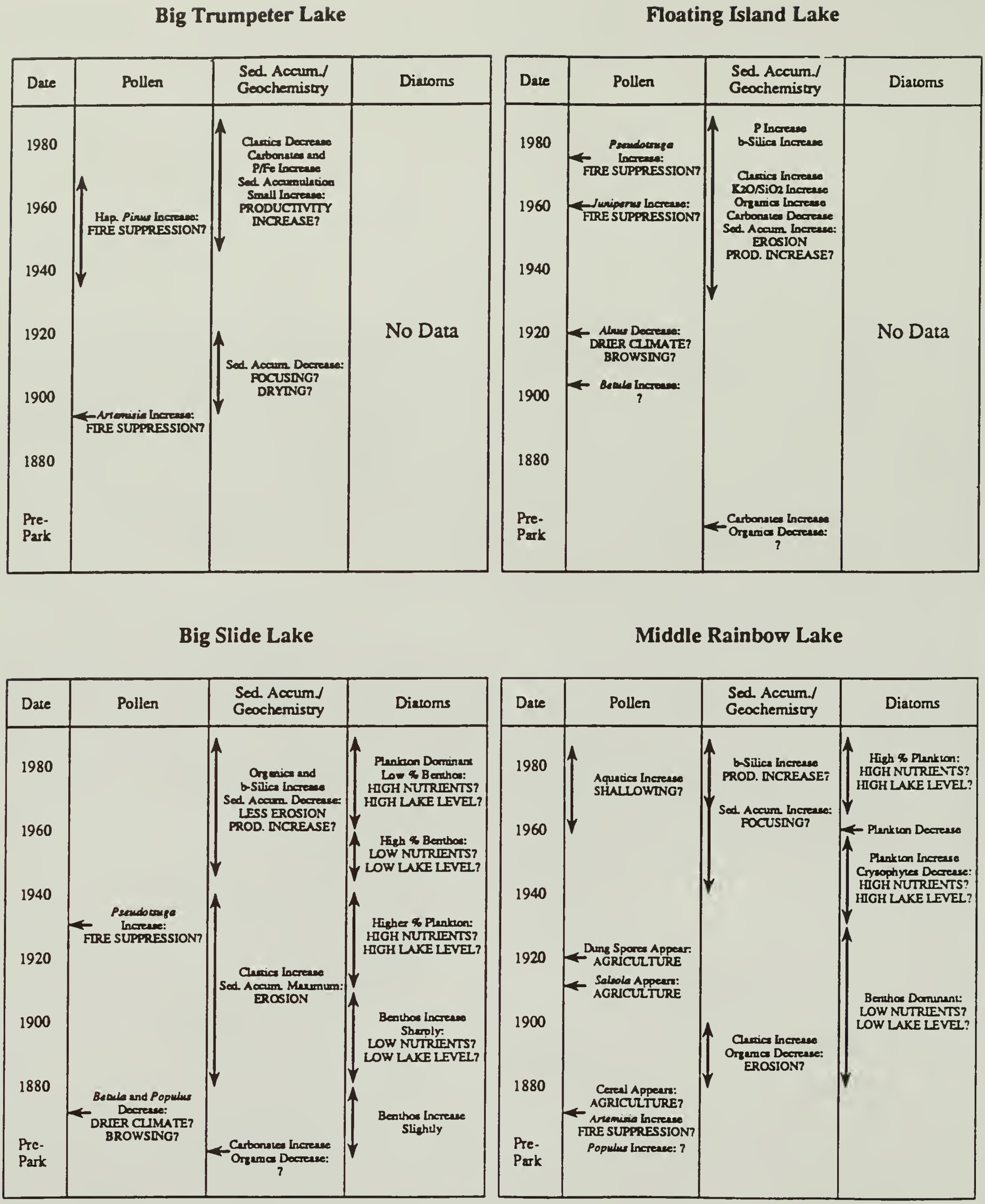

Fig. 16. Major stratigraphic changes at Big Trumpeter, Floating Island, Big Slide, and Middle Rainbow lakes, with tentative interpretations.

juniper are poorer pollen producers, and in most cases they together account for less than 10% of the total terrestrial pollen. Even at Buck, Foster, and Slough Creek lakes, where nearby forests are dominated by Douglas-fir, the pollen of *Pseudotsuga* does not exceed 5%. Because they produce so little pollen, subtle changes in the pollen record of these conifers probably have greater paleoecological significance than changes of equal magnitude for pine.

Aspen and willow, perhaps the two taxa most critical to questions of overbrowsing, are also notoriously poor pollen producers. Both can reproduce sexually or asexually, although the latter mode is more common on the northern range. Because their pollen types are represented in most levels by only a few grains, fluctuations in pollen abundance are not statistically significant. Presence or absence of *Populus* or *Salix* pollen over several levels, however, probably does indicate a change in flowering patterns within the catchment. Aspen growth and regeneration are thought to depend on regular fires. Yet, with the exception of the area around Floating Island Lake, which was partially burned in 1988, fire has not affected the study catchments during the last 115 years (D. Despain, pers. comm.). Aspen stands around most of the sites consist of mature trees that display the characteristic 'high-lining' indicative of browsing (Despain *et al.* 1984).

The pollen record of *Populus tremuloides* probably lags behind the establishment and growth of aspen trees in two ways, first in the number of years it takes for aspen suckers to develop and produce flowers (10–20 years), and second for the time it takes for trees to grow to a height at which the foliage and flowers are no longer browsed. That aspen pollen is present in early park levels and not before is consistent with the fact that most of the present trees in the northern range are about 100 years old. Pollination in these trees may be limited to a short period in their life cycle. The clones themselves are probably older, perhaps dating to the late Pleistocene, when *Populus* was well represented in the pollen record. Paleoecological data from Buckbean Fen and Cub Creek Pond in Yellowstone indicate the presence of *Populus* between 12 000 and 11 000 years ago, shortly after glaciation, when the climate was cool and moist and substrates unweathered (Baker, 1976; Waddington & Wright, 1974). Macrofossils from Buckbean Fen, however, suggest the source of this pollen was *P. balsamifera,* not *P. tremuloides.* Other Yellowstone records, including those from the northern range, do not feature *Populus* pollen in significant amounts (Gannett & Baker 1986; Whitlock, unpubl.). Following climate warming 10 000 years ago the pollen record of *Populus* is negligible throughout the park. Its decline probably reflects the restriction of *Populus* with the onset of warmer and drier conditions and development of better soils. There has probably been no establishment of aspen since the late Pleistocene, and at no time in the Holocene do the pollen data suggest that the genus was widespread in the northern range.

Birch and alder are better pollen producers than aspen or willow, and their pollen record in the northern range suggests that they were abundant in the last 150 years at only Big Slide Lake and Middle Rainbow Lake. The Big Slide Lake area presently supports a large stand of birch, despite a history of continual beaver activity. This site features the greatest decline in *Betula* pollen, although the present birch population seems healthy.

Artemisia and Gramineae both produce abundant pollen, and frequently their records are out of phase. *Artemisia* is generally thought to be favored over grasses when conditions are dry, particularly early in the growing season. *Artemisia* also replaces grass in the absence of fires and can become the dominant steppe cover within 25 years of major burning.

The curves of *Ambrosia,* Tubuliflorae, and Chenopodiineae illustrate changes in herbaceous pollen rain at the sites. Pollen of other herbs, especially insect-pollinated taxa, is present sporadically and shows no stratigraphic trends. The record of Chenopodiineae may have several interpretations, because the genus or species source cannot be identified. If the pollen comes from greasewood, saltbush, Pahute weed, or other steppe shrubs, an increase in Chenopodiineae may signify drier/warmer conditions, increased soil alkalinity, and eroding slopes. If the pollen comes from the weedy taxa of *Chenopodium* (goosefoot), it may imply greater disturbance of adjacent slopes, perhaps from increased ungulate usage. A third source is from *Chenopodium rubrum* or *Salicornia,* growing on dried exposed lake margins.

The Cyperaceae curve is attributed largely to sedge and bulrush species growing around the lake margin. In general its abundance is similar to that of 'other aquatics', which includes various submerged and floating aquatic taxa (*Potamogeton, Nuphar, Myriophyllum, Sparganium, Lemna*).

Three environmental signals appear to be recorded by the pollen data of the last 150 years. The first signal is the effect of fire suppression. In pre-park times, fires are thought to have occurred every 20–25 years in the northern range (Houston 1973). With the policy of fire suppression from about 1890 to

1973, most of the northern range did not burn. Changes in the composition of forest and grassland as a result of this fire-management policy can be seen in the pollen data from many of the lakes. Pollen records at Foster, Buck, Buffalo Ford, and Big Slide lakes show pollen increases in various conifer taxa after 1872, possibly attributable to greater pollen production from mature stands in the absence of fires. Consistent with this trend is the fact that Foster Lake contained sedimentary charcoal in pre-park levels but not above that. General closing of the forest and encroachment of conifers into steppe and grassland inferred from pollen data is corroborated by photographic evidence (Houston 1982). Conifer percentages decrease slightly during the late 1920s and 1930s at Buffalo Ford Lake and Big Trumpeter Lake, and it is likely that drought during these years inhibited production of staminate cones, although not enough to affect the pollen rain significantly. Overall, the conifer pollen stratigraphy does not correlate well with known climatic changes on a decadal scale.

The increase in *Artemisia* pollen at Slough Creek Lake, Big Trumpeter Lake, and Middle Rainbow Lake is also consistent with decreased fire frequency, which allowed sagebrush to spread at the expense of native grasses. This trend has also been observed from photographic comparisons of the northern range during the last hundred years (Houston, 1982). The decline in *Populus tremuloides*-type pollen at Buck Lake and Buffalo Ford Lake is probably an effect of fire suppression, which has led to overmature stands of aspen that no longer flower. At Foster Lake and Slough Creek Lake *Populus tremuloides*-type pollen is consistently present in park levels but less so on pre-park levels. Thus no pattern emerges that can be traced directly to climatic change.

A second signal at many of the sites is the decrease in *Salix, Betula,* and *Alnus* in the pollen record, although the timing and magnitude of the declines are highly variable. *Salix* percentages drop at Foster Lake about 1950, at Slough Creek Lake about 1960, at Buffalo Ford Lake about 1940, at Big Slide Lake about 1872, and at Middle Rainbow Lake about 1920. *Betula* percentages decrease at Buck Lake after 1890 and at Big Slide Lake after 1872. *Alnus* pollen declines at Buck Lake about 1910, at Big Slide Lake about 1872, and at Floating Island Lake about 1920. These trends probably have more than one explanation, and they may be inextricably related. The decline in willow and other shrubs has been attributed to overbrowsing by elk, deer, antelope, and moose and used as evidence to suggest that present populations of ungulates are larger than the winter range can naturally sustain for a prolonged time. Many of the willow, birch, and alder communities today indeed show signs of browsing, as well as a shift toward asexual reproduction. Both of these factors limit production of flowers, thereby fostering a decline in the pollen record. What is unclear, however, is whether intense browsing is a cause of, or a response to, a decline in the riparian zone. One argument against it being a cause is the fact that the pollen record of riparian shrubs does not show changes corresponding to historic fluctuations in the number of elk. For example, in the 1960s, when the elk population was below 5000, there is no increase in the pollen of willow, birch, alder, or aspen at any of the sites to suggest a recovery from browsing. It seems likely that the decline in shrubs is a response to episodic drought in the northern range and shifts in the patterns of animal activity. During periods of drought riparian communities are stressed not only from water deficits but also from their greater utilization as a food source by beaver and browsing ungulates. The pollen record suggests that timing of the shrub decline is metasynchronous, however, and interactions among climate, local hydrology, and animal usage apparently varies with catchment.

A final signal in the pollen record has bearing less on the northern-range history than it does on calibrating the lead-210 chronology and the timing of anthropogenic disturbance in the region. Cereal pollen, largely *Triticum,* is a good indicator of agricultural activity in the region. It appears at Foster Lake at 1920 and at Slough Creek lake and Middle Rainbow Lake as early as 1872. The Yellowstone Valley and Gardiner area were settled as early as 1860s by the mining communities of Jardine and Cinnabar (Haines, 1977). By the 1870s ranching was widespread in the area around Gardiner. Another anthropogenic indicator is *Salsola* (Russian thistle), which was brought west with construction of the Northern Pacific Railroad. Its pollen shows up after 1912 at Middle Rainbow Lake. Dung spores (*Sporormiella*) were present in Rainbow Lake sediments that date to 1920 and earlier. Apparently their source was the sheep and cattle that grazed the northwestern part of the park prior to its acquisition by the federal government.

Erosion

The only clear sedimentary evidence for increased erosion in the northern range is found at Floating Island and Big Slide lakes. At Floating Island the change to more clastic-rich sediments and higher sediment accumulation occurs between 1930 and 1940. This signal is contemporaneous with the 1932–34 construction of the road that runs along the north side of the lake. Sediment accumulation falls off after construction, as might be expected with cessation of disturbance along the lake margin (and subsequent oiling of the road surface), but remains elevated above pre-park values. The associated increase in silicate-K_2O may signify a change in the source of erosion from native soils to road-fill. Finally, the apparent decline in carbonate deposition may be related to hydrological changes and reduced inputs of dissolved carbonate caused by road building in the catchment.

It is possible that other environmental forces such as climate change or ungulate grazing are represented in the stratigraphic sequence in the Floating Island core. However, the close synchrony with road construction and the strength of the signal make it unlikely that more subtle changes could be differentiated. More importantly this signal provides a calibration for stratigraphic disturbance unrelated to direct human activity in other lakes. By this standard the only other site providing a clear indication of erosional changes is Big Slide Lake. The input of clastic materials to this site increased between 1880 and 1940, as shown by elevated sedimentation rates in three cores and a lithologic increase in silicate content. This change is notable in that Slide Lake sediments, unlike those in Floating Island Lake, are highly inorganic (owning to an unstable catchment), and any noticeable increase in clastic content must involve a major change in sediment loading to the lake.

The ultimate cause of the erosion signal in Big Slide Lake is far from clear. It begins shortly after establishment of Yellowstone park and is more or less contemporaneous with opening of the Old Gardiner Road, which passes through the Slide Lakes catchment. While it is unlikely that slope-wash from the road could directly enter Big Slide Lake (Little Slide Lake provides an upstream settling pond), road dust from summer traffic could provide a significant source of anthropogenic clastics. Use of the old road may have declined with construction of a paved road in the Gardiner River canyon. This latter event may be represented by the return to more organic sediments and the decline in sediment accumulation in Big Slide Lake after about 1940 (cf. Smol & Dickman, 1981). As at Floating Island, alternative explanations exist for the sedimentary sequence described above. Climatic change or beaver activity might affect water level and thereby influence the mat of littoral vegetation that today traps most sediment at the lake margin. Variations in ungulate activity or a reactivation of landslides in the watershed also cannot be ruled out.

Three other sites show possible evidence for periods of higher erosion. These include Foster Lake (1800–1850 and 1900–1920), Buck Lake (1860–1870), and Middle Rainbow Lake (1880–1900). In all cases the most convincing signal is a change to more silicate-rich sediments, which at Foster (1900–1920) and Buck lakes is concurrent with a small peak in sedimentation rates. The increase in sediment accumulation at these two sites is unconvincing, however, because sedimentation is elevated for a single level, and the change is relatively modest. At Middle Rainbow Lake sedimentation rates are very uncertain because of large dating errors at the base of the core. Even if these sedimentological changes do represent greater erosion, the increase is both subtle and difficult to ascribe to an environmental cause. In each case the timing is different, so climatic change seems unlikely, and, although ungulate grazing is possible, populations are poorly documented during the early history of the park. Furthermore, there is no sedimentological evidence for greater erosion in the last two decades when elk and bison reached record numbers.

Increased sediment accumulation unaccompanied by lithological change is attributed to a shift in sediment deposition pattern within the basin rather than to increased erosion. This interpretation is based on the assumption that any change in material input to the lake as a whole will alter sediment composition, whereas deposition of a greater portion of a constant sediment load at a given core site will not (Engstrom & Swain, 1986). Periods of higher sedimentation in the absence of lithologic change are evident in Buck Lake (1920–1960), Buffalo Ford Lake (1960–present), and Middle Rainbow Lake (1940–present); singular decreases in sediment accumulation are seen in the cores from Buffalo Ford Lake (1920–1950) and Big Trumpeter Lake (1890–1920). Changes in lake hydrodynamics related to variations in water level, thermal stratification, or wind stress are probably responsible for shifting the pattern of sediment deposition within these basins.

Limnological change

Sedimentological evidence for increased lake productivity includes increased concentrations of organic matter, biogenic silica, phosphorus, and in some cases carbonates, usually in conjunction with higher sediment-accumulation rates. This type of stratigraphic signal is clearly present in Buck Lake and Slough Creek Lake and possibly in Middle Rainbow Lake after 1960 and in Buffalo Ford Lake from ca. 1880 to 1920. Similar changes in sediment composition but without increased accumulation are also seen at Slough Creek Lake (1890–1920) and in Big Trumpeter Lake after 1945. Sedimentological evidence for higher productivity in Floating Island Lake and Big Slide Lake after ca. 1940 is confounded by the strong geochemical signal for erosional changes at these sites. Geochemical evidence for greater eutrophy in Buck, Slough Creek, and Middle Rainbow lakes is corroborated by the diatom data and coincides with a known increase in elk populations in the northern range during the last two decades. The signal at Big Trumpeter Lake, while less convincing, could represent the same ecological event, especially if dating uncertainties at this site (see above) are taken into account. The earlier and nearly contemporaneous changes in Slough Creek Lake and Buffalo Ford Lake sediments might likewise be related to changes in elk populations shortly after park establishment. Greater ungulate use of these catchments could increase nutrient loading and elevate lake productivity.

On the other hand, just four of our eight study sites show a sedimentological signal associated with the well-documented elk increase of the 1960s, and one of these, Buck Lake, is only marginally used for winter forage. Other factors such as climatic and hydrologic change, fire suppression, or beaver activity could be responsible either independently or in conjunction with ungulate use for changing nutrient flux to the lakes. There is no way to disentangle these environmental forces, because they are effectively contemporaneous and because the geochemical signals for eutrophication in these lakes are far too subtle.

The five Yellowstone lakes analyzed for sedimentary diatoms show differing patterns of limnological change from the early 19th century to the present. These differences indicate the importance of local factors in controlling diatom distribution and limnological history. All five sites, however, were clearly mesotrophic to eutrophic prior to the establishment of the park, indicating that watershed input of nutrients to these systems has been quite high naturally.

The diatom data suggest that during the last 150 years perturbations have occurred in each of the lake catchments that altered the relative proportions of benthic and epiphytic diatoms relative to planktonic taxa. The timing, magnitude, and duration of these perturbations vary among the lakes. In all sites studied, epiphytic and benthic diatoms increase relative to plankton sometime in the latter half of the 19th century. The magnitude of the increase is quite small in Buck, Big Slide, and Middle Rainbow lakes and probably indicates only small fluctuations in the aquatic ecosystems. The shifts are more pronounced, however, in Foster and Slough Creek lakes, suggesting greater limnological change. It is not clear whether the habitat shift in the diatom community reflects lowered nutrient availability or increased littoral area resulting from lowered water levels. The asynchroneity of these alterations suggests that water-level change in response to regional climatic change is unlikely, and that nutrient inputs to the lakes changed, perhaps as a result of lower fire frequency. The chrysophyte stratigraphies in Foster and Slough Creek lakes suggest fluctuating nutrient concentrations at these sites.

Middle Rainbow, Big Slide, and Slough Creek lakes show more frequent 20th century limnological fluctuations, so they either experienced greater environmental change or were particularly sensitive to the changes that occurred. Benthic diatom percentages in these lakes decline between 1910 and 1920 but later show a resurgence of variable duration, beginning in the 1930s at Big Slide Lake but not until the 1950s in Middle Rainbow and Slough Creek lakes. At Buck and Foster lakes, on the other hand, benthic percentages remain slightly elevated from the early 20th century through the 1950s. At all sites except Foster Lake benthic diatoms decline and plankton increases from the early 1960s to the present. Although Foster Lake shows a brief pulse of higher diatom plankton in the mid-1950s, the general trend is toward gradually lowered nutrient availability and ultimately a total loss of diatom and chrysophyte plankton.

Changing nutrient availability in the lakes, as reflected in alterations in the proportions of planktonic to benthic diatoms, could result from variable and asynchronous use of lake catchments by grazing ungulates; however, changes in the pollen data that might reflect the local presence of ungulates do not generally parallel periods of elevated nutrient concentrations as suggested by diatom data (Fig. 15, 16). Planktonic percentages in Buck, Slough Creek, Middle Rainbow, and Slide lakes are elevated in the last two decades, when increased ungulate populations are well-documented. This trend could reflect higher nutrient inputs to these systems. The diatom species composition of the post-1960s sediments, however, is quite similar to that prior to park establishment, suggesting that these lakes have not been perturbed outside their normal range. Thus it is clear that none of the lakes has been significantly enriched in comparison with their 'natural' pre-park disturbance conditions, and that the magnitude of any enrichment by ungulate populations must be small in comparison with natural nutrient yields from the catchment.

Conclusions

The principal stratigraphic changes in the sediments of the eight lakes investigated are tabulated in Figs 15 and 16, along with tentative interpretations of their significance. The most striking impression one gains from the tabulation are the asynchroneity of the stratigraphic changes among the lakes, and the large number of queries in the interpretations. These results emphasize the difficulties in deciphering the complex interactions among the environmental factors affecting the vegetation, the sediment flux to a lake, the sediment distribution within a lake, and the limnological productivity—factors such as changes in climate, fire regime, grazing and manuring by ungulates, erosion, lake morphometry and littoral vegetation, and, in the northern edge of the park, early agriculture. Climate and fire frequency can affect the vigor and distribution of certain trees and shrubs, and climate can also control the water depth and thus the biota of a small lake. Lake levels may also be affected by beaver activity, mass movement (in the case of Slide and Rainbow lakes), and possibly seismic activity. Catchment erosion is influenced by vegetation type and density, animal trampling, and climate. Lake productivity and biota are affected by nutrient influx, water clarity, and water depth. The composite record of changes in these factors may rest in well-dated lake sediments, but the present investigations illustrate the difficulties in sorting out the exact course of the environmental changes.

Nonetheless, a few conclusions can be drawn from the dated stratigraphic sequences in the northern range of Yellowstone Park. The single stratigraphic change that is relatively easy to explain is at Floating Island Lake, where the increase in sediment accumulation combined with an increase in clastics and their elemental representatives (K_2O, SiO_2) about 1935 can be attributed to runoff or dust occasioned by construction of a nearby road. The subsequent increase in organic matter may record an increase in lake productivity, which may also be related to this disturbance, although the lack of a diatom diagram for this site prevents confirmation of such an inference. The lake-sediment record of road construction was not a central objective of this investigation, but the results do show that important local landscape disturbance does significantly alter the limnological record.

Several decades of the pre-park era are recorded at most sites, and significant changes in certain profiles indicate that variations in environmental or sedimentological factors were effective under natural conditions. For example, at Slough Creek Lake in the mid-1800s a temporary maximum in carbonates, Ca, Mn, and biogenic silica may represent an episode of increased productivity, although the diatom profile does not support this inference. Buffalo Ford Lake shows an interval of low carbonates (and Ca) and high Fe in the 1800s. All sites with diatom diagrams show a relatively high trophic status for pre-park times. The two sites with active landsliding in shales (Big Slide and Middle Rainbow lakes) show a steady dominance of clastics in the profiles from bottom to top.

Profiles are slightly less complacent for the years after the park was founded in 1872 than before, implying that park management may have had some influence on lake sedimentation, although it is usually difficult to decipher the specific factors responsible. The strongest stratigraphic changes are in the diatoms, yet the patterns are not uniform among the five lakes studied, and in any case one cannot infer a progressive eutrophication as a consequence of park management. In the early years of the park an increase in conifer and *Artemisia* pollen and decrease in aspen pollen at several sites may record the beginning of fire suppression.

In the early 1900s some sites show increased sediment accumulation at the core site (Foster, Buffalo Ford, Big Trumpeter, Big Slide lakes), but in most cases the cause may be sediment redistribution (focusing) or increased algal production rather than erosion and increased sediment input to the lake. Most profiles show few changes in the 1930s to 1950s. The exception is the record of increased erosion related to road construction near Floating Island Lake. An increase in lake productivity during the last few decades is suggested for Buck, Slough Creek, and possibly Big Trumpeter, Floating Island, Big Slide and Middle Rainbow lakes by sedimentological increases in biogenic components and accumulation rates. The diatom profiles support this interpretation for the four lakes that were studied (Buck, Slough Creek, Big Slide and Middle Rainbow). Trophic conditions today, however, are not much different from what they were before the park was established. The big puzzle is why most lakes had a temporary phase implying low nutrient input at different times in the park history—the explanation here is that each lake responded differently to climatic conditions and perhaps the absence of fire, depending on its morphometry and hydrologic setting.

The case for accelerated erosion in the northern range resulting from ungulate grazing is not supported by the stratigraphic studies. Increased elk populations during the last two decades have apparently not resulted in increased erosion of the lake catchments.

Sediment composition and variability before and after the park was established are similar.

The pollen evidence for ungulate grazing on trees and shrubs is weak; most sites do show a slight decrease in the pollen profile for one or another hardwood tree or shrub (willow, aspen, alder, birch), but the dates for the decrease are highly variable from site to site, and in any case dry climatic conditions provide an alternative explanation. The case for the absence of fire as a factor in vegetation change is somewhat stronger, as represented by slight increases in conifers or in *Artemisia* at all sites. The variable times at which these changes occur may reflect the different response times of the various conifers to a change in fire regime.

The overall conclusion must be that the lake-sediment records in the northern range do not convincingly show systematic direct or indirect effects of ungulate grazing during the history of the park. It is possible that grazing pressure did impact the landscape of the northern range in ways too subtle for our paleoecological techniques to resolve, particularly against a background of high environmental variability. However, this is precisely the point we set out to resolve: do recent ungulate impacts fall within the limits of natural environmental variability. We conclude that they do.

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Major Erosive Lands in the Upper Yellowstone River Drainage Basin

Henry Shovic, Jana Mohrman, and Roy Ewing

Yellowstone National Park
Center for Resources
Box 168
Mammoth, Wyoming 82190

Abstract. Periodically high turbidity in the upper Yellowstone River system has become a subject of interest to recreational groups, scientists, and federal land managers. Although information about sediment and turbidity has been collected for major tributaries, additional data on tributary drainage characteristics are needed to facilitate an understanding of causes. No systematic study has been done to determine potential sediment source areas or to describe major erosional processes. Therefore, a reconnaissance study was initiated to provide that information. Seven major types of highly erosive lands were identified. Qualitative analysis of areal extent and sediment data point to the drainage basins of the upper Lamar River, Soda Butte Creek, and the Gardner River (primarily Mount Everts) as having by far the most highly erosive land and the largest sediment contributions to the Yellowstone River above Corwin Springs. Erosive areas and sediment contributions are substantially higher in the Yellowstone National Park portion of the study area than in the Gallatin National Forest portion.

Key words: Erosion, Gallatin National Forest, turbidity, water quality, Yellowstone National Park, Yellowstone River.

The management of Yellowstone National Park has long been the focus of controversy. The unique management objectives for the park have called for a similar management style, which has developed over the last century. Yellowstone National Park's unparalleled resources are to be preserved in their natural state, yet to be made available to the public. The public has divergent philosophies, perceptions, and interests about exactly what the management objectives mean and about their implementation.

The Yellowstone River above Livingston, Montana, is also embroiled in controversy. Its status as a blue ribbon trout stream, its high usage levels, and its freedom from impoundment give it high visibility in political and public circles. The upper reaches of the Yellowstone River are in Yellowstone National Park, Wyoming, but it passes through miles of private land between the park and Livingston. Many important tributaries are in the surrounding Gallatin National Forest. This shared ownership guarantees diversity of interests, perceptions, and philosophies on the part of the public, and controversies over management.

Soil erosion and subsequent siltation is one of those controversies. The term *soil erosion* (the movement of soil particles by wind, water, or gravity) often conjures images of farmland washing away, dust bowls, and dying fishes. Accelerated soil erosion is generally detrimental because vegetation cover and soil horizons or layers are lost, usually due to some short-term disturbance. This disturbance can be geologic (earthquakes, glaciation, etc.), vegetative (disease, fire, etc.), or climatic (storms, droughts, etc.), or can be influenced by fauna (primarily humans: Toy 1977). Erosion is also directly or indirectly responsible, however, for most of the character of our landscapes, including the magnificent landscapes of Yellowstone National Park and its neighbor, the Gallatin National Forest. Geologic erosion, the type present here, occurs at a rate slow enough to lag behind the development of stable soil profiles and vegetation cover. The character of geologic erosion is largely dependent on climate, topography, and rock types.

Accelerated soil erosion in northern Yellowstone National Park has been qualitatively investigated by geologists, by comparisons of historical photographs, by range management evaluations, and by systematic—although qualitative—observations (Keefer 1976; Houston 1982; Despain et al. 1986; C. Craig, Debris flow-dominated alluvial fans in northern Yellowstone National Park, Wyoming: depositional frequency and chronology of fan development. Research Division, Yellowstone National Park, Wyoming, unpublished manuscript). Opinions on the status of erosion in the park have been based on a mixture of this and other, sometimes inappropriate, information. No systematic effort has been made to measure or otherwise quantify contributions of various sites to produce a picture of the most important erosion processes operating in northern Yellowstone National Park and of the results of those processes.

The most recent debate over erosion involves the periodic, high turbidity of the Yellowstone River during the summer. Because recreational uses have been increasing, organized groups have taken an interest in the sources of this turbidity. The possible relation between heavy grazing of the grasslands by wildlife in the northern Yellowstone drainage to erosion and sedimentation has been discussed for many years (summarized in Coughenour and Singer 1991).

A study was started in 1985 to quantify the sediment and turbidity contributions to Yellowstone Lake in Yellowstone National Park (Ewing et al. 1986; Mohrman et al. 1988) from tributaries to the Yellowstone River above Livingston, Montana. The drainage basins in the park contributed significantly to the overall suspended sediment load of the Yellowstone River. Basins in the Gallatin National Forest also contributed to the load but to a lesser extent. The major sources of the eroded material were not determined although contributing watersheds could now be quantitatively identified.

This study was initiated to determine major erodible areas in Yellowstone National Park and in parts of the Gallatin National Forest. Our objectives were to complete an inventory of major erosional features, to provide information to researchers and land managers about important erosion processes and the location and characteristics of highly erosive sources within the study area, and to qualitatively compare with sedimentation data to provide a better understanding of major erosion processes. The inventory was to consist of two products. The first was to include major landscape groups having properties that influence erosion potential. This gave a landscape and process framework for the second, which was the actual delineation of erosive lands.

Methods and Materials

Definitions

Erosion is defined as the detachment and transfer of soil or regolith material to perennial stream courses (Kirkby and Morgan 1980). For this study, transport within those courses is not included. Mass movement and solution are included, however, as well as continuous removal of material by wind, water, or other agents (Toy 1977). Eroded material is defined as the fraction of available material less than 2 mm in diameter. This is because it is the most important size fraction in determining suspended sediment loadings and turbidity—parameters measured in the sediment study.

Ratings of erosion potential were defined based on local management guidelines and soil survey interpretations (Davis and Shovic 1984). High erosion potential means significant sediment is produced from a major site in the short term (1–10 year frequency), either by snowmelt, summer rainstorms, or hydraulic action near streams. High sites have active rills, gullies, landslides, or evidence of sheet erosion. Vegetation is absent or sparse and is affected by erosion processes. The coarse fraction (greater than 2 mm in size) of soil is less than 50% of total soil volume. Neither significant erosion pavement or other armoring by gravel or larger materials is present. Eroded material commonly reaches perennial streams within 1 year.

Moderate erosion potential means there are areas of noticeable erosion on a small proportion of a site, or significant erosion only occurs during extreme events. Because of sediment trapping areas between the eroding slope and the stream course, there is no sediment contribution to perennial streams under most conditions. The eroded material eventually enters the stream system but not as rapidly as in high as defined above. If areas have no vegetation and are near streams, over 50% of the soil volume is larger than 2 mm in diameter, or finer particles are retained in place by cementation, resulting in little fine sediment potential.

Low erosion potential means no visible active erosion. If there are relict erosion features, current transport mechanisms are ineffective in delivering material to perennial streams.

Study Area

The study area consists of the Yellowstone River drainage from the Yellowstone Lake outlet downstream to Livingston, Montana (Fig. 1). Because of limited time and resources, three subareas were prioritized for completion, based on the availability of sediment, soil, and geological data.

Priority Area One

This area includes northern Yellowstone National Park. Also included are (1) lands on the Gallatin National Forest and in private ownership;

Fig. 1. Study area and subdrainage basins. Large numbers refer to priority areas. Small numbers are drainages or subdrainages. Heavy blach lines are drainage or subdrainage boundaries. Small letters refer to drainages used in the sediment/turbidity study (Ewing et al. 1986, Mohrman et al. 1988).

(2) the Slough, Buffalo, Mol Heron, and Tom Miner drainages; (3) small areas north of Gardiner, Montana, on the western side of the Yellowstone River; and (4) the northern corner of the Soda Butte Creek drainage (drainages 1–14 and part of 15 in Fig. 1). The highest number of sediment and turbidity stations in the sediment study are in northern Yellowstone National Park and the area north, to and including Tom Miner Creek (Ewing et al. 1986; Mohrman et al. 1988). The northwest corner of area 1 is covered by the Gallatin Forest Soil Survey (Davis and Shovic 1984).

Priority Area Two

This area consists of lands west and east of the Yellowstone River in Paradise Valley, Montana (area 2, Fig. 1). The west part contains only one sediment or turbidity monitoring station (Big Creek). Part of that area is covered by a soil survey on Gallatin Forest Land (Davis and Shovic 1984). The east part of area 2 contains the majority of watersheds in the Paradise Valley that were monitored for turbidity by personnel of the National Park Service. Few landscape or soils data for the eastern part are available because of the large amount of private land and the Absaroka–Beartooth Wilderness, for which a soil survey is lacking.

Priority Area Three

This area was not inventoried in this study (area 3, Fig. 1). The National Park Service has no sediment or turbidity data for these lands. The watersheds also have limited coverage by the Gallatin National Forest

Soil Survey. Qualitative field observations made by the Forest Service during the course of the sediment and erosion studies, however, indicate these streams are not large contributors to sediment loading, and the lands in these watersheds are not likely to be highly erosive (Personal Observation).

Mapping Methods

The mapping methods used in this study were modified from those used in Forest Service wildland soil inventories (U.S. Forest Service 1987) and other large scale erosion inventories (Rickert et al. 1978). Standards for mapping unit composition follow national guidelines (U.S. Forest Service 1987). Maximum dissimilar inclusions (limiting errors) in map unit delineations or map unit descriptions is 15%. Minimum map unit delineation size is about 4 ha (10 acres). If necessary, smaller eroding areas are mapped as complexes of eroding and noneroding areas. Each priority area was mapped slightly differently, because of differences in available data.

Priority Area One

Compilation of Existing Data. Geologic maps, existing soil information, precipitation maps, literature on erosion, aerial photography, topographic maps, vegetation maps, and existing erosion data were collected and reviewed.

Preliminary Field Studies and Initial Classification. Two field investigations were conducted to familiarize the study team with the overall erosion situation. Because landscape and soil information relating to erosion is scarce in the Yellowstone National Park portion of the study area, a preliminary classification of major landscape groups was made to focus further field investigation and to develop an understanding of the erosional processes operating in the park portion. Remote sensing methods with aerial photography were used in mapping the major landscape groups (Avery 1968; Wolf 1974; Johannsen and Sanders 1982). The erosion potentials are based on theory of erosion and experience in similar landscapes (Leopold et al. 1964; Toy 1977; Kirkby and Morgan 1980). Erosion potential refers to overall tendencies, and does not imply the entire area is eroding in that manner. This map product was completed at a scale of 1:125,000 using color infrared aerial photography (1:50,000 scale), geologic maps, and information on glacial history (U.S. Geological Survey 1972a, 1972b; Pierce 1979)

Development of Initial Mapping Legend and Delineation of Units. A selection of 1:20,000 aerial photographs was used to delineate potential erosional land areas or suspect areas. Delineation was based on photo signature (appearance of the feature on aerial photographs), geologic formation (either surficial or bedrock as appropriate), and landform (Avery 1968; Wolf 1974; Johannsen and Sanders 1982). These were used to focus field studies within major landscape groups.

Twenty-five field studies were conducted during May–November 1987 (Table 1). These were carefully documented with either aerial photographs or topographic maps and color slides indexed to field notes. The field study locations were selected as representative of each major landscape group to help ensure that the major erosional processes were covered in the data collection (Table 2) and to access previously mapped suspect areas. Twenty-two field studies were carried out by members of the study team, and the remaining three were accomplished by National Park Service employees as they performed other duties.

These field studies were used to develop predictive mapping tools and a legend of erosional features. Map units were described in terms of photo signatures, landforms, and geologic materials to facilitate mapping from the office. Though the initial legend included areas of high, moderate, and low erosion, only the high areas were mapped. The remainder was discussed in text. Because of incomplete coverage at one scale, both 1:62,500 color infrared and 1:20,000 color aerial photography were used in Yellowstone National Park. Mapping in Tom Miner, Mol Heron, and Upper Slough Creek drainages and the Cooke City, Montana, area was completed using 1:62,500 black and white photography. Geologic maps as a scale of 1:125,000 and 1:62,500 were used for the area. Mapping was completed on 15-minute (1:62,500) topographic quadrangles.

Descriptions of map units are in Appendix A. Channel erosion map units or CER (Appendix A) were mapped in linear measure. To allow relative areal comparison to other kinds of map units, they were converted to areal measure by combination with an average eroding slope length on both stream banks (9.1 m; 30 feet). The value is based on weighing of estimates of slope length done during field investigations. Small perennial stream channels have about 3.0 m (10 feet) of eroding bank slope length, while large streams such as the Lamar River may have 18.3 m (60 feet) of cutbank slope length.

Areas previously mapped on aerial photos were reexamined as mapping proceeded to ensure that features were being consistently interpreted. The legend was modified as required. Another quality control evaluation involved mapping on adjacent photo flight lines, with

Table 1. Field sampling areas for priority area one.

Sample area	Location	Major landscape group	Date
FT1	Lamar	AL, LH	6/18/87
FT2	Everts	MW	5/5/87
FT3	Tower	LH	5/26/87
FT4	Northeast entrance	GT	6/4/87
FT5	Northeast entrance	GT	7/1/87
FT6	Slough–Lamar	AL	7/1/87
FT7	Reese Creek	SB, GS	7/2/87
FT8	Blacktail Plateau	GG	7/23–24/87
FT9	Flather Upper Lamar	GT, SB, GM	7/6–10/87
FT10	Flather Cache Creek	GT	7/31/87
FT11	Hayden Valley	LK, PQ	7/5–6, 18/87
FT12	Daisy Pass–Pebble	GT	8/8/87
FT13	not done		
FT14	Sevenmile Hole	PQ, SH	8/25/87
FT15	Washburn	GC	9/1/87
FT16	West Blacktail	GG	9/11/87
FT17	Lava Creek	PQ	9/11/87
FT18	Gardner Canyon	MW	9/15/87
FT19	Old Gardiner Road	GG, MW	9/18/87
FT20	Hellroaring	GG, SG	9/17/87
FT21	Stevens Creek	GG, MW	9/22/87
FT22	Specimen Ridge	GM, PT	9/24/87
FT23	Slough Creek	SG, AL	10/8/87
FT24	Exclosures	GG	varied
FT25	Fawn Pass	GG, GS	10/13/87
FT26	Mahony Upper Lamar	GT, SB, GM, AL	11/5/87

some overlap. Delineations were compared across photos to help assure consistency.

The areal extent of map units was determined with dot grids and planimeter. Linear measurements of CER's were made with a stadimeter (distance wheel). Map unit areas were totaled by drainage or sub-drainage and major landscape group. Map units were transferred to a 1:400,000 (Fig. 2) scale map of the Yellowstone National Park and Cooke City portions of the study area.

A random examination was made of photographs and final maps to determine any consistent errors in transfer, mapping, or labeling. A complete inspection of all maps was made to find any edge matching problems, labeling errors, or obvious map errors. Finally, all map units were measured and added twice.

Priority Area Two

Gallatin National Forest lands on the study area generally have a low surface erosion potential if undisturbed. Significant disturbance by ground-based management is generally necessary to produce accel-

Table 2. Priority area one field sample areas by major landscape group.

Major landscape group	Sample area
GT	FT4, FT5, FT9, FT10, FT12, FT26
SB	FT7, FT9, FT26
GM	FT9, FT22, FT26
AL	FT6, FT1, FT23, FT26
PT	FT22
PQ	FT11, FT17, FT14
SH	FT14
LH	FT3
GG	FT8, FT16, FT20, FT19, FT21, FT24, FT25
SG	FT20, FT23
LK	FT11
GS	FT7, FT25
MW	FT2, FT18, FT19, FT21
GC	FT15, FT14

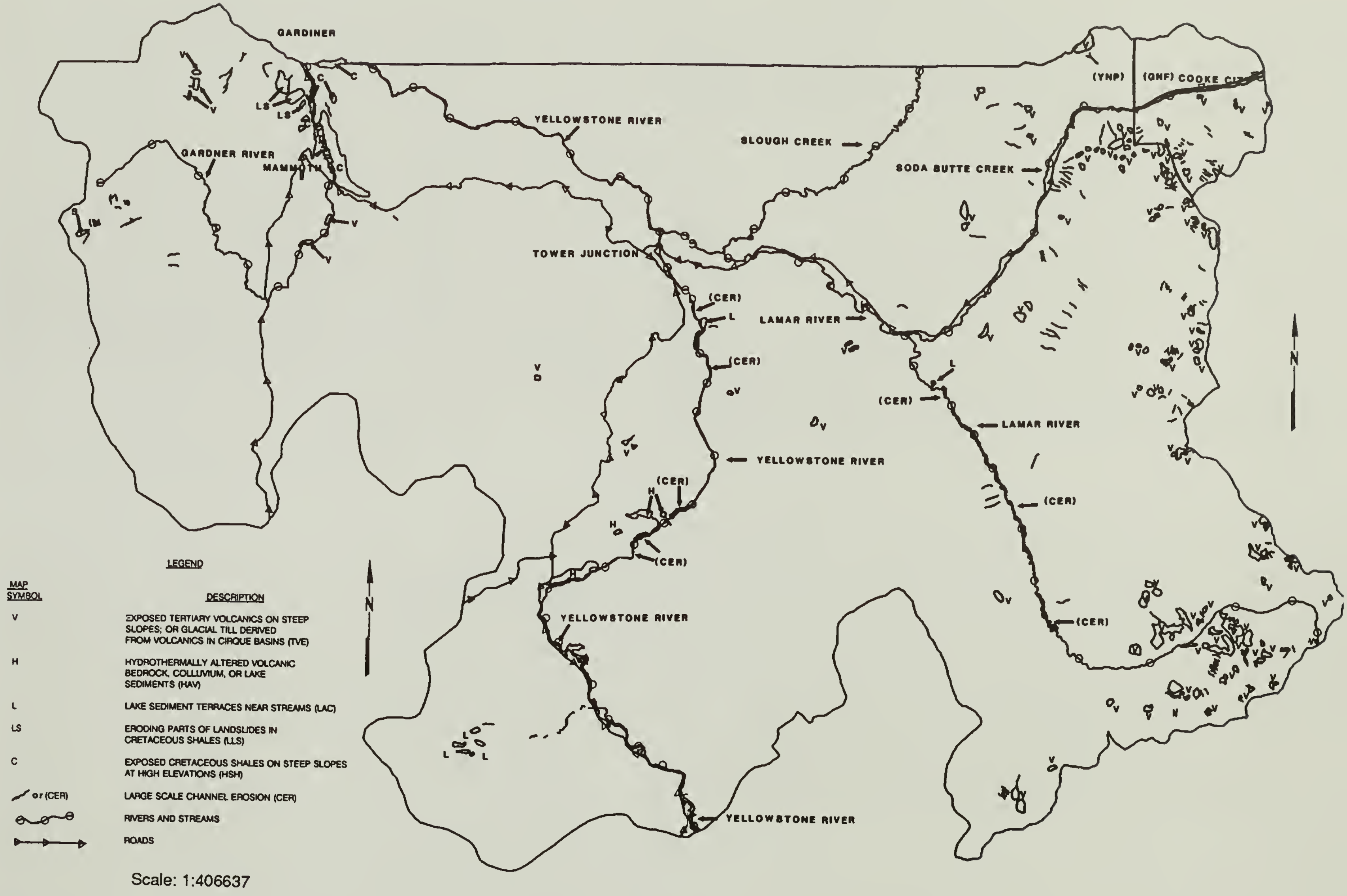

Fig. 2. Major erosive lands in northern Yellowstone National Park, Wyoming; Cooke City area, Montana; and part of the Gallatin National Forest.

erated erosion. This is based on data for lands in the northern Rocky Mountains and the Gallatin National Forest (U.S. Forest Service 1981; Davis and Shovic 1984). Therefore, map unit definitions were based on areas having recent disturbance (timber harvest units less than 10 years old from U.S. Forest Service timber stand data) and occurrence in soil survey map units rated as having a low potential for sediment control. The disturbed areas were mapped on 1:62,500 topographic maps. Private land included within forest boundaries was not evaluated.

Results and Discussion

Areas with High Erosion Potential in Priority Area One

Descriptions of map units having high erosion potential are in Appendix A. Figure 2 illustrates map unit distribution for Yellowstone National Park and the Cooke City area and part of the Gallatin National Forest within priority area one. Areal extent is given for each high map unit for individual areas and subdrainage basins (Table 3) monitored in the sediment study (Ewing et al. 1986; Mohrman et al. 1988), for priority area one. These are summarized by major drainage basins in Table 4. To develop a perspective of erosional landscapes related to actual sedimentation, erosive lands in each drainage basin are discussed below in terms of areal extent, physical characteristics, associated major landscape groups, and qualitative relations to the sediment study (Ewing et al. 1986; Mohrman et al. 1988). A semi-quantitative ranking of areal extent versus sediment loadings was completed for selected basins. Finally, a ranking of erosive land area versus drainage basins and major landscape groups was completed.

A few areas were excluded from mapping. About 5% of the area south of Cooke City was not mapped because there was no photo or geologic coverage available. A few identified high sources are on the Yellowstone River from Tower Junction to Blacktail Bridge in the Black Canyon. Because of poor accessibility and time constraints, these were not verified in the field nor mapped. Some probable high areas are

Table 3. Area of map units having high erosion potential by subdrainages in priority area 1.

	Map unit area (ha)							Total
Subdrainage[a]	V	CER	L	H	LS	C	S	(ha)
Upper Lamar above Soda Butte (1)	1,426	71	16					1,563
Soda Butte (2)	591	24						615
Slough (3)	20	5						25
Yellowstone River above Lamar (4)	91	15	185	228				519
Lava above picnic ground (5)		1						1
Lava Creek picnic ground to Gardner River (6)						98		98
Gardner West (7)	66	13			94	500	20	693
Reese (8)	55	1						56
Mol Heron (9)	43	2				8		53
Yellowstone above Corwin, below Gardner River (10)		5			79	16		100
Tom Miner (11)	39	1						40
Blacktail (12)								0
Lamar between Soda Butte and Yellowstone River (13)	28							28
Yellowstone River below Corwin, above Tom Miner (14)								0
Hellroaring area (15)						82		82
Total by map unit	2,409	138	201	228	173	704	20	3,873
Percent of total map unit area	62	4	5	6	4	18	1	100%

[a] Numbers in parentheses ( ) are subdrainages from Fig. 1.

Table 4. Area of map units having high erosion potential by drainage basins in priority area one; Northern Yellowstone National Park, Cooke City, Montana area; and part of the Gallatin National Forest.

Drainage basin[a]	Map unit area (ha) V	CER	L	H	LS	C	S	Total (ha)	Drainage area (ha)	% of area
Upper Lamar above Soda Butte (1)	1,476	71	16					1,563	88,238	1.8
Soda Butte (2)	591	24						615	26,326	2.3
Upper Lamar + Soda Butte (1+2)	2,067	39	16					2,122	114,564	1.9
Slough (3)		20	5					25	56,964	0.04
Yellowstone River above Lamar (4)[c]	91	15	185	228				519	89,781	0.6
Lamar (total) (1+2+13+3)[c]	2,115	100	16					2,231	182,085	1.2
Lava (5+6)		1				98		99	12,007	0.8
Gardner (5+6+7)[c]	66	13			94	599	20	792	52,340	1.5
Reese (8)[c]	55	1						56	3,439	1.6
Mol Heron (9)	43	2				8		45	10,883	0.5
Yellowstone above Corwin, below Gardner (BLA)(10)[b,c]		5			79	16		100	4,266	2.3
Tom Miner (11)		39	1					40	17,049	0.2
Blacktail (12)[b,c]								0	21,083	0

[a] Numbers in parentheses ( ) refer to subdrainage areas.

[b] These are subdrainages of sediment study basins but are included because they are significant parts of the northern ungulate winter range.

[c] Drainages are discussed in text.

near Lamar Mountain in the southeast part of the study area. Though photo signatures indicate active erosion potential, they were not mapped because of lack of field verification. Total area of these unmapped areas is probably less than 50 ha.

Erosive Lands in Individual Stream Drainage Basins

The Lamar River Drainage. This drainage basin consists of the Upper Lamar above Soda Butte Creek, Soda Butte Creek, Slough Creek, and the Lamar between Soda Butte Creek and the Yellowstone River. Of these, the Soda Butte drainage has the highest proportion of highly erosive land (2.3%; Table 4). The map units are primarily V, which include glacial till in high elevation cirque basins, derived primarily from volcanic rocks in the Lamar River Formation. Also, the oversteepened, large glacial trough walls (major landscape group GT, Appendix B) provide an efficient intermittent transport system to Soda Butte Creek. Many of these intermittent channels are also eroding into moraines and Paleozoic shale bedrock on the lower portions of the trough walls (Map Unit CER, Appendix A).

The kinds and amounts of eroding land in the Soda Butte drainage are related to their contribution described in the sediment study (Ewing et al. 1986; Mohrman et al. 1988). The drainage had a consistent and relatively high sediment discharge during the 1985 and 1986 snowmelts. In 1985, Soda Butte Creek's snowmelt discharge greatly exceeded that of the Gardner River, despite having about half the drainage area of the Gardner (26,326 vs. 52,340 ha; Table 4).

Summer sediment discharge ranked similarly for both years of the sediment study. This discharge varied greatly for Soda Butte Creek, depending on the intensity and duration of summer rainstorms. For example, the sediment discharge from an intermittent trough wall tributary was measured at 114,960 tons per day, after a heavy day-long rain. This represented the largest transported load during a single event by the Yellowstone River or any of its tributaries during the 2-year study. This suggests that heavy summer rains realize a significant portion of the erosion potential of the Soda Butte drainage.

The upper Lamar River above Soda Butte Creek also has a relatively high proportion of eroding land (1.8%). Most lies near stream headwaters on glacially oversteepened cirque headwalls and scarps (V, Appendix A). The eroding slopes of volcanic rocks with poor induration are generally in the Wapiti Formation. High snowmelt rates and summer thunderstorms have eroded this rock into badland topography, a combination of bare slopes having dense dendritic drainage patterns and rapid erosion.

The second major kind of erosive land is characterized by large-scale channel side-cutting on the Lamar River below Cold Creek to the area south of Cache Creek (CER, Appendix B.). This often occurs in lake sediments that front on the stream channel and show evidence of rotational slumping and mud flows. These sediments are remnants of glacial and near postglacial lakes formed at the end of the Pleistocene. They are now being eroded by streams to their angle of repose.

Again, the relatively high proportion of erosive lands is reflected in the sediment data. The Lamar River upstream of Soda Butte Creek ranked high in summer turbidity and for the season as a whole during 1985–86 (Ewing et al. 1986; Mohrman et al. 1988).

Slough Creek has a relatively low proportion of eroding land (0.04%). This basin has large areas of hard, Precambrian age metamorphic and Tertiary igneous intrusive rocks in the lower three-fourths of the drainage. Also, extensive piedmont glaciation removed steep trough walls or fluvial slopes from many of Slough Creek's tributary valleys, leaving a subdued topography (Pierce 1979). Headwater areas have steep cirque basins, but these were formed in well-indurated volcanic rocks. Cliffs are much more common than rapidly eroding slopes. Slough Creek had a low contribution to turbidity during 1985, ranking low in overall average turbidity as well as having low snowmelt and summer values (Ewing et al. 1986).

The Lamar River drainage as a whole has 2,231 highly erosive hectares of a total of 3,875 total erosive hectares or over half the entire highly erosive area in priority area one (Tables 3 and 4). Ewing et al. (1986) and Mohrman et al. (1988) indicate the Lamar drainage makes major sediment contributions to the Yellowstone River, proportional to the amount of highly erodible land in its tributary drainages.

Yellowstone River Above the Lamar River. The Yellowstone River between the Yellowstone Lake outlet and the confluence with the Lamar River comprises a large drainage basin with a moderate amount of highly erodible land (0.6%; Table 4). Most of the land is underlain by Quaternary volcanic rocks, which have high permeability and low erosion potential (major landscape group PQ). These have been covered with a thin mantle of permeable glacial till. Almost all highly erodible land is either in lake sediments or hydrothermally altered volcanic rocks that front on or near the Grand Canyon of the Yellowstone (map units L or H). Some channel erosion is present (map unit CER). Map units are on steep cut slopes or in landslides, resulting from rapid downcutting of the Yellowstone River (major landscape group SH and LH). Some delineations are in the Hayden Valley where Trout Creek and Alum Creek have cut into lake sediment benches and terraces.

The sediment study indicated that the Yellowstone River drainage is a significant sediment source, often ranking next to the Lamar River in sediment discharge. During 1986, measured summer sediment discharge for the Yellowstone River drainage was greater than the Lamar's. Lower turbidity rankings may be related to suspended particle type and size produced by eroding hydrothermally altered rocks (Mohrman et al. 1988).

Blacktail Plateau. The Blacktail Plateau (area 12, Fig. 1), is south of the Yellowstone River between Tower Junction and Gardiner, Montana. It includes rolling, grassy moraines with some forest (major landscape groups GG and GM). Precipitation is relatively low here (Soil Conservation Service. Average annual precipitation (inches)—1953–56—Yellowstone National Park. State office, Bozeman, Montana, unpublished), and streams do not have the high peak flows occurring in the eastern part of the study area. The plateau had no major areas of high erosion potential (Table 4). The turbidity data agree with the general scarcity of highly erosive features in this area. Although no streams in this area were monitored in the sediment study, indirect comparison of turbidity stations above and below this reach of the Yellowstone River suggest that it is not a substantial sediment source (Ewing et al. 1986).

The Gardner River Drainage. The picture is different for the Gardner River drainage basin, where there is a relatively high proportion of highly erosive land (1.5%). Though most of the landscape is rolling moraine, there are significant areas of mass wasting (ancient landslides). Glacial troughs and cirques and scoured peaks in shales, sandstones, and limestones (major landscape groups GM, MW, and GS) occur in the western part of the basin. Precipitation is variable, and vegetation ranges from alpine turfs to shrubland. Map units are V, CER, LS, C, and S. Steep volcanic scarps, channel erosion, actively eroding landslide debris, shale or mudstone scarp slopes (Mount Everts and environs east of Mammoth, Wyoming), and high elevation shale scarps are common features. Though debris fans make up the lower parts of Mount Everts, because of their relatively old age (200–800 years; C. Craig, Debris flow-dominated alluvial fans in northern Yellowstone National Park, Wyoming: depositional frequency and chronology of fan development. Research Division, Yellowstone National Park, Wyoming, Unpublished manuscript) they are not included in highly erosive lands. In the short term (10–30 years) they are relatively stable, except for channel erosion.

Almost 530 ha of the 599 ha of steep shale or mudstone scarp slopes (Map Unit C) were measured on Mount Everts. The upper slopes of Mount Everts are nearly bare of vegetation, especially on south facing slopes. Soils have a high salt and clay content. Crusts form on the soil surface, increasing runoff potential (except where broken up by animal, hail, or thunderstorm activity). The Gardner River has cut away at the base of the slope in places, especially in the Gardner Canyon, accelerating hillslope retreat. These characteristics are consistent with sedimentation data (Mohrman et al. 1988). Morhman et al. (1988) conclude that the Gardner River basin is a significant source during snowmelt and during summer rains.

The Reese Creek Drainage. The Reese Creek drainage is relatively small (3,439 ha), but it has a relatively high proportion of erosive area (1.6%; Table 4). It is primarily a glacial trough in volcanic rocks, with some shale at high elevations (major landscape group GS). The shale areas are not obviously eroding, but steep, west facing trough walls in the center of the drainage are responsible for channel erosion and debris flows into the stream (map units V, CER). Morhman, et. al. (1988) indicate this small drainage basin is a moderate sediment producer but is often dewatered during the summer months. The kinds of map units present imply some summer sediment would occur (if not dewatered) with thunderstorm activity, especially in the lower two-thirds of the drainage.

Boundary Line Area (Stevens Creek). This drainage includes the Boundary Line area (locally called the BLA), and extends from the western side of the Yellowstone River at Gardiner, Montana, to the edge of the Reese Creek drainage, and from that drainage north to the Mol Heron drainage. It is the northern part of subdrainage 10 (Fig. 1). Area 10 has about 2.3% highly erosive lands (Table 4). These are limited to shale scarp slopes near and within ancient landslides in shales and mudstones of Cretaceous age. The overall area of erosive lands is small, however (about 100 ha). This area was not monitored in the sediment study.

Tom Miner Creek and Mol Heron Creek. These drainages are both primarily in the Gallatin National Forest. Both drainage basins contain a small amount of erosive land (Table 4). The Tom Miner Creek drainage, however, has significant unmapped private land in its center. Though both drainages are largely volcanic in lithology, rocks are more indurated than those in eastern Yellowstone National Park, as evidenced by the presence of cliffs on cirque basins and steep slopes, rather than the eroding slopes common in less competent rocks. Some Cretaceous sedimentary rocks exist in the Mol Heron drainage. Landforms are largely fluvially modified glacial valleys, lacking obvious trough shapes.

Ewing et al. (1986) and Mohrman et al. (1988) measured a moderate sediment production from Mol Heron Creek during snowmelt and from Tom Miner Creek during snowmelt and summer. Erosive land proportion is low, however. There were some point sources identified below federal land that may contribute a substantial part of this sediment.

Ranking of Erosion and Sediment Discharge

The above rankings of erosive land and comparisons to sediment data have been largely qualitative. This is because of the reconnaissance nature of the erosion study, and because methods of data collection and analysis are quite different between the two studies. A semi-quantitative ranking, however, can be made between sediment discharge from selected drainages and the total erosive hectares present (Table 5).

The first of the two major groupings of drainages (includes Lamar–Tower, Yellowstone from Lake to Tower, Soda Butte, and the Gardner River drainages) ranks above the second group by a factor of 8 or more for both erosive area and sediment discharge. This indicates consistency between estimates of sediment contribution and erosive area. More detailed interpretations of rankings are inappropriate here because erosive areas vary some in erosion potential. Though all are high as defined above, variation between individual map units can skew any strictly quantitative correlation based on this table or one built on sediment yield and proportion of erosive lands.

Ranking of Erosion Potential by Drainage Basins

An understanding of the relative distribution of eroding land drainages and subdrainages can be gained by ranking on area of contributing erosive lands (Table 6). Note that the first four are an order of magnitude larger than the remainder. By this measure the most erosive land is contained in the Upper Lamar River, Gardner River, Soda Butte Creek, and Yellowstone River (from Tower Junction to the Yellowstone Lake Outlet) drainage basins.

Ranking by proportion of highly erosive land gives a different picture (Table 7). The top five areas are Soda Butte Creek, BLA, Upper Lamar River, Reese Creek, and the Gardner River drainages. Their

Table 5. Ranking of sediment discharge (average of means for 1985 and 1986 snowmelt) and highly erosive land area for selected drainage basins in priority areas 1 and 2.

Drainage	Subdrainage[a]	Sediment discharge (tons/day)	Total erosive area (ha)
Lamar at Tower	1,2,3,13	2,575	2,231
Yellowstone above Tower	4	975	519
Soda Butte	2	277	615
Gardiner River	5,6,7	160	792
Tom Miner	11	22	40
Mol Heron	9	21	45
Big	[b]	16	0
Reese	8	6	56

[a] Subdrainages from Fig. 1.
[b] From priority area 2, Fig. 1.

proportions exceed the remainder by a factor of 3 or greater. These are the most erodible areas in a geomorphic sense, though because of other factors they may not contribute the most sediment to streams. The important erosion processes in these areas are eroding glacial till in high drainages (map unit V in the Soda Butte Creek drainage), eroding shale scarp slopes (map units C and LS in the Boundary Line area (BLA) and the Gardiner River drainage), and eroding glacial headwalls in poorly indurated volcanic rocks (map unit V in the Upper Lamar River and Reese Creek drainages).

These map units make up 84% of the highly erosive lands in priority area one, underlining their importance to stream sediment contribution in the overall area (Table 3). Channel side-cutting into alluvium or lake sediments (Map Unit CER) is much lower in total area. CER map units are located directly on major streams in these areas, however, raising their importance beyond the areal extent. Almost all the remaining areas are steep slopes (hydrothermally altered slopes or lake sediment scarps) or eroding landslides.

Ranking of Erosion Potential by Major Landscape Groups

Because erosional landscapes were defined in northern Yellowstone National Park via the major landscape groups (Appendix B; Fig. 3), one can make inferences about erosion potential in various landform–geology–vegetation groups. Table 8 lists the extent of highly erosive lands in each major landscape group. These can be ranked by erosive land area to indicate which landscapes have the greatest contribution to erosion (Table 9). The highest contributions are from small glacial troughs and cirques in Tertiary volcanic rocks (GC); lands having landslides and stream breaks composed of mudstones,

Table 6. Ranking of drainage basins and subdrainage basins by area of highly erosive land.

Drainage or subdrainage	Map area (ha)
Upper Lamar	1,563
Gardner	792
Soda Butte	615
Yellowstone River above Lamar	519
Yellowstone River above Corwin Springs, below Gardiner (BLA)	100
Reese	56
Mol Heron	53
Tom Miner	40
Drainages below Tom Miner (Big, Suce, etc.)	37
Slough	25
Blacktail	0

Table 7. Ranking of drainage basins and subdrainage basins by proportion of highly erosive land.

Drainage or subdrainage	Map proportion (%)
Soda Butte	2.3
Yellowstone River above Corwin Springs, below Gardiner (BLA)	2.3
Upper Lamar	1.8
Reese	1.6
Gardner	1.5
Yellowstone River to Lake (above Lamar)	0.6
Mol Heron	0.5
Tom Miner	0.2
Drainages below Tom Miner (Big, Suce, etc.)	0.2
Slough	0.04
Blacktail	0

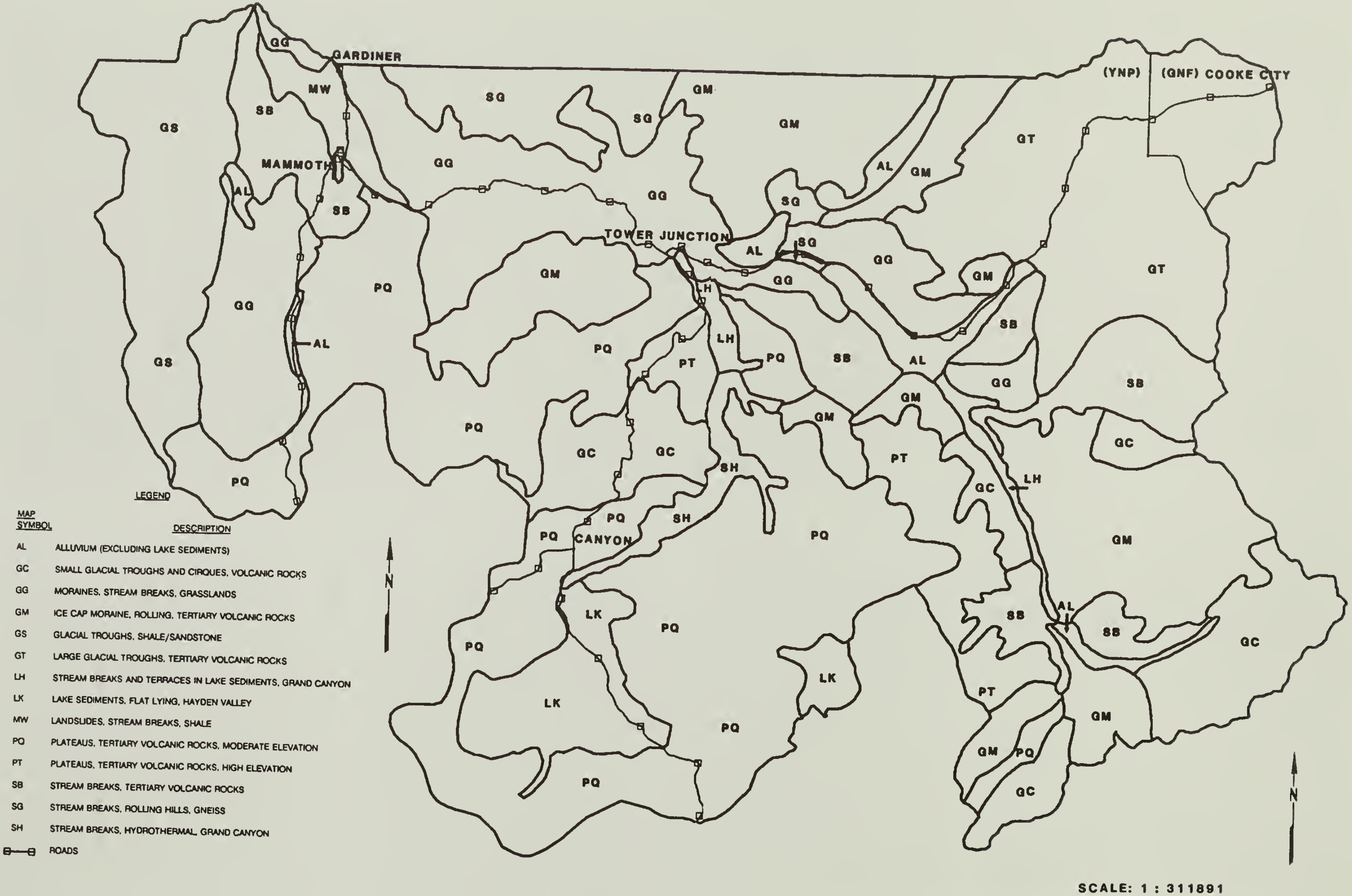

Fig. 3. Major landscape groups in northern Yellowstone National Park, Wyoming; Cooke City Area, Montana; and parts of the Gallatin national Forest, Montana.

Table 8. Area of map units with "high" erosion potential by major landscape group for the Yellowstone National Park portion and Cooke City area in priority area 1.

Major landscape group	Map unit area (ha)							Total (ha)[a]	Major landscape group area (ha)	% of major group area
	V	CER	L	H	LS	C	S			
AL								0	6,667	0
GC	796	23						819	22,745	3.6
GG	16	1				91		108	39,509	0.3
GM	168	5						173	50,529	0.3
GS	55	9					20	84	18,451	0.5
GT	693	43						736	31,585	2.3
LH		17	51					68	2,721	2.5
LK		5	95					100	11,396	0.9
MW		5			165	646		816	3,293	24.8
PQ	33	1		7				41	78,477	0.1
PT								0	11,707	0
SB	399	9				10		418	23,763	1.8
SG								0	8,338	0
SH	8	6	16	201				231	3,687	6.3
Total	2,168	124	162	208	165	747	20	3,594	312,867	1.1

[a] These totals include only map units within Yellowstone National Park, where Major Landscape Groups are defined, and are different from those in Table 3.

shales, and volcanic debris (MW); large glacial troughs in Tertiary volcanic rocks (GT); and stream breaks (SB, not including the Grand Canyon of the Yellowstone), also in Tertiary volcanic rocks. These lands are concentrated in the eastern part of the study area (GC, GT, SB), and near Mammoth Hot Springs, Wyoming, in the northwestern end of Yellowstone National Park (MW). About 78% of the erosive lands in northern Yellowstone National Park is contained in these major landscape groups. These major landscape groups make up only 26% of the entire area, showing most erosion occurs on a small subset of geologic–landform–vegetation combinations.

The major landscape groups can also be ranked by proportion of highly erosive land (Table 10). Landscapes that have the highest erosion rates by proportion are MW, hydrothermally altered stream breaks (SH), and small glacial troughs and cirques in Tertiary volcanic rocks (GC). Although they have some features in common with other landscapes, it is the combination of features that seems to produce erosive potential. For example, low elevation glacial moraines with grassland or forest have a low proportion of highly eroding land (GG, GM) but also do not have the steep slopes, the relatively high precipitation, and the lack of vegetation common in GC. Glacial troughs and cirques have these three characteristics but may not necessarily be highly erosive. The cirques in sandstone and shale (major landscape group GS) have a low proportion of erosive lands; but slopes are steep and precipitation is relatively high, as in the erodible GC. In this case, rock characteristics alone apparently have low potential for predicting occurrence of highly erosive lands.

Table 9. Major landscape group's ranked by area of highly erosive land for the Yellowstone National Park portion and Cooke City area in priority area 1.

Major landscape group	Map area (ha)
GC	819
MW	816
GT	736
SB	418
SH	231
GM	173
GG	108
LK	100
GS	84
LH	68
PQ	41
AL	0
SG	0
PT	0

Areas of Moderate Erosion Potential in Priority Area One

Areas of moderate erosion potential were not mapped, but we describe them here. Extensive areas of

Table 10. Major landscape groups ranked by proportion of highly erosive land for Yellowstone National Park portion and Cooke City are in priority area 1.

Major landscape group	Map proportion (%)
MW	24.8
SH	6.3
GC	3.6
LH	2.5
GT	2.3
SB	1.8
LK	0.9
GS	0.5
GM	0.4
GG	0.3
PQ	0.1
SG	0
AL	0
PT	0

rolling glacial moraines with incised stream drainages exist, some relict from outwash periods and some with underfit perennial streams (see major landscape group GG, GM; Fig. 3; Appendix B) In these areas, stream banks and relict stream breaks occasionally have bare slopes but are not actively eroding. Stream breaks sometimes are underlain by weathered basalt, particularly on the Blacktail Plateau.

Areas of hydrothermally altered Quaternary basalts, gravels, and colluvium, along with some older volcanic rocks, have a moderate erosion potential. These are not highly erodible, probably because of cementation. They occur in the Grand Canyon of the Yellowstone and are scattered throughout the park in thermal areas associated with streams.

The Burnt and Deep Creek drainages south of Specimen Ridge contain areas that have photo signatures representing a possible moderate erosion rating. Time constraints prevented field verification.

Lake sediments of Bull Lake age exposed in the Hayden Valley (major landscape group LK) are occasionally incised by relict stream courses and are bare of vegetation. Sediment production, however, is buffered by well vegetated terraces and stream flood plains.

High-elevation cirques and slopes near Mount Washburn and other peaks are bare of vegetation in some places. Permeable soils and many rock fragments apparently stabilize the bare soil, allowing only occasional gullying or rill erosion. Similar landscapes are in the central peaks of the southern Gallatin National Forest, which also have some areas of moderate erosion potential.

The lower portion of the Mount Everts escarpment is composed of glacial moraines, ancient debris flows, and alluvial fans. Although this is a moderate source, incised debris flow channels that originate in the highly erosive upper part dissect this area.

Highly Erosive Areas in Priority Area Two

Priority area two (Fig. 1) was evaluated within Gallatin National Forest boundaries, outside of the Absaroka–Beartooth Wilderness. The distribution of these map units is not shown in the figures but is enumerated in the tables.

The criteria for high erosion potential were met in only a few areas. Drainages below Tom Miner (Table 6) contain only 37.2 ha of highly erosive land (0.1% of drainage area). It is possible that there are some high sources in parts of drainages not evaluated; however, geology, landforms, and vegetation patterns make extensive areas unlikely. Suce Creek does have a small area of sandstone and shale that has a potential for erosion.

Results of sediment studies relate well to these findings. Streams in this part of the study area are relatively low sediment and turbidity contributors during snowmelt and were dry during most of the summer (Mohrman, et al., 1986). Also, a high proportion of the sediment and water transported by the Yellowstone River originates upstream from Corwin Springs, indicating priority area two drainages have a small overall contribution. Gallatin National Forest data indicate sediment production and turbidity are low for measured streams (Big, Mill, and West Fork Mill creeks; Glasser and Jones 1982).

Erosion on Private Lands

This study did not assess erosion in portions of drainages under private ownership, with the exception of a small amount of the Mol Heron Creek drainage. Privately owned lands comprise an important part of several drainages monitored for suspended sediment or turbidity; namely, Tom Miner, Mol Heron, and Big creeks. Large areas of private land occur on both sides of the Paradise Valley below these drainages (Fig. 1).

Ewing et al. (1986) and Mohrman et al. (1988) located several significant erosion features in privately owned areas. An eroding rotational earth slump in ice-marginal glacial lake sediments contributes a substantial amount of suspended sediment to lower Tom Miner Creek. Another mass wasting feature is located on the East River Road, just south of Wanigan in Paradise Valley. Runoff localized in the active slump–mudflow moves material onto the road, where surface wash and maintenance equipment transport it to the Yellowstone River. Other sediment-contributing sources identified during aerial photo interpretation or field investigation include the canyon area of Mol Heron Creek north of Cinnabar Mountain and the Beattie Gulch area north of Reese Creek from Gardiner to Yankee Jim Canyon.

Conclusions

Measurements and results from the sediment studies compared to areal extent of highly erosive lands and rankings of erosive lands in this study all point strongly to the upper Lamar River, Soda Butte Creek, and the Gardner River (primarily Mount Everts) drainage basins as by far the most important sediment producers in the Yellowstone River above Corwin Springs. The area is believed to contain the major sources for sediment and turbidity measured at Livingston. Sediment contributions are much higher in the Yellowstone National Park portion of the study area. Highly erosive land is noticeably lacking on the Gallatin National Forest portion.

These differences are not easily explained in a reconnaissance study such as this, but some hypotheses can be offered. The Gallatin National Forest and Yellowstone National Park both have broadly similar lithologies, similar glacial histories, and similar climates. Some important differences existed, however. Yellowstone National Park was largely covered by a thick ice cap, while the Gallatin National Forest was glaciated primarily from local, mountaintop sources. The volcanic rocks of the Gallatin have been only generally mapped but seemingly differ widely from those in the eastern part of the park. Also, landforms on the Gallatin National Forest are more representative of postglacial hillslope processes such as fluvial (water) erosion than are those in the park. Many areas in the park still bear scars of the violence of meltwater floods in the last parts of the Pleistocene.

The Yellowstone region is moving toward equilibrium with the present environment. Geographically, this is represented by a transect from the steep relict glacial peaks and remnant lake sediments of Yellowstone National Park to the more stable, fluvially influenced Gallatin National Forest. The kinds of materials that are most erosive in Yellowstone National Park (lake sediments in major drainages, weakly consolidated but steep mountain slopes, landslides in clay materials, salt laden shales, and hydrothermally altered rocks) do not occur on the Gallatin National Forest (Davis and Shovic 1984). Lithology changes along the transect from relatively erodible volcaniclastics to more stable volcanic rocks, and from shales and limestones to Precambrian metasediments.

The landscapes in Yellowstone National Park, and to a lesser extent the Gallatin National Forest, seem to be in a state of transition. Their landforms and dominant erosional processes reflect the transition as the entire system approaches an equilibrium with the present. The landscapes and soils in northern Yellowstone National Park are relatively young (Davis and Shovic 1984; Trettin 1986). Almost the entire park was covered with ice until about 13,000 years ago (Pierce 1979), and high mountain tributary glaciers scoured and steepened the highest peaks (major landscape groups GC and GS). Much of the park was covered with an ice cap, which has left dominant characteristics on today's topography (major landscape groups GM, GG, PT, and PQ). Some areas were deeply carved by ice from the Beartooth Plateau (major landscape group GT). During deglaciation, the tributary glaciers melted before the main outlet glacier, causing lakes and moraines to form in many areas. Extensive silty sediments are left where these glacial lakes were located especially in Hayden Valley and along major streams (major landscape group LK and LH). These sediments are being eroded now (map unit CER and L).

Geologically recent events have also influenced the characteristics of the landscape. The active deformation of the central part of the study area has probably influenced stream channel characteristics and the stability of slopes. Deformation in the last 100 years is on the order of 250–500 mm (Smith and Braile 1984).

Relatively recent volcanism has influenced the character of the exposed rocks. The dominant rocks in this portion of the study area are volcanic formations of Quaternary and Tertiary ages. The younger rocks tend to be rhyolites, welded tuffs, or basalts (major landscape group PQ; Appendix B). Older rocks that occur in the eastern parts of the park are combinations of sediments, lava, volcaniclastics, and ash flows from large, andesitic volcanos. These rocks are often weakly consolidated. Though these areas are often mapped as containing similar bedrock, significant differences in rock type may influence susceptibility to weathering and erosion (Smedes and Prostka 1972). These differences have not been consistently mapped in the Gallatin National Forest or in Yellowstone National Park, but observations in this study indicate landscapes in the Wapiti Formation seem more highly erosive than the Lamar River Formation, at least in Yellowstone National Park (map units V, major landscape groups GC, GT, and SB).

The eroding sedimentary and volcanic rocks near Mammoth (major landscape group MW) are also related to bedrock, climate, and glacial erosion. They are weakly consolidated, Cretaceous-aged mudstones and shales of the Landslide Creek formation, with some welded tuff. Ancient and recent landslides in these materials were apparently triggered by glacial oversteepening. Some are still active, especially those facing the Gardner River.

The systematic observations in this study indicate that large-scale erosional features are characterized by landscapes reflecting the above kinds of geological and climatological events. Drainagewide sediment loads are related to the extent of those erosional features. Also, only a small amount of land is highly erosive in any basin. Further assessments of the reasons for observed levels of stream sedimentation should be based on knowledge of these landscape features.

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Appendix A. Erosive Land Map Unit Descriptions

The following format is used for the descriptions:

SYMBOL: The identifier as given on Fig. 2. Symbols in parentheses ( ) are the identifiers used in mapping on 15-minute quads. A short description is given, summarizing the central concept of the Map Unit.
SUMMARY: This is an overall summary of the Map Unit.
REGOLITH: This is the unconsolidated material overlying bedrock. It is used because no soils information was gathered other than texture of eroding sediments, rock-fragment content, and erosion status.
LANDFORM: This is the character of the map unit, as visible from aerial photographs.
VEGETATION: existing on the site.
LITHOLOGY: description of geologic formations.
EROSION PROCESS: This is a summary of the kinds of erosion occurring in the Map Unit, with probable contributing factors.
COMMENTS: extent, location, any cautions or miscellaneous descriptive data.

[HER does not appear on Fig. 2, because it was mapped only on the Gallatin National Forest, near Mill Creek.]

SYMBOL: **CER** (Large scale channel erosion)
SUMMARY: Large-scale channel–bank erosion on perennial streams. Materials are from a variety of sources. They are often representative of another Map Unit but are mapped as a linear feature because they are too narrow to accurately portray at the scale of mapping.
REGOLITH: Glacial outwash, exposed, weathered shale or volcanic rocks, glacial till, landslide features, lake sediments. All are moderately fine to medium textured with many to few rock fragments. Some areas are hydrothermally altered.
LANDFORM: Variety of landforms, ranging from stream-cut terraces, stream breaks, cirque basins, glacial trough walls, rolling glacial moraines, landslides.
VEGETATION: variable but usually sparse
LITHOLOGY: variable
EROSION PROCESS: variable, depending on the conditions and materials. Includes mass wasting and surface wash.
COMMENTS: These occur throughout the study area at moderate to high elevations, usually on steep slopes on ephemeral streams. However, they are also common on major streams, such as the Lamar River, and in the Grand Canyon of the Yellowstone and major tributaries.

SYMBOL: **C** (CSH) (Exposed Cretaceous shales and mudstones on steep slopes)
SUMMARY: Mudstones and shales exposed in steep landslide scarps and on steep fluvial slopes, at low elevations; shales are Cretaceous in age; slopes are immediately postglacial to recent in age
REGOLITH: Weathered shale and mudstone; moderately fine to fine textures with few rock fragments; some glacial till; sandstone interbedded in places
LANDFORM: Steep landslide scarps and steep fluvial slopes or stream breaks on incised drainageways, some debris flows, fans, and incised channels
VEGETATION: sparse or absent; where present, usually alkali-tolerant plants
LITHOLOGY: common parent material is the Cretaceous Landslide formation and other Cretaceous shales and mudstones interbedded with sandstones; some surficial deposits
EROSION PROCESS: overland flow, channelized erosion, debris flows; these slopes have been oversteepened, probably by a combination of glacial erosion, faulting, and stream cutting; they are now are retreating to their angle of repose, which is likely to be fairly gentle considering the poorly indurated material
COMMENTS: occurs primarily on Mount Everts, near Slide Lake, and near the old road from Mammoth to Gardiner

SYMBOL: **H** (HAV) (Hydrothermally altered volcanic bedrock, colluvium, or lake sediments)
SUMMARY: hydrothermally altered volcanic conglomerates, vent facies and tuff on steep slopes on major streams; some altered lake sediments or colluvium
REGOLITH: medium textured, weathered and altered poorly consolidated or poorly indurated volcanic-derived materials
LANDFORM: very steep stream breaks
VEGETATION: absent or sparse
EROSION PROCESS: overland flow, rill erosion; transport at base of slopes by high water or storm events; translational or rotational mass movement
COMMENTS: these are almost entirely in the Grand Canyon of the Yellowstone River

SYMBOL: **HER** (Highly erosive areas on the Gallatin National Forest)
SUMMARY: recent ground disturbance by logging and roads in areas highly erodible if disturbed.
REGOLITH: generally colluvium and till derived from volcanic rocks of Tertiary age
LANDFORM: stream breaks and steep glacial moraines
VEGETATION: generally forested
LITHOLOGY: tertiary volcanic rocks (Absoroka supergroup)
EROSION PROCESS: channelized erosion on roads and in skid trails
COMMENTS: these are few in number and occur on the west side of the Yellowstone River above Tom Miner Basin, on Gallatin National Forest lands

SYMBOL: **S** (HSH) (Exposed shales on steep slopes at high elevations)
SUMMARY: bedrock composed of shale and sandstone exposed at high elevations by glacial scour and subsequent stream erosion; slopes are postglacial in age; rocks are generally Cretaceous or older
REGOLITH: surface materials are moderately fine to medium textured and are weathered from bedrock
LANDFORM: scarp slopes on glacially scoured slopes at high elevations near heads of drainages; bedrock channels of ephemeral streams on high glacially scoured slopes
VEGETATION: generally sparse or absent
LITHOLOGY: Cretaceous or older shales of the Amsden formation or the Ellis group, and other formations; beds are generally steeply dipping
EROSION PROCESS: glacial erosion has left shale exposed; it is readily eroded by stream-bank and channel erosion, and overland flow.
COMMENTS: these are not extensive and occur on the western edge of the study area near Fawn Pass, Quadrant and Little Quadrant Mountains

SYMBOL: **L** (LAC) (Lake sediment terraces near streams)
SUMMARY: lake sediments of glacial or near postglacial age; on terraces or benches cut by streams; in landslides on streams
REGOLITH: moderately fine (clay) to silty lake sediments with some sand or gravel lenses or beds
LANDFORM: terrace scarp slopes fronting on major perennial streams; high, steep channel banks, active landslides fronting on major streams
VEGETATION: scattered tilted trees, hydrophytic vegetation, meadow or grassland in Hayden Valley.
LITHOLOGY: surficial deposits, of Recent and Pinedale age; in Hayden Valley there are older sediments of Bull Lake age
EROSION PROCESS: mass movement, stream-bank erosion, overland flow
COMMENTS: these are primarily located in the upper Hayden Valley

SYMBOL: **LS** (LSS) eroding parts of landslides in Cretaceous shales or mudstones
SUMMARY: steep slopes in landslides from shales interbedded with some sandstone; bedrock is Cretaceous in age; other areas are slump blocks formed in post-Pinedale glacial lake–outwash–debris flow deposits; landslides are generally postglacial in age
LANDFORM: internal scarps and oversteepened internal toeslopes on lobate landflows
REGOLITH: moderately fine textured soil materials with sodium influence from the parent bedrock. Glacial till is often mixed with the landslide material
VEGETATION: sparse, alkali-tolerant plants
LITHOLOGY: Common parent formations and deposits are the Landslide shales and mudstones; glacial deposits and debris flow deposits; surficial deposits
EROSION PROCESS: overland flow, slumps, channelized erosion within intermittent streams; mass movement at stream edge due to high water or storm events
COMMENTS: these occur primarily north of the town of Mammoth, in the Boundary Line area near Reese and Stevens creeks; and on the western banks of the Gardner River in the Gardner Canyon

SYMBOL: **V** (TVE) Exposed Tertiary volcanics on steep slopes; or glacial till derived from volcanics in cirque basins
SUMMARY: volcanic rocks, either detritus and till in cirque basins or exposed bedrock at high elevations by glacial erosion; usually postglacial in age; rocks are Tertiary in age
REGOLITH: there are two major groups; the first is poorly indurated volcanic rock, composed of andesite flows and conglomerates, and ash or tuff deposits; the second is glacial till derived from volcanic rocks made up of hard andesite flows and some volcanic conglomerates; in both instances, textures are medium to moderately fine
LANDFORM: for Group 1, cirque basins dissected by incised stream channels; these are usually at the heads of tributaries of large U-shaped valleys; they have high stream gradients; for Group 2, highly dissected badlands, cirque headwalls, and scarps

VEGETATION: generally absent, but a few areas have alpine turf with scattered trees on ridges; cirque moraine deposits may have whitebark pine forest cover or scattered subalpine fir

LITHOLOGY: Group 1 is commonly the Lamar River formation; Group 2 is primarily the Wapiti formation; there are a few delineations of Quaternary basalt on Tower Creek and on the Gardner River east and south of Bunsen Peak

EROSION PROCESS: recent glacial erosional scarps and depositional materials, high stream flow peaks, and lack of vegetation combine to encourage high erosion rates; processes are stream bank and stream channel erosion, and overland flow; intermittent debris avalanches, torrents during peak flows and shallow mass movements in regolith; rotational slumps and other mass movements on channel banks

COMMENTS: Group 1 is primarily in the northeast corner of the study area; Group 2 is primarily in the northeast and eastern parts of the study area.

Appendix B. Major Landscape Groups

AL	alluvium (excluding lake sediments)
GC	small glacial troughs and cirques, volcanic rocks
GG	moraines, stream breaks, grasslands
GM	ice cap moraine, rolling, Tertiary volcanic rocks
GS	glacial troughs, shale/sandstone
GT	large glacial troughs, Tertiary volcanic rocks
LH	stream breaks and terraces in lake sediments, Grand Canyon
LK	lake sediments, flat lying, Hayden Valley
MW	landslides, stream breaks, mudstones
PQ	plateaus, Quaternary volcanic rocks, moderate elevation
PT	plateaus, Tertiary volcanic rocks, high elevation
SB	stream breaks, Tertiary volcanic rocks
SG	stream breaks, rolling hills, gneiss
SH	stream breaks, hydrothermal, Grand Canyon

AL

LANDFORM: stream alluvium in major drainages

PARENT MATERIALS AND STREAM CHARACTERISTICS: stream gravel, kames, other ice marginal deposits; medium and moderately coarse textured soils, humic alluvium

EROSION POTENTIALS: low to moderate

VEGETATION: mostly meadow grasses, marsh, riparian vegetation

SLOPES: gentle to flat, some rolling

LITHOLOGY: surficial deposits

MAJOR FORMATIONS, MEMBERS: pk, sg, fa (recent to postglacial)

REPRESENTATIVE PHOTO: 259-145 (FL 7) Color IR YNP flight

GC

LANDFORM: U-shaped, glacial troughs and glaciated peaks, cirques, and headwalls; high elevation (greater than 8,000 feet); results of small valley glaciers in late Pinedale time; parallel and trellis drainage patterns, fluvial dissection common on highest peaks

VEGETATION: sparse to dense forest, alpine turf

PARENT MATERIALS AND STREAM CHARACTERISTICS: shallow to deep regolith; high to medium stream gradients; high peak flows

EROSION POTENTIALS: low to high, depending on lithology and elevation

SLOPES: moderate to very steep

LITHOLOGY: tertiary volcaniclastics, flows

MAJOR FORMATIONS, MEMBERS: Tl, Tt, Tw

REPRESENTATIVE PHOTO: 277-8 (FL 5) Color IR YNP flight

GG

LANDFORM: low elevation, ground and lateral moraine with some glaciofluvial modified moraine; slopes variable; less than 7,800 feet, less than 8,500 feet on south slopes; dendritic drainage patterns

VEGETATION: mostly grass, some scattered forest; dense forest south of Gardners Hole

PARENT MATERIALS AND STREAM CHARACTERISTICS: variable glacial till and fluvial modified till; soils are medium to moderately coarse textured; streams have variable gradients, most are intermittent; low stream gradients, metamorphic rocks near Buffalo Plateau; mostly perennial in Gardner's Hole area

EROSION POTENTIALS: low

SLOPES: rolling, moderate

LITHOLOGY: surficial deposits; bedrock is Precambrian metamorphic rocks and Tertiary volcaniclastics

MAJOR FORMATIONS, MEMBERS: variable

REPRESENTATIVE PHOTO: 259-149 (FL 7) Color IR YNP flight

GS

LANDFORM: U shaped, glacial troughs and glaciated peaks, cirques, and headwalls; high elevation (greater than 8,000 feet); parallel and trellis drainage patterns

VEGETATION: variable, dense to sparse forest, alpine turf, rockland

PARENT MATERIALS AND STREAM CHARACTERISTICS: shallow to deep soils, medium to moderately fine textured soils; high to moderate stream gradients, high peak flows

EROSION POTENTIALS: moderate

SLOPES: moderate to very steep; concave and long

LITHOLOGY: sandstone, shale, some limestone; dikes

MAJOR FORMATIONS, MEMBERS: Cp, Kmk, Ps, Trt, Mm, Pq, Kl, Cp (variable age)
REPRESENTATIVE PHOTO: 277-99 (FL 3) Color IR YNP flight

GM

LANDFORM: moderate-relief ground moraine; overridden by ice cap; slight modification by fluvial processes
PARENT MATERIALS AND STREAM CHARACTERISTICS: glacial till; deep soils; streams have little alluvial fill, low to moderate stream gradients; coarse dendritic drainage patterns; some streams are entrenched with alluvium in large, flat-bottomed drainages
VEGETATION: dense forest, alpine turf, some low-elevation meadow near Blacktail Plateau
EROSION POTENTIALS: moderate
SLOPES: rolling, complex; mostly moderate slopes
LITHOLOGY: volcaniclastic rocks: andesite, basalt, some welded tuff
MAJOR FORMATIONS, MEMBERS: Tw, Tlr, Tl (Tertiary)
REPRESENTATIVE PHOTO: 259-3 (FL 8) Color IR flight (YNP)

GT

LANDFORM: U shaped valleys (valley glacial troughs), glacial features only slightly modified; high elevation summits; parallel or trellis drainage patterns, some deranged on moraines
VEGETATION: dense to sparse forest, alpine turf, rockland, talus
PARENT MATERIALS AND STREAM CHARACTERISTICS: mostly glacial till, little reworking, bedrock with shallow soils; some stream alluvium, though outwash, braided stream courses present; high gradient streams, high energy stream flows, high peak flows
SLOPES: mostly steep, concave, some ares of hummocky moraine
EROSION POTENTIALS: high
LITHOLOGY: volcaniclastic rocks: andesite, basalt; some limestone, sandstone and shale
MAJOR FORMATIONS, MEMBERS: Tw, Tlr, Cs, Dot, (Tertiary, Cambrian, Devonian)
REPRESENTATIVE PHOTO: 259-4 (FL 8) Color IR YNP flight

LH

LANDFORM: stream breaks in moderately fine to medium textured materials on the lower Grand Canyon of the Yellowstone, Lamar River, and major tributaries, with parallel drainage patterns
VEGETATION: meadow, forest
PARENT MATERIALS AND STREAM CHARACTERISTICS: lake sediments, streams empty directly into major stream channels, few buffer areas, mass failures common; moderately fine to medium textured soils; incised, high gradient streams
EROSION POTENTIALS: high
SLOPES: steep to moderately steep
LITHOLOGY: lake sediments, some kames, terrace gravels, landslide debris, some welded tuff
MAJOR FORMATIONS, MEMBERS: pkl, pk, (post glacial to recent), Ts (Tertiary)
REPRESENTATIVE PHOTO: 259-157 (FL 6) Color IR YNP flight

LK

LANDFORM: flat to rolling glaciolacustrine and glaciofluvial deposits (possibly Bull Lake age); some glacial moraine; overridden by ice cap; pinnate to dendritic drainage patterns; mostly in Hayden Valley, White Lake area
VEGETATION: grasses, meadows, some riparian
PARENT MATERIALS AND STREAM CHARACTERISTICS: soils are medium to moderately fine textured; low stream gradients, meanders common, large alluvial flats
EROSION POTENTIALS: low to high
SLOPES: flat to moderately steep; slopes are short and complex
LITHOLOGY: surficial deposits
MAJOR FORMATIONS, MEMBERS: pk, pkl, bu, some sg, fa (post glacial to recent)
REPRESENTATIVE PHOTO: 385-85 (FL 5) Color IR YNP flight

MW

LANDFORM: a mixture of ancient landslides, steep stream breaks, glaciofluvial deposits, and glacial moraine; deranged, parallel, and dendritic drainage patterns
VEGETATION: bare ground, grass, meadow, scattered trees
PARENT MATERIALS AND STREAM CHARACTERISTICS: moderately fine to moderately coarse textured soils; streams have high to moderate gradients
EROSION POTENTIALS: high
SLOPES: moderate, rolling to very steep, complex, long to short
LITHOLOGY: bentonitic landslide debris, mudstones, some welded tuff
MAJOR FORMATIONS, MEMBERS: Kl, Ls, Tlc, some Qyh (variable age)
REPRESENTATIVE PHOTO: 277-96 (FL 3) Color IR YNP flight

PQ

LANDFORM: plateaus covered by relatively shallow glacial till, overridden by ice cap; low relief with little fluvial modification (except where entrenched by streams); parallel or weakly dendritic drainage patterns that are widely spaced, and partially dependent on bedrock structure

VEGETATION: forest

PARENT MATERIALS AND STREAM CHARACTERISTICS: mostly shallow regolith (deep near Canyon); stream gradients are moderate to low; streams are in alluvium or entrenched valleys; regolith is weathered glacial till and weathered bedrock; some Bull Lake Till; much subsurface water flow due to permeable soils and bedrock

EROSION POTENTIALS: low to moderate

SLOPES: straight to convex, moderate length, gently to moderately sloping with steep stream sideslope

LITHOLOGY: relatively young rhyolite or hard, welded tuff; some Tertiary volcaniclastics at high elevations; some basalt

MAJOR FORMATIONS, MEMBERS: Qpu, Qyl, Qsl, Qpo (Quaternary)

REPRESENTATIVE PHOTO: 251-161 (FL 6) Color IR YNP flight

PT

LANDFORM: high elevation plateaus covered with shallow glacial till; overridden by ice cap; little fluvial modification; disordered and dendritic drainage patterns (greater than 8,600 feet in most areas); greater than 7,600 feet near Grand Canyon of the Yellowstone)

VEGETATION: alpine turfs, whitebark pine forest, some stunted, scattered, open-canopy forest

PARENT MATERIALS AND STREAM CHARACTERISTICS: glacial till, deep to shallow soils, many bedrock exposures, little stream development; low gradient streams in alluvium (little lake sediment; moderately fine textured sediments in alluvial areas

EROSION POTENTIALS: low to moderate

SLOPES: flat to gently rolling

LITHOLOGY: volcaniclastics; flows, breccias, conglomerates

MAJOR FORMATIONS MEMBERS: Tl, Tt, Tlr (Tertiary)

REPRESENTATIVE PHOTO: 259-143 (FL 7) Color IR YNP flight

SB

LANDFORM: Stream breaks, modified from glacial moraines in an ice cap situation and from exposed bedrock; dendritic to parallel drainage patterns

VEGETATION: Scattered forest on south slopes, dense to scattered forest on north slopes

PARENT MATERIALS AND STREAM CHARACTERISTICS: modified glacial till, some colluvium; shallow soils; streams are well-defined, nonbraided, often incised, moderate stream gradients

EROSION POTENTIALS: moderate to high

SLOPES: complex, straight to convex, mostly steep, long

LITHOLOGY: volcaniclastic rocks, andesite, basalt

MAJOR FORMATIONS, MEMBERS: Tl, Tw, Tlr (Tertiary)

REPRESENTATIVE PHOTO: none

SG

LANDFORM: rolling to steep stream-dissected slopes (highly modified glacial moraine, most till is gone); ice cap situation; dendritic drainage patterns; near Black Canyon are some stream terraces and gravels

VEGETATION: scattered forest

PARENT MATERIALS AND STREAM CHARACTERISTICS: metamorphic rocks; shallow soils with much bedrock exposed; streams have high gradients with little alluvium

EROSION POTENTIALS: low

SLOPES: gentle to steep

LITHOLOGY: gneiss and schist; some volcanic rocks

MAJOR FORMATIONS, MEMBERS: pCg (PreCambrian)

REPRESENTATIVE PHOTO: 385-74 (FL 4)

SH

LANDFORM: steep to very steep stream breaks with some hydrothermal alteration (Grand Canyon of the Yellowstone and some major tributaries)

VEGETATION: variable, with many bare slopes

PARENT MATERIALS AND STREAM CHARACTERISTICS: various tuffs, rhyolite flows, talus, medium to coarse textured soils (depending on characteristics of parent rock and type of hydrothermal alteration); high stream gradients, most streams intermittent, except for Yellowstone River and major tributaries

EROSION POTENTIALS: moderate to high

SLOPES: steep to very steep, straight, long

LITHOLOGY: tuffs, flows, conglomerates, with some stream gravels and other exhumed stream sediments

MAJOR FORMATIONS, MEMBERS: Tlr, Qjb, Qpu (mostly Quaternary)

REPRESENTATIVE PHOTO: 385-82 (FL 5) Color IR flight (YNP)

Soil Quality, Erosion Potential, and Site Productivity on Landscapes in Northwestern Yellowstone National Park, Wyoming

Henry F. Shovic

Soil Scientist

Abstract. The grasslands and shrublands north of Mammoth Hot Springs, Wyoming, are a critical part of the northern range. Though small in extent (4,065 ha), the area provides important winter range for a variety of species. The objective of this paper is to report on grass and shrub site productivity and erosion parameters for landscapes in the study area and their relation to inherent landform, soil, and vegetation characteristics. About 33% of the study area has clayey, salt affected soils. These soils are poor plant growth media, with low water holding capacity, high root resistance, poor aeration, and possible sodium toxicity. They have many surficial rock fragments, further reducing productivity. Almost half of the study area has moderate or high erosion potential. It is probable that steep slopes, high clay content, salt concentration, and other inherent properties of the landscape are primarily responsible for that potential. About 6% of the area has been highly disturbed through intensive agriculture and habitation. This contributes to the unnatural look of some parts of the study area, as well as reducing productivity and influencing erosion. The study area has been observed to have high winter use by ungulates and also appears to have these landscape characteristics. High wildlife usage has undoubtedly contributed to average vegetative coverage, vegetative species dominance, and erosion status. However, its importance is confounded by inherent ecosystem properties and past disturbances described above. The ecosystems in the survey area are combinations of parameters: landforms (unstable landslides, steep slopes, erodible mudstones), soils (salt and clay concentration, large numbers of rock fragments), and vegetation (salt tolerant, or otherwise unproductive habitat types with inherently low cover, exotic or introduced species) all influenced by the relatively dry climate. These factors (and past disturbance) significantly influence soil productivity, site productivity, and erosion potential. Given the character of these environmental variables, the intensity of their effects may confound a cursory analysis of the apparent effects of present wildlife usage. Therefore, assessments of the reasons for the area's appearance should be based on examination of all relevant ecological parameters as well as that usage.

Key words: Elk, erosion, grasslands, productivity, shrublands, soil quality.

The grasslands and shrublands north of Mammoth Hot Springs, Wyoming, are a critical part of the northern range. Though small in extent, the area provides important winter range for a variety of species. This paper interprets the results of a soils investigation in this area (H. F. Shovic, A. Rodman, D. Neprud, and J. Lane. Soils investigation of the Reese Creek–McMinn Bench–Mammoth area, northwestern Yellowstone National Park. Division of Research, Yellowstone National Park, unpublished report). That investigation was completed to provide information on soils and landscape relations, soil interpretations for management activities, and spatial depiction of disturbed areas; in support of the ongoing soil survey of Yellowstone National Park. The objective of this paper is to report on grass and shrub site productivity and erosion parameters for landscapes in the study area and their relations to inherent landform, soil, and vegetation characteristics.

Study Area

The study area (about 4,065 ha) is in northwestern Yellowstone National Park (Fig. 1). It includes the Stevens Creek area, McMinn Bench, the Rainbow Lakes area, part of northern Mount Everts, and Elk Plaza. The southern boundary is Mammoth Hot Springs, Wyoming. The northern boundary is Reese Creek and the Yellowstone River.

The area was purchased in the 1930's by the National Park Service. A residence and related outbuildings are in the Stevens Creek area. Unused irrigation ditches are common in the area, with some large, eroded breaches at higher elevations. Plant

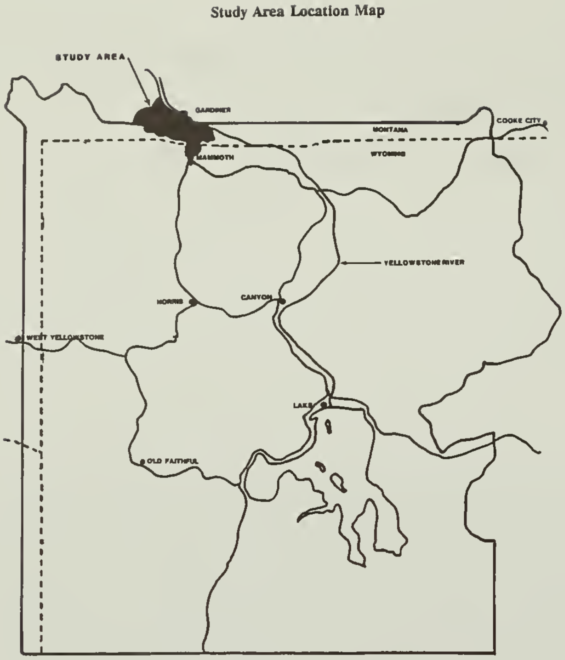

Fig. 1. Location of the study area with respect to Yellowstone National Park.

communities in and near these ditches are commonly different from those on upland sites. Gravel pits, unused landfills, and building foundations are present in the area. A reservoir (known as Ice Lake) is near Stevens Creek. An abandoned railroad grade transects the lower elevations. Unused roads lead to Rainbow Lakes and Ice Lake.

Elevations range from 1,585 m near the Yellowstone River to 2,075 m on the slopes above McMinn Bench. Landforms include earthflows and block glides, landslide scarps, stream cut terraces and small valleys, glacial moraine, and steep stream breaks. Vegetation is commonly grasses and shrubs. Slopes are moderate (2–35%) with some steeper scarps. Topography includes rolling, chaotic hills, nearly flat terraces, and gently undulating to moderately steep slopes (Pierce 1979; Fraser 1962; Waldrop and Hayden 1962; Morrison–Maierle, Inc., Geologic investigation, Gallatin National Forest, U.S. Forest Service, Bozeman, Montana, Project 916-081-01). Most of the topography is relatively young (Pleistocene or Holocene).

Landslide vegetation is sparse, with sage (*Salvia* spp.), bitterbrush (*Purshia* spp.), greasewood (*Sarcobatus* spp.), needlegrass (*Stipa* spp.), and other dry-environment species. Some flat terraces were farmed in the 1940's and have a sparse cover of wheatgrass (*Agropyron* spp.), mustards (*Brassica* spp.), and other annuals. Higher elevation vegetation on Mount Everts is moist grassland. The Mammoth area has a mixture of scattered pine (*Pinus* spp.), sage, and grassland. Introduced (exotic) species are present throughout the study area.

The lithology of parent materials varies from Cretaceous sediments and Tertiary volcanics to gravelly or bouldery glacial till derived from a variety of rock types (Fraser 1962). The climate is relatively warm and dry (compared to the remainder of Yellowstone National Park), with from 25 to 41 cm of precipitation. The area often is free of snow in the winter, and snowmelt occurs in May or early June. Mean temperatures range from –1° C (minimum) to 13° C (maximum) with a mean annual temperature of 5.5° C (Yellowstone National Park, unpublished weather data).

Soils in the northern two-thirds of the study area are unique to the region. They are formed in periglacial and preglacial landslide debris, stream alluvium, glacial outwash, and glacial till (H. F. Shovic, A. Rodman, D. Neprud, and J. Lane. Soils investigation of the Reese Creek–McMinn Bench–Mammoth area, northwestern Yellowstone National Park. Division of Research, Yellowstone National Park, unpublished report). High levels of sodium are common and affect productivity, erosion potential, and plant communities. The soils compact and seal when wet partly because of high clay contents. Wind erosion occurs during dry periods. Soils in the southern one-third of the area have formed in a variety of materials, including weathered travertine, glacial till, landslide debris, and weathered shale and sandstone. These soils are nonsodic, with moderate to low fertility.

Methods

The carrying capacity of any area is largely dependent on its capacity to produce edible vegetation on the variety of sites present. This productivity is dependent on a variety of abiotic and biotic factors. These include soil quality, degree of disturbance (e.g., management input), climate, and vegetative community (Pritchett 1979). Soil quality (or soil productivity) is defined as "the capacity of a soil to sustain plant growth under a specified set of conditions" (Hausenbuiller 1972:223). Soil quality is largely dependent on those soil properties that affect aeration, the supply of water, and the supply of essential nutrients. Important properties are soil texture, rock fragment content, organic matter content, condition of the soil surface, and presence of salts.

Disturbance can take the form of soil alteration by management or erosion. Accelerated erosion removes fertile topsoil and reduces infiltration, as well as increasing sediment in streams (Hausenbuiller 1972:381). The soil can also be altered by management through compaction or removal.

In this study, climate is assumed to be constant. This is because of the relatively small areal extent of the study area (4,065 ha), the relatively small variation in elevation (490 m), and the relatively constant northerly aspect.

Soil productivity (soil quality), erosion status, and site productivity are discussed below. These are interpretations of soil and site characteristics (H. F. Shovic, A. Rodman, D. Neprud, and J. Lane. Soils investigation of the Reese Creek–McMinn Bench–Mammoth area, northwestern Yellowstone National Park. Division of Research, Yellowstone National Park, unpublished report) based on map unit descriptions and soil taxonomy (Soil Survey Staff. Soil taxonomy. U.S. Soil Conservation Service, unpublished).

Interpretations were made for the entire study area at the scale of the soil survey.

Soil Productivity

Soil productivity is a component of site productivity. Ratings are relative and are based on soil texture, rock fragment content in the soil, rock fragments on the soil surface, fertility, and sodium status in the soil (Table 1). In this area, the presence of calcium carbonate in the solum (in the absence of high sodium levels) is related to soils having relatively high fertility (Soil Survey Staff. Soil taxonomy. U.S. Soil Conservation Service, unpublished).

High soil productivity means there are no soil limitations to plant growth. Soils with high ratings generally have medium textures, few rock fragments, high fertility, and are on moderate slopes. Moderate soil productivity means there are no severe limitations to plant growth, but there are more rock fragments and lower water holding capacity (less clay) than from soils rated high. Low soil productivity means there are significant limitations to plant growth, such as high sodium status, or large numbers of rock fragments.

Following are some exceptions to the criteria used in Table 1. Soils having moderate levels of salt (as evidenced by pH above 8.5 but without other physical indicators of high sodium status) are rated as moderate. Significant disturbance to the soils, such as high compaction levels, removal of surface soil, or covering with asphalt are given low soil productivity. Irrigation in some disturbed fields may have raised salt levels above natural conditions. The low rainfall and slow soil permeability would contribute to its persistence after irrigation has ceased.

Erosion Potential

Erosion potential is a relative measure of the soil's tendency to erode under grazing pressure, wind, and water. Factors used in rating are slope steepness, plant cover, soil texture, sodium status, and number of rock fragments on the surface. An exception is Map Unit D11, which is rated low in spite of steep slopes. The soils in the railroad grade are permeable and not likely to produce runoff.

High erosion potential is defined as having significant sediment produced from a major site in the short term (1–10 year frequency), either by snowmelt, significant summer precipitation, or hydraulic action within or near streams. An example is the SCH map unit which is located next to active stream and river channels. High sites have active rills, gullies, landslides, or evidence of sheet erosion. Vegetation is absent or sparse and is affected by erosion processes. The coarse fraction of soil is less than 20% of total soil volume. There is no significant erosion pavement, nor other armoring by gravel or larger materials. Material commonly reaches perennial streams the same year as eroded.

Moderate erosion potential refers to areas that have noticeable erosional features, but the proportion of the site actively eroding is low, or erosion takes place only during extreme precipitation. There may be no perennial stream effect under most conditions be-

Table 1. Criteria for rating soil productivity.

Soil productivity rating	Soil texture	Rock fragments (%) (surface/subsurface)	Soil fertility	Sodium or salt	Landform
High	Medium (silty)	<20 / <20	High	Low	Swales
Moderate	Mod. coarse, Medium (loam)	>20 / <50	Moderate	Low	Rolling
Low	Mod. fine, fine	>50 / >50	Low to moderate	High	Any

cause of sediment trapping areas on the eroding slope. The eroded material eventually moves off-site but not as quickly as in the high category.

Low erosion potential refers to cases where no evidence of active erosion is present. There may be relict forms of past erosional processes, such as post glacial channels or scarps.

Rating criteria are given in Table 2. The ratings are based on the factors given above and map unit descriptions and are modified as necessary by field experience.

Site Productivity

Site productivity is a measure of potential productivity expected on a site in terms of plant growth. Ratings are based on soil productivity, habitat types, erosion potential, and plant cover. Plant communities are represented by habitat types (Despain 1990), which have a general relation to vegetative production poten- tial. This potential is realized to a greater or lesser extent depending on soil quality and degree of site dis- turbance (Despain 1990).

High site productivity means that average long-term annual production is the highest in the study area. Moderate and low site productivity indicate relative intermediate and low long-term production (see Table 3 for rating criteria). A range of production is given for each rating, based on limited data from southwestern Montana (H. F. Shovic, A. Rodman, D. Neprud, and J. Lane. Soils investigation of the Reese Creek–McMinn Bench–Mammoth area, northwestern Yellowstone National Park. Division of Research, Yellowstone National Park, unpublished report). These values are not meant to be site specific. "D" (disturbed map) units are not rated for site productivity. This is because production values are not known for the plant communities on those sites.

Results and Discussion

Table 4 contains a list of map units, areal extent, and relative proportions in the study area. These map units correlate to those mapped in Fig. 2, which is a schematic representation of the soil maps in an unpublished report (H. F. Shovic, A. Rodman, D. Neprud, and J. Lane. Soils investigation of the Reese Creek–McMinn Bench–Mammoth area, northwestern Yellowstone National Park. Division of Research,

Table 2. Criteria for rating erosion potential.

Erosion rating	Slope[a] (%)	Cover (%)	Soil texture	Sodium or salt	Rock fragments (%)
High	>45	<15	Mod. fine, fine	Any	<20
Moderate	45>...>10	50>...>15	Any	Yes	50>...>10
Low	<10	Any	Any	Any	>50

[a] When parent material is glacial till, slope category is not used unless texture is moderately fine. In this case erosion rating is moderate.

Table 3. Criteria for rating site productivity.

Site productivity rating (kg/ha)[a]	Soil productivity	Common habitat type[c]	Erosion potential	Average cover (%)
High (1356–2182)	High	ARTR/FEID or FEID/AGSP	Low	>50
Moderate (493–1355)	Moderate to low	ARTR/FEID or FEID/AGSP	Low	>50
Low[b] (211–492)	Low	AGSP/POSA or SAVE/AGSM or others	High to moderate	<20

[a] Range of values is in air dried annual production (H. F. Shovic, A. Rodman, D. Neprud, and J. Lane. Soils investigation of the Reese Creek–McMinn Bench–Mammoth area, northwestern Yellowstone National Park. Division of Research, Yellowstone National Park, unpublished report).

[b] ARTR/AGSP always rated as having low productivity.

[c] ARTR/FEID = *Artemesia tridentata/ Festuca idahoensis*; FEID/AGSP = *Festuca idahoensis/ Agropyron spicatum*; AGSP/POSA = *Elymus spicatum/ Poa sandbergii*; SAVE/AGSM = *Sarcobatus vermiculatus/ Elymus smithii*; ARTR/AGSP = *Artemesia tridentata/ Elymus spicatum*; habitat types follow Despain (1990) and Mueggler and Stuart (1980).

Table 4. Areal extent of map units in the study area.

Map unit	Acres	Hectares	Percent of total
FGT	130	53	1.3
FLD	291	118	2.9
FMC	492	199	4.9
FME	209	85	2.1
FMF	526	213	5.2
FOW	99	40	1.0
FST	137	55	1.4
GTC	883	357	8.8
GTF	196	79	1.9
GTM	2,126	860	21.1
LSI	1,250	506	12.4
LSP	1,132	458	11.2
LSV	509	206	5.1
RSC	712	288	7.1
RSF	139	56	1.4
SCH	631	255	6.3
SFL	79	32	0.8
D01	86	35	0.9
D02	89	36	0.9
D03	10	4	0.1
D04	51	20	0.5
D05	7	3	0.1
D06	1	1	0.1
D07	12	5	0.1
D08	28	11	0.3
D09	1	1	0.1
D10	35	14	0.3
D11	70	28	0.7
D12	3	1	0.1
D13	2	1	0.1
D14	3	1	0.1
D15	10	4	0.1
D16	99	40	1.0
Totals	10,048	4,065	100.4

Yellowstone National Park, unpublished report). Each map unit is a unique combination of soils, vegetation, topography, and geologic material; or a particular kind of disturbance. Map unit descriptions are in the Appendix. Table 5 gives ratings for soil productivity, site productivity, and erosion potential for each map unit. These ratings are based on the rating criteria in Tables 1, 2, and 3 and on field experience of the author.

Some inherent landscape properties and historical events affect erosion potential, soil conditions, and vegetation. About 33% of the study area has clayey, salt affected soils (Tables 4 and 5; H. F. Shovic, A. Rodman, D. Neprud, and J. Lane. Soils investigation of the Reese Creek–McMinn Bench–Mammoth area, northwestern Yellowstone National Park. Division of Research, Yellowstone National Park, unpublished report). These soils are poor plant growth media, with low water holding capacity, high root resistance, poor aeration, and possible sodium toxicity. They have many surficial rock fragments, further reducing productivity.

All of the area has low or moderate long term site productivity (Table 5). Small areas (too small to separate at this scale of investigation) have high productivity (e.g., swales with silty soils in map unit GTM; H. F. Shovic, A. Rodman, D. Neprud, and J. Lane. Soils investigation of the Reese Creek–McMinn Bench–Mammoth area, northwestern Yellowstone National Park. Division of Research, Yellowstone National Park, unpublished report). Those labeled low or moderate make up only a small part of the study area. Site productivity is also related to soil productivity and habitat type (Table 5; Appendix). These parameters are probably relatively unaffected by animal effects.

About 6% of the area has been highly disturbed in the past (highly disturbed units; i.e., "D" units in Tables 4 and 5, Appendix, and Fig. 2). Most of this disturbance is in highly visible areas. Note the location of the "D" (disturbed) map units and those marked with an asterisk ("*," Fig. 2). To a local observer, these areas look unnatural because of low vegetative cover, debris, foundations, or soil disturbance. This disturbance has significantly altered soil properties, which in turn affects vegetation composition and productivity. Apparently, a large part of the area was heavily grazed by cattle in the early part of this century (Donald Despain, plant ecologist, Yellowstone National Park, personal communication). The effects of this widespread disturbance probably are still present.

Almost one-half of the study area has moderate (23%) or high (26%) erosion potential (Tables 4 and 5). A significant part of the area is unstable compared to surrounding landscapes. It is geologically young and is still adjusting to current environmental conditions. Though causative factors were not separated in this study, it is probable that steep slopes, high clay content, salt concentration, and other inherent properties of the landscape are primarily responsible for the erosion potential.

The effects of heavy wildlife usage on the northern range (summarized in Coughenour and Singer 1991) has been the subject of much discussion. Some suggested effects are high erosion, low plant cover, and an increase in introduced species. The study area described here has been observed to have high winter use by ungulates and also seems to have the listed landscape characteristics. High wildlife usage has

Fig. 2. Schematic Soil/Landscape Map of the study area.

Table 5. Management interpretations and pertinent soil conditions for each map unit.

Map unit	Soil productivity	Site productivity	Erosion potential	Comments
FGT	Moderate	Low to moderate	Low	Unit near Gardiner has compacted layers and exotic species
FLD	Low	Low	Low	Large number of rock fragments
FMC	Moderate	Moderate	Low	
FME	Low to moderate	Low	High	Salt and sodium can be present; entrenched, erosive stream channels
FMF	Moderate to high	Low to moderate	Low	Units near Gardiner have irrigation channels, some foundations, and evidence of plowing
FOW	Low to moderate	Low	Low	Large number of rock fragments can be present
FST	Low to moderate	Low	Moderate	Unit near Gardiner has some evidence of use as stockyard, with many exotic species; salt can be present in root zone
GTC	Low to moderate	Low to moderate	Low	
GTF	Moderate	Moderate	Moderate	
GTM	Moderate	Moderate	Low	
LSI	Low	Low	Moderate	Salt and sodium can be present in root zone
LSP	Low	Low	High	Salt and sodium can be present in root zone
LSV	Low to moderate	Low to moderate	Moderate to high	Salt and sodium can be present in root zone; LSVa has low productivity
RSC	Low	Low	Moderate	Many rock fragments
RSF	Low	Low	Moderate to high	Many rock fragments
SCH	Moderate	Moderate	Low to high	Active stream channels; high erosion only near active streams
SFL	Moderate	Low	Low	Many exotics in part of unit; probably grazed or plowed
D01	Low		Low	Actively used site
D02	Moderate		Low	Highly disturbed
D03	Low		Low	Highly disturbed
D04	Low		Moderate to high	Highly disturbed
D05	Low		Low	Highly disturbed
D06	Low		Low	Highly disturbed
D07	Low		Moderate	Highly disturbed
D08	Low to moderate		Low	Highly disturbed
D09	Low		Low	Highly disturbed
D10	Moderate		Low	Highly disturbed
D11	Low		Low	Highly disturbed
D12	Low		Low to moderate	highly disturbed
D13	Low		Low	Highly disturbed
D14	Low		Low	Highly disturbed
D15	Low		Low	Partially disturbed; soil productivity moderate in undisturbed parts
D16	Moderate		Low	Highly disturbed

undoubtedly contributed to average vegetative coverage, vegetative species dominance, and erosion status. Its importance, however, is confounded by inherent ecosystem properties and past disturbance described above. The ecosystems in the survey area are combinations of parameters: landforms (unstable landslides, steep slopes, erodible mudstones), soils (salt and clay concentration, large numbers of rock fragments), and vegetation (salt tolerant, or otherwise unproductive habitat types with inherently low cover; exotic or introduced species) all influenced by the relatively dry climate. These factors (and past disturbance) significantly influence soil productivity, site productivity, and erosion potential. Given the character of these environmental variables, the intensity of these environmental variables may confound any apparent effects of present wildlife usage. Therefore, assessments of the reasons for the area's appearance should be based on examination of all relevant ecological parameters as well as that usage.

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Appendix. Map Unit descriptions.[1]

Detailed soil descriptions for each of these map units are in H. F. Shovic, A. Rodman, D. Neprud, and J. Lane (Soils investigation of the Reese Creek–McMinn Bench–Mammoth area, northwestern Yellowstone National Park. Division of Research, Yellowstone National Park, unpublished report). Habitat types follow Despain (1990) and Mueggler and Stuart (1980).

Map Unit FGT

Topography: The landforms are coalescing alluvial fans with broad, convex slopes. Slopes range from 0 to 3%. The drainage patterns are weakly radial.

Vegetation: Natural vegetation is grassland and sparse shrubland. Habitat types are primarily bluebunch wheatgrass (*Agropyron spicatum*)/Sandberg bluegrass (*Poa sandbergii*), with some big sagebrush (*Artemisia tridentata*)/bluebunch wheatgrass occurring at the base of the fan and within fan channels. The native vegetation has been disturbed and the present vegetation is primarily (60–80%) invading exotics. Vegetative cover varies from 10 to 40%.

Parent Material (geology): The source material for the fans is Cretaceous sandstone, siltstone, mudstone, and Pleistocene glacial till. There have been some surficial additions by glacial floods of the Yellowstone and Gardner rivers.

Soil Description: Subrounded boulders and stones make up 30–40% of the soil surface. The soils are well drained with fine to medium textures and dark colored surface layers. The surface textures are mainly loams and clay loams. Soil reaction (pH) is usually 8.0 or slightly higher. The accumulation of calcium carbonate can occur at depths greater than 20 cm. The soil fertility is moderate. Both local and glacially imported rock fragments occur within the soil and vary from 35 to 85% of the profile.

Soil Distribution: The percentage of sand and rock fragments generally increases upslope toward the apex of the fan and within fan channels. Some areas have more rock fragments on the surface and are similar to map unit FLD. The swales have fewer rock fragments and resemble map unit FMF.

Map Unit FLD

Topography: Landforms include glacial flood deposits and eroded terraces. Slopes range from 0 to 20%. These features are located on valley bottoms and sides. Drainage patterns are weak to absent. This unit is differentiated from map unit GTM by the higher percentage of large rock fragments on the surface.

Vegetation: Natural vegetation is shrubland. Habitat type is mainly big sagebrush/bluebunch wheatgrass, though summits and south facing slopes are limited to a bluebunch wheatgrass/Sandberg bluegrass habitat type. Vegetative cover varies between 30 and 50%.

Parent Material (geology): The unit is made up of stream channel deposits from postglacial floods. The floods were probably the result of rapid draining of ice-dammed lakes during and immediately after deglaciation. In some areas, the surface material contains loess (wind blown silt). The rock types include Precambrian intrusive volcanics, Tertiary extrusive volcanics, and Cretaceous sedimentary rocks.

Soil Description: Rounded and subrounded boulders, with some cobbles and stones make up 40 to 60% of the soil surface. Soils are well drained with medium to coarse textures and dark colored surface layers. Surface textures are mainly loam, with some areas of silt loam and sandy loam. Soil reaction (pH) is slightly below 8.0 at the surface and 8.0 in the subsurface layers. Soil fertility is moderate and calcium carbonate usually occurs in the sandier, subsurface layers. Subrounded boulders, stones, and cobbles make up 35 to 70% of the soil and become more abundant with increased depth. At 25 cm, rock fragments make up approximately 70% of the profile.

Soil Distribution: Finer surface textures occur on lower slope positions.

Map Unit FMC

Topography: Landforms are alluvial fans with broad, convex slopes. They are located on valley sides and

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[1] From H. F. Shovic, A. Rodman, D. Neprud, and J. Lane. Soils investigation of the Reese Creek–McMinn Bench–Mammoth area, northwestern Yellowstone National Park. Division of Research, Yellowstone National Park, unpublished report.

bottoms. Slopes range from 8 to 20%. Drainage patterns are weakly radial to dendritic.

Vegetation: Natural vegetation is shrubland and grassland. Habitat types are mainly big sagebrush/ Idaho fescue (*Festuca idahoensis*) and big sagebrush/bluebunch wheatgrass with some areas of bluebunch wheatgrass/Sandberg bluegrass. Vegetative cover varies from 35 to 70%. Root density is high in the top 10cm of the soil.

Parent Material (geology): The alluvial fan deposits are derived from local sandstone and rhyolitic bedrock. There are occasional glacial erratics within the soil.

Soil Description: Angular and subangular gravels and cobbles, with some subrounded stones make up from 2 to 40% of the soil surface. Soils are well drained, with medium to coarse textures and dark colored surface layers. Surface textures are mainly sandy loams with some loamy sands. Surface soil reaction (pH) varies between 7.3 and 8.1. Calcium carbonate may occur in the subsoil at depths greater than 10 cm. Salt and/or sodium may occur in the soil profile. The soils have moderate fertility. Rock fragments are generally angular and subangular gravels and cobbles. The amount of rock fragments within the profile varies widely (5–50%) but become more abundant with increasing depth.

Soil Distribution: Surface rock fragment percentage increases toward the head of slopes and within fan channels.

Map Unit FME

Topography: The landforms are coalescing alluvial fans with dissected slopes and entrenched stream channels. Slopes range from 5 to 45%. The drainage patterns are strongly parallel.

Vegetation: The natural vegetation is sparse grassland and sparse shrubland. The habitat type is usually bluebunch wheatgrass/Sandberg bluegrass, with some big sagebrush/bluebunch wheatgrass occurring at the base of the fan and in fan channels. Vegetative cover ranges from 10 to 60%.

Parent Material (geology): The source material of these fans is mainly Cretaceous sandstones, siltstones, and mudstones. Because some of the bedrock is marine in origin, there are areas high in calcium carbonate and other salts. A small percentage of the surface stones are glacial erratics.

Soil Description: Angular and subangular cobbles make up 5-to 35% of the soil surface. The soils are well drained with medium textures and light and dark colored surface layers. They are finer textured than map unit FMC. The surface textures are mainly loams. Clay accumulation can occur in the subsoil. Soil reaction (pH) varies from 8.0 to 8.5. Calcium carbonate may occur below 20 cm. Salt and/or sodium accumulations can occur in the subsoil below 40 cm. Soil fertility is usually low. The amount of rock fragments within the profile ranges from 5 to 30%. Most are subangular to subrounded gravels and cobbles.

Soil Distribution: The proportion of sand in the soil tends to increase toward the apex of the fan. Rock fragments become more abundant toward the apex and within fan channels. Fan bases have the finest textures and the lowest abundance of rock fragments.

Map Unit FMF

Topography: The landforms are coalescing alluvial fans with broad, convex slopes. Slopes range from 2 to 10%. The drainage patterns are weakly radial.

Vegetation: Natural vegetation is grassland and sparse shrubland. The major habitat type is bluebunch wheatgrass/Sandberg bluegrass, with some big sagebrush/bluebunch wheatgrass occurring at the base of the fan and within fan channels. Vegetative cover varies from 35 to 65%.

Parent Material (geology): The source material for the fans is Cretaceous sandstone, siltstone, mudstone, and Pleistocene glacial till.

Soil Description: Less than 5% of the surface is covered by angular gravels. The soils are well drained with medium textures and light colored surface layers. The surface textures are mainly loams. Soil reaction (pH) is between 7.8 and 8.3. The accumulation of calcium carbonate can occur from the surface down to 30 cm below the surface. The soil fertility is high. Rock fragments within the profile vary from 0 to 20%, abundance usually increases with depth. They are rounded and generally small in size.

Soil Distribution: The percentage of sand and rock fragments in the soil generally increases upslope toward the apex of fans and within fan channels.

Note: The area just southeast of the old Gardiner Cemetery is different from others within this map unit. Here, soils are moderately fine to fine textured with few rock fragments. Cracks up to 5 cm wide are common on the surface. Soils have formed in slope-wash from landslides and may be high in sodium.

Map Unit FOW

Topography: The landforms include gently sloping glacial outwash fans and kame terraces that are both flat and hilly. They are located on valley sides. Slopes vary from 5 to 50%. Drainage patterns are weakly deranged to parallel.

Vegetation: Natural vegetation is grassland and shrubland. Habitat types are big sagebrush/bluebunch wheatgrass and bluebunch wheatgrass/Sandberg bluegrass. Vegetative cover varies from 20 to 40%.

Parent Material (geology): Both outwash fans and kame terraces are composed of stratified or semistratified material. Because the material originates from glaciers, it is a combination of eroded local and distant bedrock. The rock types include acid and basic extrusive volcanics, sandstones and finer grained sedimentary rocks, travertine, and intrusive volcanics.

Soil Description: Rock fragments make up 20–50% of the surface. The soils are well drained with coarse to medium textures and light to dark colored surface layers. Kame deposits tend to have loam or sandy loam surface textures with few rock fragments throughout the profile. Outwash deposits have a loam surface texture and contain abundant subrounded rock fragments of all sizes. The soil fertility is moderate.

Soil Distribution: Soil type is primarily controlled by the method of deposition.

Map Unit FST

Topography: The landforms are alluvial fans with convex slopes. Slopes range from 5 to 15%. The drainage pattern is weakly radial.

Vegetation: Natural vegetation is shrubland. The major habitat type is greasewood/western wheatgrass (Agropyron smithii). The vegetative cover ranges from 35 to 50%. Greasewood is tolerant of saline and sodic conditions in the soil. The distribution of the greasewood/western wheatgrass habitat type may indicate places where salt and/or sodium enriched water reaches the root zone.

Parent Material (geology): The source material for these fans are Cretaceous sedimentary rocks and Pleistocene landslides.

Soil Description: Angular and subangular gravels and cobbles cover up to 30% of the soil surface. The soils are well drained with coarse to medium textures and dark colored surface layers. Surface textures range from loam to loamy sand. Surface soil reactions (pH) are 8.0 and above. Soil fertility is low. Free calcium carbonate occurs throughout the soil profile. Because of parent material, these soils have high soluble salt concentrations in the root zone (see Salt and Sodium in Soils for an explanation on saline, saline–sodic, and sodic effects on soil). Subangular to subrounded rock fragments occur in the soil profile. The abundance of rock fragments usually increases with depth.

Soil Distribution: The percentage of sand and rock fragments in the soil generally increases upslope toward the apex of fans and within fan channels. High salt concentration may occur anywhere within the unit.

Map Unit GTC

Topography: The landforms are moderately to steeply sloping, glaciated mountain slopes with some areas of outcropping bedrock. Slopes range from 15 to 60%. The drainage pattern is weakly dendritic to deranged. Outcrops of local bedrock make up 10 to 30% of the map unit.

Vegetation: The natural vegetation is shrubland and grassland. The major habitat types are big sagebrush/bluebunch wheatgrass, big sagebrush/Idaho fescue, and bluebunch wheatgrass/Sandberg bluegrass. Vegetative cover varies from 30 to 60%. Sanady soils tend to habve a bluebunch wheatgrass/ Sandberg bluegrass habitat type, while loamier soils support big sagebrush/Idaho fescue or big sagebrush/ bluebunch wheatgrass.

Parent Material (geology): The unit is a combination of glacial till, weathering bedrock, and colluvium. The bedrock is primarily Cretaceous sandstone and hard units of Tertiary volcanics.

Soil Description: Rock fragments make up 20–40% of the soil surface. The soils are somewhat excessively drained with medium to moderately coarse textures and light and dark colored surface layers. Soil color reflects weathered bedrock color. The surface textures are loams and sandy loams. Soil fertility is moderate. Free calcium carbonate may occur throughout the soil profile. Rock fragments, angular to rounded, vary from 5 to 40% within the profile.

Soil Distribution: Soils in deeper till are similar to those in map unit GTM. As soils become shallower (closer to bedrock), the percentage of sand and angular rock fragments increases. Soils on steep slopes are a mixture of till and residuum.

Map Unit GTF

Topography: The landforms are steep to moderately sloping glaciated mountain ridge tops and slopes. Slopes vary from 20 to 65%. Drainage patterns are weakly parallel to dendritic. Outcrops of bedrock do occur but are rare within this unit.

Vegetation: The natural vegetation is grassland and shrubland. The major habitat types are bluebunch wheatgrass/Sandberg bluegrass and big sagebrush/ Idaho fescue. Vegetative cover varies from 50 to 70%. The bluebunch wheatgrass/Sandberg bluegrass habitat type occurs on more clayey soils and southerly slopes, while the more loamy soils and northerly slopes support big sagebrush/Idaho fescue habitat type.

Parent Material (geology): This unit is a combination of glacial till, weathering bedrock, and colluvium. The bedrock is Cretaceous siltstone, mudstone, and bentonite.

Soil Description: Rock fragments make up 0 to 30% of the soil surface. The soils are well drained with moderately fine textures and dark colored surface layers. Soil color reflects the color of weathered bedrock. Surface textures range from loam to clay loam. Soil fertility is high. The amount of rock fragments within the profile varies. Most rock fragments are subrounded.

Soil Distribution: The soils in deeper till are similar to those in map unit GTM. As the soils get shallower (closer to bedrock), the clay percentage of the soil increases. North-facing slopes tend to have more loam surface textures than do south-facing slopes.

Map Unit GTM

Topography: Landforms include moderately sloping, glaciated valley side slopes and hummocky, nearly level to rolling moraines in valleys. Slopes range from 0 to 40%. Drainage patterns are weakly dendritic or deranged. There are a few rounded, subdued rock outcrops.

Vegetation: Natural vegetation is shrubland, grassland, and moist meadow with a few Douglas-fir trees on some protected sites. Major habitat types are big sagebrush/bluebunch wheatgrass, big sagebrush/ Idaho fescue, and bluebunch wheatgrass/Sandberg bluegrass. Vegetative cover generally varies from 30 to 75% and up to 90% in moist meadows. The big sagebrush habitat types usually occur on the north and northeast facing slopes in surface soils with high silt and organic matter contents. The bluebunch wheatgrass/Sandberg bluegrass habitat type generally grows on southerly slopes and has a lower percent vegetative cover.

Parent Material (geology): Surficial deposits of glacial till make up most of this unit. These deposits are Pleistocene in age and are derived from a variety of rock types, including Precambrian crystalline rocks, Tertiary volcanic rocks, Mississippian limestones, travertine, and Cretaceous sedimentary rocks.

Soil Description: Rounded and subrounded cobbles, stones, and boulders make up 10 to 40% of the soil surface in most areas. Soils are well drained with moderately coarse to fine textures and dark colored surface layers. Surface soil texture is mainly loam and sandy loam but varies from silt loam to loamy sand. Subsoil texture is most often loam. Soils in this map unit often have an accumulation of clay in the subsoil. Surface soil reaction (pH) is between 7.0 and 8.0 and is usually slightly higher with depth. Calcium carbonate is common in subsurface layers and sometimes occurs in the surface soil. Salt and/or sodium accumulations can occur in the subsoil, usually 20 m or more below the soil surface. The soils usually have high fertility. Rock fragments make up from 10 to 50% of the profile.

Soil Distribution: Surface soils on north and northeast facing slopes often have high silt and organic matter contents. Soils on southerly slopes are shallower and have less silt and less organic matter in the surface soil then northerly slopes.

Map Unit LSI

Topography: Landforms are a hummocky, rolling, chaotic mixture of small hills, swales, and depressions. The topography is more subdued and rounded than in map unit LSP. Slopes range from 0 to 55%. Drainage patterns are dendritic, with common eroded gullies. Upper parts of landslides are marked by steep scarps and composed of large bedrock blocks, while lower parts are lobate mudflows. Rounded and subrounded glacial stones and boulders (erratics) are common on the surface.

Vegetation: Natural vegetation is shrubland and sparse grassland. There are some Douglas-fir and aspen near the upper boundary. Major habitat types are big sagebrush/bluebunch wheatgrass, bluebunch wheatgrass/Sandberg bluegrass, and meadow types. Meadows occur in swales and open depressions where the surface soil is high in silt and organic matter. Vegetative cover is greater than in map unit LSP. It ranges from 15 to 45% and up to 85% in meadows. Cover is associated with the texture of the surface layer, clayey soils having the lowest cover and medium textured soils having higher percent cover. Root density is also related to clay content. Between 15 and 30 cm, the lowest root densities are associated with clayey textures and the highest with sandy loam textures.

Parent Material (geology): These landslides occurred during the last glacial period. Their appearance has been modified by glacial erosion and deposition. The unstable slopes were probably the result of glacial erosion on water-lubricated bentonitic bedrock. The bentonite is overlain by volcanic breccias. Slide debris is angular dacitic and andesitic rock fragments in a bentonitic matrix, sometimes covered by a thin mantle of glacial till.

Soil Description: Local angular and subangular gravels and cobbles, with glacially derived rounded and subrounded stones and boulders, make up 30–60% of the soil surface. Soils are well drained with dark to light colored surface layers. Surface textures are mainly loam and sandy loam with some areas of clay, clay loam, and silt loam. They tend to have more silt and sand than those in map unit LSP because of a mantle of till that varies in depth. Subsurface textures are clay or clay loam. The soil reaction (pH) below 12 cm is generally above 8.0. In most places there is an accumulation of sodium and/or salt throughout the soil profile (see Salt and Sodium in Soils for an explanation on saline, saline-sodic, and sodic effects on soil). This reduces plant productivity and increases erodibility. Soil fertility is low to moderate. Angular gravels make up 5 to 15% of the soil profile. Rock fragments generally increase in abundance with increasing depth.

Soil Distribution: In general, the surface soil on the upper portion of these landslides is deeper and has less clay than surface soils on the lower portions of the landslides. On the lower portion of the landslide; surface soils in depressions and swales have loam, silt loam, or sandy loam textures, while the surface soils on summits, shoulders, and south facing slopes have higher clay contents because they have probably lost or never had the mantle of glacial till. This distribution of surface textures results from local erosion and redeposition of the original landslide material.

Map Unit LSP

Topography: Landforms are a hummocky, rolling, chaotic mixture of small hills, swales, and depressions. Slopes range from 0 to 55%. Drainage patterns are dendritic, with common eroded gullies. Upper parts of landslides are marked by steep scarps and composed of large bedrock blocks and till, while lower parts are lobate mudflows.

Vegetation: Natural vegetation is shrubland and sparse grassland. There are some Douglas-fir and aspen near the upper boundary of the landslides. Habitat types are bluebunch wheatgrass/Sandberg bluegrass, big sagebrush/bluebunch wheatgrass, big sagebrush/Idaho fescue, greasewood/western wheatgrass, and meadow types. Bluebunch wheatgrass/Sandberg bluegrass habitat type tends to occur in soils with clay loam surface textures. Big sagebrush habitat types occur in soils with loamy surface textures. Meadows occur in swales and open depressions where the surface soil is high in silt and organic matter. Greasewood/western wheatgrass habitat type occurs in closed depressions. Vegetative cover generally ranges from 10 to 60% and up to 70% in meadows.

Parent Material (geology): These landslides occurred just after the last glacial period. The unstable slopes were probably the result of glacial erosion on water-lubricated bentonitic bedrock. The bentonite is overlain by volcanic breccia. Slide debris is angular dacitic and andesitic rock fragments in a bentonitic matrix, with some glacial till.

Soil Description: Subrounded, subangular, and angular gravels and cobbles make up 10 to 60% of the soil surface. Soils are well drained, with fine textures, and dark colored surface layers. Subsurface textures are clay or clay loam, while surface layer textures vary with landscape position. Surface textures are mainly clay loam and loam, with some areas of clay, silt loam, and sandy loam. Soil reaction (pH) in the subsoil is generally above 8.0. In many places there is an accumulation of sodium throughout the profile and salt in the subsoil (see Salt and Sodium in Soils for an explanation on saline, saline–sodic, and sodic effects on soil). This reduces plant productivity and increases erodibility. Soil fertility is low to moderate. Angular gravels make up 0 to 20% of the soil profile.

Soil Distribution: Surface soil layers on the upper portion of landslides have loam and sandy loam textures. Soils on the lower portions of the landslides; small summits, shoulders of slopes, and south facing slopes have clay or clay loam surface textures, while surface soils in footslopes and toeslopes (depressions and swales), tend to have loam, silt loam, or sandy loam textures. This distribution of surface textures is due to local erosional and depositional modification of the original landslide deposit.

Map Unit LSV

Topography: Landforms are a hummocky, rolling, chaotic mixture of scarps, stream channels, small hills, swales, and depressions. The unit is characterized by high surface variability and indications of recent movement, such as slip scars and leaning trees. Slopes range from 0 to 55%. Drainage patterns are deranged to dendritic.

Vegetation: Natural vegetation is sparse shrubland, sparse grassland, moist meadows, and some riparian and forested areas. The forested areas occur along water courses and contain aspen and Douglas-fir. The major habitat types are big sagebrush/Idaho fescue and big sagebrush/bluebunch wheatgrass, with some greasewood/western wheatgrass and bluebunch wheatgrass/Sandberg bluegrass. Meadows occur in swales and at lower slope positions where soils are high in silt and organic matter. The greasewood/ western wheatgrass habitat type often occurs in depressions. Vegetative cover varies from 15 to 50% in most areas, and up to 100% in meadows and along water courses.

Parent Material (geology): This unit contains recently reactivated landslides and a postglacial landslide with high soil variability. The slide debris is mainly a bentonitic matrix with angular rock fragments of dacitic and andesitic composition. The older landslide in the western portion of the study area (labelled LSVa on Fig. 2) contains mostly dacitic rock fragments.

Soil Description: Rock fragments, mostly angular gravels and cobbles with some rounded boulders and stones, make up 30–60% of the soil surface. The soils are well to moderately well drained with dark to light colored surface layers. Surface soil textures are highly variable. They include sandy loams, clay loams, loams, and silt loams. Soil reaction (pH) varies from 7.3 to 8.0. In many places there is an accumulation of sodium throughout the profile and salt in the subsoil (see Salt and Sodium in Soils for an explanation on saline, saline–sodic, and sodic effects on soil). This reduces plant productivity and increases erodibility. Soil fertility is low to moderate. Rock fragments make up 20–60% of the soil profile.

Soil Distribution: Soil distribution is related to landslide deposition and is highly variable.

Map Unit RSC

Topography: The landforms are steep to moderately-sloping, straight hillslopes and cliffs, often with small fans and colluvium at the base of slopes. Slopes range from 3% on summits to 70% on hillsides. Drainage patterns are strongly to weakly parallel. Rock outcrops makes up 15 to 30% of this map unit.

Vegetation: The natural vegetation is shrubland and grassland, with some scattered trees and barren areas. The major habitat types are big sagebrush/bluebunch wheatgrass and bluebunch wheatgrass/Sandberg bluegrass. Scattered common juniper (*Juniperus commonis*) and Douglas-fir (*Pseudotsuga mensiesii*) occur in the unit along the Gardner River. Vegetative cover varies between 0 and 50%. The distribution of habitat types is related to surface soil textures. In general, grasslands occur on loams and clay loams, while shrublands occur on sandy loams and loamy sands.

Parent Material (geology): The soils in this unit originate from weathering bedrock and colluvium. In the area on and near Mount Everts (southern part of the study area), the bedrock is Cretaceous sandstone, with some siltstone. Near Sepulcher Mountain to the north, bedrock is primarily hard units of Tertiary volcanics.

Soil Description: Rock fragments make up 20–90% of the soil surface. The soils are somewhat excessively drained with medium to coarse textures. Surface layers are light colored with loam, sandy loam, or loamy sand textures. Soil reaction (pH) at the surface varies from 7.0 to 8.0. The soils are generally shallow to bedrock. Soil fertility is low. Angular rock fragments make up from 2 to 80% of the soil profile. Rock fragment abundance generally increases with increasing depth.

Soil Distribution: Depth of soil is strongly related to bedrock proximity. Soils are deepest at the bases of slopes and midway between rock outcrops.

Map Unit RSF

Topography: The landforms are steep, straight hillslopes and cliffs, often with small fans and colluvium at the base of slopes. Slopes range from 40 to 70%. Drainage patterns are strongly to weakly parallel. Rock outcrops make up 30% of this map unit.

Vegetation: The natural vegetation is shrubland, grassland, and scattered trees. There are also some barren areas. The major habitat types are big sagebrush/bluebunch wheatgrass, bluebunch wheatgrass/Sandberg bluegrass, and areas of scattered common juniper and Douglas-fir. Vegetative cover varies between 0 and 50%. The distribution of vegetation is related to slope, depth to bedrock, and surface soil textures. Scattered trees are most abundant in the northern section of the unit along the Gardiner–Mammoth road.

Parent Material (geology): The soils in this unit originate from colluvium over weathering bedrock. Along the Gardner River, bedrock is interbedded sandstones and shales. In other areas bedrock is mudstone. The influence of till-type materials (glacial till colluvially redeposited) is strongest in the northern portion of the unit along the Gardiner–Mammoth road.

Soil Description: Angular stones, cobbles, and gravels make up 25–60% of the soil surface. Subrounded glacial erratics are found in the northern half of the unit along the Gardiner–Mammoth road. The soils are well drained with fine to medium textures and a few areas with coarse textures. Surface layers are dark colored with loam and clay loam textures. Soil reaction (pH) is greater than 8.0 at the surface. The soils are often shallow to bedrock. Soil fertility is low in most areas but moderate in the northern portion of the unit along the Gardiner–Mammoth road. Angular rock fragments are generally abundant within the profile.

Soil Distribution: Depth of soil is strongly related to bedrock proximity. Soils are deepest at the bases of slopes and midway between rock outcrops. Soil texture is related to bedrock type. Soils derived from interbedded sandstone and shales have loam and sandy loam textures, while soils forming from fine-grained rock types have loam and clay loam textures.

Map Unit SCH

Topography: Landforms are stream bottom deposits, including channels, small terraces, and flood plains. Slopes range from 0 to 15%. They abut major streams and rivers.

Vegetation: Natural vegetation is shrubland and sparse forest. Englemann spruce, Douglas-fir, lodgepole pine, and aspen occur along water courses. The major habitat types are big sagebrush/Idaho fescue and big sagebrush/bluebunch wheatgrass. Vegetative cover ranges from 30 to 50%.

Parent Material (geology): The unit is composed of alluvial material deposited from various sized streams and rivers. Material includes channel-fill, bar, and over-bank deposits. Near smaller streams, rock types are mainly local with some glacial erratics concentrated within stream channels. River deposits have a high concentration of reworked glacial drift.

Soil Description: Rock fragments make up 20–60% of the soil surface. Soils are well drained with medium to coarse textures and dark colored surface layers. Surface soil textures are mainly loam, with some sandy loam and loamy sand. Soil reaction (pH) is generally near 8.0. Soil fertility is moderate. Rock fragments within the profile vary from 5 to 70%. Soil texture and the percentage of rock fragments often varies abruptly with depth.

Soil Distribution: Rock fragments and sand in the surface layer become more abundant near channels. The mode of deposition causes soil textures and rock fragment abundance to be highly variable both laterally and with depth.

Map Unit SFL

Topography: The landform is a broad, gently sloping floodplain from a stream. The slopes range from 0 to 2%. The drainage patterns are weakly parallel or braided.

Vegetation: The natural vegetation is grassland and shrubland. The habitat types are bluebunch wheatgrass/Sandberg bluegrass and big sagebrush/bluebunch wheatgrass. The native vegetation has been disturbed and the present vegetation is 10–35% invading exotics. Vegetative cover varies from 30% in the grassland to 40% in shrubland. The shrubland occurs around the edge of the unit and makes up 25% of the total.

Parent Material (geology): The material is primarily floodplain deposits from streams. This material was deposited on top of or against glacial flood deposits. The boundary area of the unit is a mixture of both types of deposit.

Soil Description and Distribution: Surface rock fragments only occur where the unit grades into glacial flood deposits (FLD) or stream deposits (SCH). In those areas, gravels and cobbles occupy up to 35% of the soil surface. The soils are well drained. Surface soils are coarse textured and dark colored. The surface soil texture is very fine sandy loam. The gradational areas referred to above have coarse sandy loam textures. Soil fertility is moderate.

Map Unit D1

Topography: This map unit contains the town of Gardiner, Montana. The landform is a generally flat to gently sloping river terrace. Slopes range from 0 to 10%.

Vegetation: The native vegetation was probably similar to map units FMF and FLD. The present vegetation is urban plants and invading exotics.

Parent Material (geology): Sandy, gravelly, and bouldery alluvium make up most of the unit. Mode of deposition is probably flooding of the Yellowstone River, with both in-channel and over-bank deposits.

Soil Description and Distribution: Undifferentiated.

Map Unit D2

Topography: This area is mainly a flood plain with some gently rolling terrain. This unit is located in the Yellowstone River valley bottom. Slopes vary from 0 to 5%. Remains of irrigation ditches cross the surface.

Vegetation: Natural vegetation is grassland or shrubland. The native vegetation in this unit has been artificially altered by irrigated agriculture. The present vegetation is mostly exotics. Vegetative cover is approximately 35%.

Parent Material (geology): The unit is composed of silty, clayey, and sandy alluvium. Irrigated agriculture has altered the top 9 cm with plowing and additions of organic matter and fertilizers.

Soil Description: Surface rock fragments make up 0 to 2% of the soil surface. Soils are well drained with fine textures and dark colored surface layers. Surface soil texture is silty clay loam. The soil reaction (pH) is 8.0 at the surface and 7.5 or slightly above in the subsurface. These soils have moderate fertility. Rock fragments in the soil make up less than 5% of the profile.

Soil Distribution: The unit has been altered by irrigated agriculture. The plow layer (top 9 cm) has had the most additions of fertilizer and organic matter. Plowing may also have compacted the soil below 9 cm. The mode of deposition has resulted in textural variations with depth. These different layers are affected differently by the irrigation process and result in various vegetation patterns.

Map Unit D3

Topography: This area is flat, or gently sloping, abandoned building sites.

Vegetation: Barren areas and sparse grassland with a high percentage of exotic species are common.

Parent Material (geology): Mainly the same as map unit GTM, with one small area similar to LSP.

Soil Description and Distribution: Rock fragments make up greater than 35% of the soil surface. Soils are moderately coarse textured, shallow and underlain by asphalt or rock foundations. Subsoil is exposed. For more soil information, see map unit GTM (or map unit LSP for the southern area).

Map Unit D4

Topography: This unit contains berms and excavations from abandoned irrigation ditches. Side-slopes are 0 to 30%, though ditches are on contours. Berms can be up to 8 feet high with ditches up to 10 feet deep on steep slopes (greater than 45%).

Vegetation: Barren areas alternate with grassland and shrubland. Exotic species are common.

Parent Material (geology): The irrigation ditches pass through map units FOW, FMC, FMF, FST, RSC, and SCH. Locate the specific area of interest on Fig. 2, then see the appropriate map unit for a description of parent material.

Soil Description and Distribution: Soils are medium to moderately coarse textured depending on location of ditch. Subsoils are exposed, with topsoil piled in berm. Soils have many rock fragments. More detailed soil information is given with map units SCH, FMC, FMF, FST, RSC, and FOW (see explanation in Parent Material section above).

Map Unit D5

Topography: The area is flat or gently sloping (excavations for borrow pits and foundations).

Vegetation: Vegetation is sparse grassland and shrubland with exotic species common. Barren areas occur within the map unit.

Parent Material (geology): See map unit FMF.

Soil Description and Distribution: Soils are moderately coarse textured with many rock fragments. Subsoils are exposed.

Map Unit D6

Topography: The area contains trenches once used as rifle range target areas, structures remaining behind the trenches, and large berms, up to 3 m in height.

Vegetation: Vegetation is sparse grassland or shrubland with exotic species common. Barren areas occur within the map unit.

Parent Material (geology): See map unit FMF.

Soil Description and Distribution: Soils are moderately coarse textured with some rock fragments. Subsoils are exposed. For more soil information, see map unit FMF.

Map Unit D7

Topography: Landforms are a mixture of benches, terraces, and hills. Slopes vary from 0 to 40%. Part of this area is an abandoned landfill. Trash, concrete slabs, asphalt, and other refuse are common in the area. A section of the area has been recontoured.

Vegetation: Vegetation is grassland and shrubland, sparse in places. Exotic species are common.

Parent Material (geology): See map units LSP and FST.

Soil Description and Distribution: Some soils are salt and sodium affected. For more soil information, see map units LSP and FST.

Map Unit D8

Topography: The unit contains abandoned road grades.

Vegetation: Vegetation cover is variable, depending on the severity of cuts and fills, and age of abandonment. The variability does not match that of the surrounding, undisturbed areas. Species are a mixture of natives and exotics.

Parent Material (geology): The abandoned road grades pass through map units LSI, LSP, RSC, and SCH. Locate the specific area of interest on Fig. 2, then see the appropriate map unit for a description of parent material.

Soil Description and Distribution: Soils are generally moderately coarse to medium textured with many rock fragments. Subsoils to subsurface layers are exposed, depending on road and slope gradients. Some areas are compacted. More detailed soil information is given with map units LSI, LSP, RSC, and SCH (see explanation in Parent Material section above).

Map Unit D9

Topography: The map unit contains an earth-fill dam for the abandoned Ice Lake reservoir.

Vegetation: Vegetation is grassland and sparse shrubland, with a combination of native and exotic species.

Parent Material (geology): See map unit LSI.

Soil Description and Distribution: Soils are moderately coarse to medium textured with many rock fragments. The dam is mainly composed of substratum material.

Map Unit D10

Topography: The area is gently sloping and contains abandoned irrigated fields and the settlement of Stephens Creek.

Vegetation: Vegetation is a mixture of native and exotic species.

Parent Material (geology): The map unit has been influenced by a variety of depositional events. Locate the specific area of interest on Fig. 2 then look up the adjacent map unit (FMC, GTM, SCH, or SFL) for a description of parent material.

Soil Description and Distribution: Soils are variable but probably have been either plowed or compacted. More detailed soil information is given with map units

FMC, GTM, SCH, and SFL (see explanation in Parent Material section above).

Map Unit D11

Topography: This unit contains an abandoned railroad grade. The grade has either been built up into a berm or cut into the hillside.

Vegetation: The vegetation is sparse grassland with barren areas.

Parent Material (geology): The abandoned railroad grade passes through map units D2, D16, FGT, FLD, LSP, and SCH. Locate the specific area of interest on Fig. 2, then see the appropriate map unit for a description of parent material.

Soil Description and Distribution: Soils on the track bed and partway down berm sides are human-made. Soil materials are clinker, ashes, and cinders. Soils are coarse textured with many small rock fragments. Subsoils and substrata are exposed on cuts. More detailed soil information of undisturbed units in the area is given with map units LSI, LSP, RSC, and SCH (see explanation in Parent Material section above).

Map Unit D12

Topography: This area contains abandoned gravel pits.

Vegetation: The vegetation is sparse grassland with some barren areas.

Parent Material (geology): See map unit FLD.

Soil Description and Distribution: Soils are coarse textured, with many rock fragments. Subsoils or compacted substratum is exposed. For more soil information see map unit FLD.

Map Unit D13

Topography: The area is flat to gently sloping and contains remnants of building sites or parking areas.

Vegetation: Vegetation is sparse grassland with exotic species common. The unit contains some barren areas.

Parent Material (geology): See map unit FLD.

Soil Description and Distribution: Soils are moderately coarse textured with many rock fragments. They are shallow and underlain at 5 to 10 cm by asphalt paving or foundations. For more soil information see map unit FLD.

Map Unit D14

Topography: This unit is an abandoned coal mine. Structures have been removed, and slopes have been somewhat recontoured. A waste rock pile and some timbers remain in the area.

Vegetation: The vegetation has been covered or removed and barren areas remain.

Parent Material (geology): See map unit RSF.

Soil Description and Distribution: Soils are fragmental. Rock fragments make up 90% of the soil profile. For more soil information see map unit RSF.

Map Unit D15

Topography: The landforms are alluvial fans with slopes ranging from 5 to 15%. The areas have been impacted by trampling and contain small ditches, refuse, stone foundations, and remnants of road grades.

Vegetation: The vegetation is primarily exotic species with some greasewood. There are some barren areas in the unit.

Parent Material (geology): See map unit FST.

Soil Description and Distribution: The soils are similar to those in map unit FST but have been compacted.

Map Unit D16

Topography: The landform is mainly a flood plain with some gently rolling terrain. This unit is located in the Yellowstone River valley bottom. Slopes vary from 0 to 5%. Remains of irrigation ditches cross the surface.

Vegetation: Natural vegetation is grassland or shrubland. The native vegetation in this unit has been artificially altered by irrigated agriculture. The present vegetation is mainly exotic species. Vegetative cover is approximately 35%.

Parent Material (geology): The unit is composed of silty and sandy alluvium. Irrigated agriculture has altered the top 9 cm with additions of organic matter and fertilizers.

Soil Description: Surface rock fragments make up 0–2% of the soil surface. Soils are well drained with medium textures and dark colored surface layers. The surface texture is loam. The soil reaction pH is 8.1 at the surface and varies between 8.3 and 7.6 in the subsurface. These soils have moderate fertility. Rock fragments in the soil make up less than 5% of the profile.

Soil Distribution: The unit has been heavily altered by irrigated agriculture. The plow layer (top 9 cm) has had the most additions of fertilizer and organic matter. Plowing may also have compacted the soil below 9 cm. The mode of deposition has resulted in textural variations with depth. These different layers are affected differently by the irrigation process and result in various vegetation patterns.

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[Editor's note: Fig. 1 contains same information but is formatted differently]

Ungulate herbivory of willows on Yellowstone's northern winter range

Francis J. Singer, Lauryl C. Mack, and Rex C. Cates

Authors are research scientist, Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, Colorado 80523; research assistant, Research Division Yellowstone National Park, Wyoming 82190; professor, Department of Botany, Brigham Young University, Provo, Utah 84602.

Abstract. Effects of unmanaged populations of large mammalian herbivores, especially elk (*Cervus elaphus*) on vegetation is a concern in Yellowstone National Park, since wolves (*Canis lupus*) are extirpated, ungulate migrations are altered by human activities and the disruption of natural process is possible. Stands of low, hedged (height-suppressed) willows (*Salix* spp.) are observed throughout the greater Yellowstone National Park area where high densities of wintering elk or moose (*Alces alces*) exist. The height of 47% of the willow stands surveyed on Yellowstone's northern winter range has been suppressed. Mean leader use of willows of all heights was 22% in the winter of 1987–88, increased to 60% in winter 1988–89, following the drought and fires of 1988, then declined to 44% in 1989–90 and winter 1990–91. Height-suppressed were about one-half as tall as (43 ± 2 cm, $\bar{x} \pm$ SE) as tall willows (83 ± 4 cm). Percent twig use of suppressed willows in summer (25%) and winter (59%) was significantly more than for intermediate or tall stands ($P < 0.05$). Suppressed willows produced about one-fourth the aboveground annual biomass compared to taller willows; even after 27 or 31 years of protection, previously-suppressed willows produced only one-third the aboveground biomass of taller willows, suggesting suppressed willows grow on sites with lower growth potential. Growth conditions for willows on the northern winter range may have declined due to a warmer and drier climate this century, locally reduced water tables—because of the decline in beaver (*Castor canadenis*) or fire suppression may be responsible for the observed changes. Tall and intermediate-height willows contained higher concentrations of nitrogen and they exhibited more water stress than height-suppressed willows of the same species. More xeric growth conditions this century than last century, especially during the decades of the 1920's, 1930's and 1980's, may explain the low growth rates and lower chemical defenses against ungulate herbivory for height-suppressed willows. We propose a more xeric climate and locally-reduced water tables likely contributed to the willow declines on the northern winter range, but that the proximate factor in the declines was herbivory by native ungulates.

Key Words: ungulate herbivory, browsing of willows, *Salix* ecology, willow water stress, and secondary compounds

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Declines in willow (*Salix* spp.) abundance, distribution and stature on Yellowstone's northern range this century have been locally dramatic. Some willows were removed by park staff to facilitate hay culture during the early part of this century, but heavy browsing pressure, hedging, and declines were documented on many other stands (Houston 1982). Most of the declines in willows on the northern winter range apparently occurred during the 1920's through 1940's. Willow pollen in sediment samples decreased from 1900 to 1940 at 6 of 8 ponds (Engstrom et al. 1991), while willow cover declined from 1% to about 0.4% cover over the area during the past century on the northern range based upon photographic comparisons (Houston 1982:129). Willows are a very minor component of this particular grazing ecosystem. Elk (*Cervus elaphus*) number 21 per km^2, but their diets are mostly grasses (75%) and <1% willows (Singer and Norland 1994). Moose (*Alces alces*) consume more willows, but their densities are very low (<0.1 per km^2). The willow declines may be due to: (1) possibly unnatural concentrations of wintering elk (Grimm 1939, Patten 1968, Lovaas 1970, Beetle 1974, Chadde and Kay 1991), (2) declines in beaver (*Castor canadensis*) numbers on the northern winter range during the 1920's and 1930's, (3) the colonization or reappearance and increase in moose numbers on the northern winter range during 1911–50 (Walcheck 1976, Chadde and Kay 1988), (4) plant stress as a result of the droughts of 1919–36 in the greater Yellowstone area, (5) reductions in wildfires due to modern fire suppression (Houston 1973, 1982), and (6) reduced concentrations of secondary defensive compounds for willows on dry or otherwise marginal growth sites.

Willows that invade fertile, recently disturbed sites typically grow beyond the height of browsing by large herbivores through rapid vertical growth rates and large belowground storage of nutrients and energy (Bryant et al. 1983). Willows of reduced canopy size and height, i.e., suppressed willows, are observed throughout the greater Yellowstone area including Yellowstone National Park (YNP) and the Jackson Hole areas where high densities of elk and moose spend the winter (Gruell 1980, Houston 1982, Chadde and Kay 1991). Photographs from the 1860 through 1890 period show no suppressed willows (Houston 1982, Chadde and Kay 1991) and park managers are concerned if the current reduced stature of willows is either a consequence of natural processes or the effects of European man on elk populations (National Park Service 1988).

Ungulate–vegetation dynamics on Yellowstone's northern winter range provides an opportunity to monitor the effects of natural regulation of ungulates by the National Park Service in a protected ecosystem. Yellowstone National Park managers embarked on a policy of natural regulation management of ungulates within the park's boundaries in 1968, following 35 years of intensive artificial reductions of elk and bison (*Bison bison*) populations (Cole 1971, Houston 1982). Natural regulation in Yellowstone is not a scientific experiment, in that no similar control situation [with wolves (*Canis lupus*)] exist, and the extent of disruption of historic ungulate migrations by human activities outside of the park is unknown (Coughenour and Singer 1991). In spite of alterations in abundance, stature and form of limited types of woody browse (*Salix* spp., *Populus tremuloides* Michx., *P. trichocarpa* T.&G., *P. angustifolia* James) this century, Houston (1982) and Baur (1987) consider any plant changes following natural regulation to be within the bounds of expected changes. Grasses and forbs fluctuated more in response to climate changes than to ungulate densities (Houston 1982, Coughenour et al. 1994), while declines in woody riparian browse species this century were attributed to a lack of fires in an area that frequently burned, a drier and warmer climate, local reductions in water tables, and lower flooding frequency than during the 19th century (Houston 1982). Reductions in elk population to 20–30% of estimated ecological carrying capacity (ECC) in the 1960's (Houston 1982, Coughenour 1994) resulted in no significant difference in percent leader use of willows and only 11% increase in heights (Singer et al. 1994). Alternatively, Chase (1986) and Chadde and Kay (1988, 1991) concluded human activities, such as extirpation of wolves, alterations of elk migrations, increases in elk densities, and decline in beaver significantly altered ungulate–riparian vegetation relations this century on the northern winter range.

We examined 3 biological hypotheses:

1. Herbivory by large native ungulates is responsible for height suppression of willows on the northern winter range.
2. Drought-mediated water stress in willows results in reduced annual growth and contributes to height suppression of willows by large herbivores.
3. Drought or herbivore–mediated reductions in potential defensive metabolites or increases in primary nutrients in willows increase palatability

of willows to ungulates and subsequent suppression of willows.

We examined these hypotheses by comparing willow stands that varied with respect to height, location, and by comparing willow stands protected within ungulate exclosures to adjacent browsed willows. We observed the short-term effects of drought on willow herbivory in 1988–90, following the most server summer drought of this century. Summer precipitation (June–August) in 1988 was only 36% of the 29-year average and June–August daytime temperatures were 3° C above average (Singer et al. 1989).

Study Areas

Our study was conducted primarily in a 148 km^2 area of Slough Creek, Soda Butte Creek, and Lamar River tributaries of the upper Yellowstone River on the upper elevations of the northern winter range as described in Houston (1982), and on 3 study plots at lower elevations (Mammoth, Blacktail, Junction Butte). Study sites were located both within Yellowstone National Park, and outside the park boundary on the Gallatin National Forest in upper Slough and Soda Butte Creeks. Elevations of sample sites ranged from 1,890 m to 2,448 m. Average annual precipitation ranged from 30 cm per year at the lowest site near Mammoth, Wyoming to 55 cm at intermediate elevations in the Lamar Valley, to approximately 100 cm at the highest study sites near Cooke City, Montana (Houston 1982). Snowfall typically accumulates to depths of 15–45 cm at the lower sites and 60–80 cm at the upper study sites. The climate is characterized by long, cold winters and short, cool summers.

The northern winter range is approximately 800 km^2 in size, of which approximately 41% is coniferous forest (*Pseudotsuga menziesii*, *Picea engelmanni*, *Abies lasiocarpa*, *Pinus contorta*) and about 55% is grassland or sagebrush/bunchgrass (mostly *Artemisia tridentata/Festuca idahoensis*). Only about 4% of the northern winter range is classified as riparian, and only about 0.4% of the northern winter range is dominated by willows (Houston 1982:87). Houston (1982) reported that most willow/sedge (*Carex* spp.) communities were dominated by Geyer willow (*Salix geyeriana* Anderss.), Bebb willow (*S. bebbiana* Sarg.), false mountain willow (*S. pseudomonticola* Bebb), Booth willow (*S. boothii* Bebb) and Wolf willow (*S. wolfii* Bebb), while a few willow stands on sand and gravel bars were dominated by linear-leaved willows (subfamily *S. exigua* Nutt., *S. farriae* Ball). Willow stands occur only on the most mesic sites, in swales, seeps, draws, and streamsides.

Four species of ungulates on the northern winter range were observed to browse willows, elk, moose, mule deer (*Odocoileus hemionus*) and bison, but of these, only elk in lower elevations, and moose in higher elevations of the northern winter range are important browsers. Elk densities on the northern winter range ranged from 21 elk per km^2 in 1987 to 18 elk per km^2 in 1990 (Singer et al. 1989, Singer and Mack 1993). Moose densities were about 9–15 moose per km^2 in early winter near the highest elevation willow stands (Singer and Mack 1993), but few moose wintered in the middle or lower portions of the winter range (<0.1 moose per km^2). Moose were the primary ungulate herbivore in the highest elevation willow stands in winter (2,100–2,250 m) and elk the primary ungulate herbivore in the lowest stands (1,890–2,070 m), but both species potentially occurred at all elevations during winter. Beaver and hare (*Lepus* spp.) use of willows was insignificant at our study sites.

Methods

Landscape Level Measurements

We mapped willow stands in the northern winter range from the junction on the Lamar River and Slough Creek in the northeastern corner of the northern winter range and upstream to the head waters of Slough Creek and Soda Butte Creek. The mapping study area (148 km^2) totaled 19% of the entire northern winter range, and 23% of the northern winter range within Yellowstone National Park (YNP). We mapped all willow stands >0.3 ha in size from 1:32,000 color aerial photographs and ground surveys in the study area. Areas of each willow stand were calculated from dot grids. Ungulate densities were obtained from fixed-wing aircraft surveys early each winter (Dec.–Jan.), 1985–90, in each of 66 count units on the northern winter range as described in Singer (1991). We additionally sampled 3 willow stands from lower elevation core elk winter range at Junction Butte, Blacktail Deer Creek and Mammoth Hot Springs. Ungulate exclosures at these locations provided browsed and unbrowsed willow communities for sampling.

Willow Stand Measurements

Willow species abundance and production were measured in 15 randomly-located circular macroplots of 9.3 m in size in each willow stand; only 5–10 macroplots could be placed in the smallest (<0.1 ha) willow stands. The height of the tallest live leader, widest shrub crown diameter, perpendicular shrub diameter, and the species of each aboveground willow clump were recorded. Percent dead portion of each willow clump was estimated. On every fourth individual shrub of each species, the number of rooted stems, number of shoots per stem, length, height, and basal diameter of current annual growth (CAG), and diameter at the tip or browse point of 10 randomly selected shoots were recorded. Shoot measurements were gathered on the same stands in 1987, 1988, 1989, and 1990. Percent twig use of willows by ungulates was measured along 3–5 (depending on the size of the willow stand) permanently-marked 100 m transects located in a representative sample of willow stands. Along the transects, from 15 to 30 1-m circular plots were randomly located and the center of the plot was inconspicuously tagged below the shrub crown. These marked shrubs were then relocated twice a year. Winter willow use was recorded prior to leaf bud break (May), and summer use was recorded prior to leaf-drop (August) 1987–90. The total number of shoots and the number browsed were recorded in each plot. Almost no willow growth occurred after the summer readings were taken in early August, therefore, nearly all summer leader use was assumed incorporated into the winter tallies of shoot use. The height and total diameter of the willow plant, length, basal diameter, and diameter at browse point or tip, and the height from the ground to the apical bud or to the browse point were recorded on a sample of 50 browsed and unbrowsed shoots. Height classes were determined using summer height measurements at the end of each growing season (August) in 1986 to 1990. Heights of willow communities were divided into 3 categories based upon graphical analysis: (1) height-suppressed = nearly all plants were ≤80 cm, (2) intermediate = plants were 81–120 cm tall, and (3) tall willows = most plants were 121+ cm. Suppressed communities tended to be browsed at a uniform height, intermediate stands to a lesser extent, while tall stands were of diverse heights.

Bite size removed by ungulates was estimated from each browsed twig following the method of Pitt and Schwabb (1990). Bite size was calculated for winter and summer seasons from the formula:

$$BS = 100\,(Dp\text{–}Dt)/Db\text{–}Dt$$

where BS=bite size, Dp=twig diameter at the point of browsing, Db=basal diameter of browsed twig, and Dt=mean diameter of a representative sample of unbrowsed twig tips (Pitt and Schwabb 1990). This equation differed from bite size determined by twig length differences by only 4–6% (Jensen and Urness 1981) and it accurately predicted bite size for 4 of 6 shrub species (Pitt and Schwab 1990).

Aboveground biomass estimates were calculated for each willow species in each willow stand according to methods used by MacCracken and Viereck (1990) following Telfer (1969) and Oldemeyer (1981). An average number of aboveground willow clumps per macroplot was calculated for each stand. The average number of twigs per shrub, average twig length, and average green diameter at base were calculated from the annual twig measurements on the 1-m plots. Average twig weight was calculated from a linear regressions of dry weight (dependent variable) against twig length and basal green twig diameters at the base of the current annual growth (independent variables) (MacCracken and Viereck 1990). Log–log predictor regressions were calculated only for abundant species with adequate data (9 species in 1988, 5 species in 1989, and 5 species in 1990). Separate regressions were calculated for each willow species each year and each season (winter, summer) since the regressions varied between seasons and years. The r values were high for each species (range r = 0.78–0.97; mean r = 0.87, SE = 0.13; n = 19) and the plots of the residuals followed a normal distribution. The biomass of each willow species was estimated from the estimated twig weights × average number of twigs per plant × the number of shrubs per plot. Leaves were included in the summer twig weights; the presence of leaves accounted for the summer–winter differences in the regressions.

Plant Level Measurements

Forage quality was determined from shoots of height-suppressed, intermediate and tall willows for 3 species (Geyer, Wolf, and Booth willows) about 1 August of each year. At each study community, a minimum of 5 g of stem and leaf sample were taken from 5 randomly-selected shrubs. Twigs were gathered from the primary browse zone, 0.5–1.5 m. Samples were oven-dried for 48 hours at 50° C–60° C. Kjeldahl N (Assoc. Off. Anal. Chem. 1970) and in vitro digestibility (Tilley and Terry 1963), was analyzed at the Nutritional Analysis Lab, Colorado State University.

Moisture stress of willows was measured with a Scholander pressure bomb (PMS Instrument Co., Corvallis, Oregon) during the summer of 1989. Two readings were recorded from 10 plants of the 3 most common species per site. We sampled water stress on height-suppressed, intermediate, tall, protected (in ungulate exclosures for 27 or 31 years) and nearby unprotected height-suppressed willows at 3 exclosure sites. Water stress of willows was measured pre-dawn (0300–0600 hr) under conditions of minimum water stress and minimum transpiration for each plant to reduce variations due to fluctuations in day-time temperatures and cloud cover. The distal 12 cm of each willow shoot was cut, rushed to a Scholander pressure bomb, and the water potential was measured.

Twig collections for analysis of secondary metabolites paralleled the water stress sampling program; the same grazed and protected locations (height category × grazing) were sampled. Total tannins were analyzed by the butanol–HCl method. Approximately 300 mg of frozen tissue was ground under liquid nitrogen using a mortar and pestle, and then extracted in 70% acetone (3.5 ml × 3 times). Acetone was removed by passing nitrogen over the supernatant, reconstituted to 7 ml, and filtered (0.45 µm nylon filter). Buffered hemoglobin solution was used as the protein substrate. After the tannin containing willow extract was combined with the hemoglobin solution, unbound protein was read on a Coleman Spectrophotometer at 595 nm. The tannin content was expressed as mg/g dry weight.

Analysis for condensed tannins followed the methods of Porter et al. (1986) and Martin and Martin (1982) with all aspects optimized for each willow species analyzed. Twig and foliage tissue was freeze dried and foliage was separated from the twigs. In order to standardize the amount of twig and foliage tissue analyzed in each sample, 180 mg dry weight of twig tissue was combined with 120 mg dry weight of foliage tissue for each sample. This sample (300 mg) was added to 7 ml H_2O and extracted by sonication for 5 min. An aliquot (0.2 ml) of extract was added to 4.8 ml methanol. One ml of the methanol/H_2O solution was placed in an 8 ml glass vial fitted with a teflon-lined screw cap. Six ml of 95/5 butanol/HCl solution and 0.2 ml of 2% (w/v) of ferric ammonium sulfate dodecahydrate in 2 M HCl was added to each sample. Hydrolysis was carried out in tightly-capped vials by thoroughly shaking and heating in an oven at 95° C for 40 min. Following cooling, the absorbance was determined at 520 nm which was the optimal wavelength for these species. Tannin concentration was calculated by comparing the resulting absorbances to a standard curve of tannin isolated from each willow species (0.02%, w/v in methanol) serially diluted across the concentration ranges known to occur for each species.

Statistical Analysis

Nutritional levels and plant moisture stress were compared among willow height categories and grazed and protected (exclosed) sites with ANOVA ($P < 0.05$). Percent leader use, plant heights, and willow production were normally distributed and were analyzed with ANOVA and regression analysis. Differences in willow use between years, sites, and species, were compared with the non-parametric ranked Friedman 2-way analysis of variance because sample sizes on the permanently-marked utilization transects varied among years (some transects were lost and did not recover after the fires of 1988 or were inaccessible due to flooding some years), and their variances of means were not homogeneous. The Bonferroni approach (Neu et al. 1974, Miller 1981, Byers et al. 1984) was used to calculate experiment-wide confidence intervals on the proportional use of willows of each species by ungulates. Confidence intervals on percent leader use were compared to availability of willow species to evaluate disproportionate use. The terms use, avoided, and expected imply willow use greater than, less than, or equal to availability at the $P = 0.10$ level, respectively. Multiple regression analysis was used to compare percent leader use and annual biomass production with the variables of precipitation, a year effect, ungulate density in the same count unit containing each willow stand, and elevation.

Results

Landscape and Stand Level Observations

Willow herbivory was sampled in 42 browsed willow communities during 3 summers (1988, 1989, 1990) and 4 winters (1987–88, 1988–89, 1989–90, 1990–91). Ten browsed willow communities were classified as suppressed, 11 as intermediate and 21 browsed communities as tall. Suppressed and intermediate browsed stands were more prevalent at lower elevations and tall stands were more common at higher elevations (Fig. 1). Some tall stands, however, also occurred at lower elevations. Annual (summer plus winter) percent leader use varied significantly between years (Friedman test, $P < 0.05$) and was highest during the severe winter of 1989 following the fires of 1988. Summer leader use did not vary between years ($P < 0.05$).

Greater diversity of willow species was observed in taller willow stands (Table 1). An average of only 2.6 ± 0.3 species were found per macroplot in suppressed stands, 3.3 ± 0.3 species in intermediate, and 4.0 ± 0.5 species in tall stands (Mann Whitney U-tests, $P < 0.05$). Bebb and False Mountain willows were found mostly in low elevation, suppressed stands, while Drummond, Farr, and Barclay willows were found mostly in tall stands. Bebb willow reaches greater heights outside of study sites, where specimens 3–4 m in height were observed. False Mountain willow apparently competes poorly for shade in the absence of browsing; False Mountain is less abundant inside exclosures than in adjacent browsed stands (Chadde and Kay 1988, Singer et al. 1995).

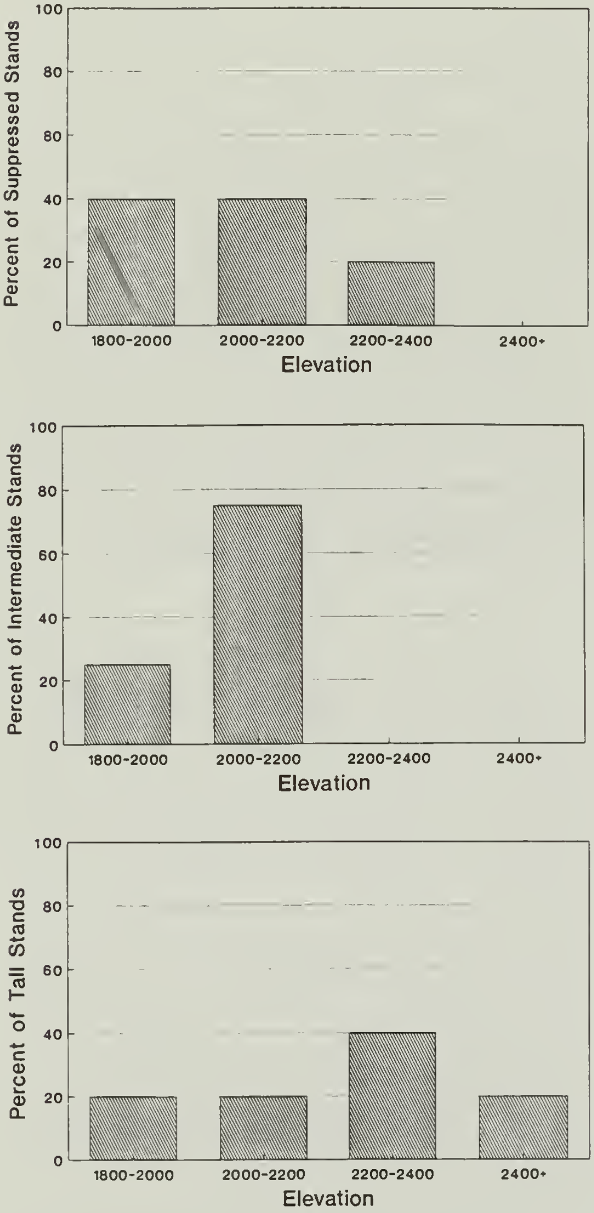

Fig. 1. The percentage of willow stands in each height class (suppressed, intermediate and tall) broken down by elevation. Missing bars indicate that there were no stands of that height class at that elevation.

Our hypothesis was that tall willows on the study area were better defended chemically, and therefore less preferred by herbivores than intermediate or suppressed willows. This hypothesis could only be examined in 3 willows that were found in all 3 height categories; comparatively taller growing Geyer and Booth willows, and the shorter, determinate growing Wolf willow. Browsing preferences varied amongst height categories for these 3 species. Geyer and Booth willows were used less than expected in tall willow stands, greater than expected in intermediate height stands, and greater than or at availability when occurring in height-suppressed stands (Table 1), a trend generally supporting our hypothesis. Wolf willow also was used proportionately less (0.088) in tall stands than in both intermediate and height-suppressed (0.233), but these patterns were not significant (Table 1).

Percent leader use during winter varied among willow species at only 19% of the 52 locations-winters (13 locations × 4 winters, Friedman tests, $P < 0.05$), and all species at a site were therefore pooled for subsequent analysis. Percent leader use varied among the 3 height classes of willows during winter and was greatest for suppressed willows (ANOVA, F = 17.3, $P < 0.001$, Table 2). Length of twig removed (cm), or bite size, was least for suppressed willows (ANOVA, F = 10.6, $P < 0.001$, Table 2).

Ungulate winter densities were higher in the valley bottoms near willow stands ($\bar{x} = 36$ elk/km) than for the northern winter range as a whole ($\bar{x} = 21$ elk/km). Ungulate winter densities were less near tall willow stands ($P < 0.05$, Table 2) compared to the other height categories, but there was no difference between suppressed and intermediate stands ($P > 0.05$).

Suppressed willow twigs were also browsed more in summer ($\bar{x} = 25\%$ leader use) than were intermediate or tall willows ($\bar{x} = 14\%$). Bite sizes were largest during summer on suppressed willows, and least on intermediate willows (ANOVA, F = 74, $P < 0.001$, Table 2). Unbrowsed shoots of suppressed willows were 21% shorter than shoots from intermediate and tall willows (Table 2, $P < 0.05$). Willow bite size relative to current annual growth (CAG) was equivalent in winter among the height classes of willows. Relative bite size during summer was also largest (75% of shoot length) for suppressed willows.

Aboveground willow production varied between years (Friedman test, $P < 0.05$, Fig. 3). Production increased markedly in 1989 following the wettest

Table 1. Proportional availability and use of willow species within willow communities of 3 height categories by ungulates on Yellowstone's northern winter range during 4 winters, 1987–90.

Height category: willow species	No. shoots samples	Proportionate availability	Proportionate use	Use compared availability
Suppressed (High Elevation):				
Wolf	25,481	1.000[1]	.230	[2]
Suppressed (Low Elevation):				
Bebb	2,578	.345	.297	—
False Mountain	2,245	.301	.318	0
Geyer	1,554	.208	.244	+
Booth	1,090	.146	.1410	
TOTAL	7,467			
Intermediate:				
Wolf	8,805	.445	.235	—
Geyer	1,808	.091	.169	+
Booth	9,160	.463	.596	+
TOTAL	19,773			
Tall:				
Wolf	8,820	.095	.088	0
Geyer	12,979	.140	.123	—
Booth	20,399	.220	.175	—
Drummond	40,549	.438	.523	+
Farr	7,796	.084	.059	—
Barclay	2,039	.022	.032	+
TOTAL	92,582			

[1] Only Wolf willow present, no preference analysis conducted.

[2] Bonferroni= 0.10 experiment-wide confidence intervals.

+ denotes use greater than, 0 use at, and - use less than availability, according to the Neu et al. (1974) test. The test was conducted on each height category separately.

Table 2. Ungulate abundance, estimated bite sizes and percent of CAG length removed on browsed shoots in suppressed, intermediate and tall willow stands on Yellowstone's Northern Winter Range 1987 to 1991.

	Suppressed		Intermediate		Tall	
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Unbrowsed shoot length, (cm)	11.8	1.5a	25.2	2.8b	17.9	1.9b
Summer:						
Ungulate species browsing	E,M,D,		M,ED		M	
Percent leader use	25	3a	14	3b	14	2b
Estimated bite size (cm removed)	8.9	1.2a	4.6	0.7b	8.4	1.9a
Approximate % length of shoot removed (unbrowsed length minus cm removed)	75%		18%		47%	
Winter:						
Ungulate species browsing	E,M		E,M,B		M	
Elk and moose density[1]	49	4a	52	3a	8	1b
Percent leader use	59	5a	43	8c	32	3c
Estimated bite size (cm removed)	5.7	0.9a	9.6	1.4b	10.4	1.6b
Average % length of each shoot removed (unbrowsed length minus cm removed)	48%		38%		47%	

[1] Elk and moose density were the combined average of actual counts of the species from fixed-wing aircraft in count units surrounding the sample stands, winters 1987–91. Percent leader use and bite size are described in the "Methods" section.

n = no. of 1 m^2 utilization plots read each season.Ungulate species: E-elk, M-moose, D-deer, B-bison. Different letters indicate a significant difference between height categories (ANOVA, $P < 0.05$).

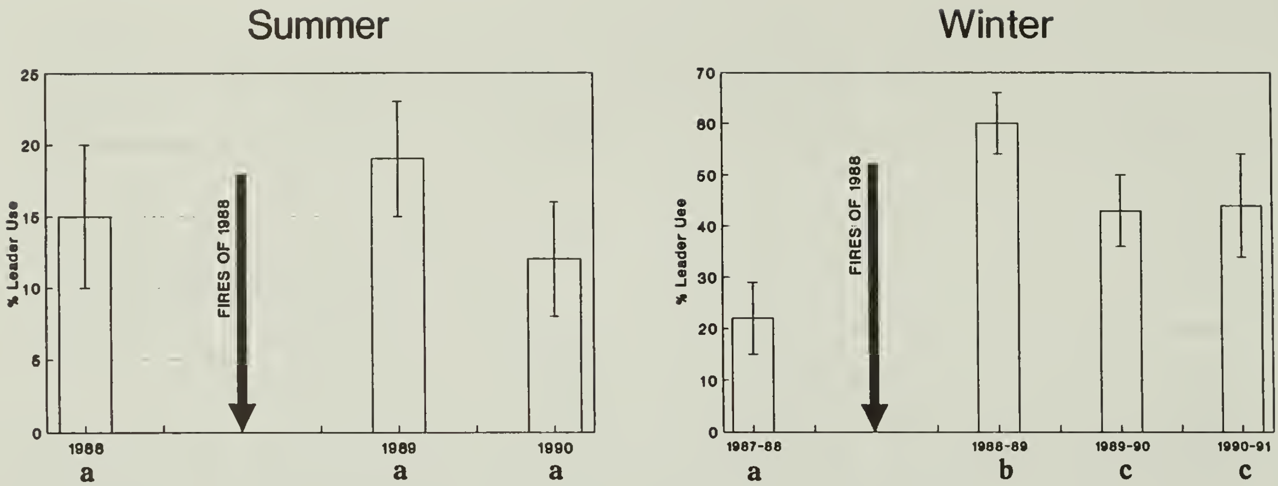

Fig. 2. Percent leader use on all willows summers and winters 1987–88 through 1990–91 on Yellowstone's northern winter range $(\bar{x} \pm \text{SE})$. Different letters denote significant differences in use levels between years according to Friedman test ($P < 0.05$).

winter of the decade, but production was least in 1990 following 2 winters of heavy browsing pressure. Suppressed willows produced only 28% as much biomass as did tall willows, and intermediate willows produced 73% as much biomass as did tall willows (Friedman test, $P < 0.05$, Fig. 3). Formerly suppressed willows, after protection for 31 years inside exclosures, still produced only 35% as much biomass as did tall willows (94 g/m for protected formerly-suppressed willows, n = 60 plots located inside of 4 exclosures, versus 272 g/m for tall willows).

Aboveground willow production increased with increasing elevation and increasing precipitation during the previous year and decreasing ungulate density the previous winter (multiple regression, r = 0.44, F = 5.2, $P < 0.008$). The relation was significant in 1988 (r = 0.67, F = 9.3, $P < 0.001$) and in 1989 (r = 0.94, F = 36.9, $P < 0.001$), but not in 1990 (r = 0.12, F = 0.52, $P = 0.68$). Elevation and precipitation are positively correlated on the northern winter range (Houston 1982), and aboveground biomass was best explained when both elevation and precipitation were used together (r = 0.67, $P < 0.001$). The relationship between biomass and ungulate density during the previous winter approached statistical significance (F = 2.75, $P = 0.11$), but there was no association between willow biomass and ungulate density 2 winters prior (r=.02, F = 0.49, $P = 0.49$). Willow biomass was negatively associated with percent leader use 2 winters before (r = 0.53, F = 23.3, $P < 0.001$).

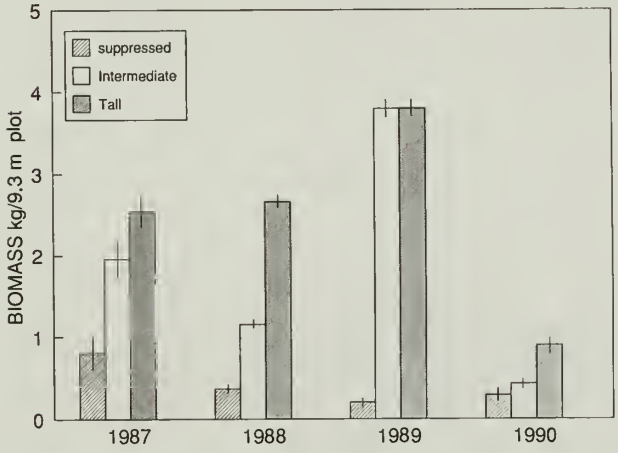

Fig. 3. Annual aboveground production of current annual growth $(\bar{x} \pm \text{SE}, \text{g/m}^2)$ in suppressed, intermediate and tall willow communities, 1988–90, on Yellowstone's northern winter range.

Percent leader use was associated with aboveground willow biomass produced the previous summer, by ungulate density and by year (F = 14.2, $P < 0.0001$). However, only 24% of the variation in leader use was explained by these 3 variables. Percent leader use in the current year was not associated with either bite size (r = 0.02, F = 0.56, $P = 0.46$), or by percent leader use the previous year (r = 0.04, F = 1.19, $P = 0.18$).

Tall willows had higher nitrogen (N) concentration than suppressed willows in 1988 and 1989, and higher *in vitro* digestibility than suppressed willows in 1990 ($P < 0.05$, Table 3). Intermediate willows had higher N concentration in 1990, but lower N concentration in 1988 ($P < 0.05$) compared to suppressed willows. There was a tendency for higher N concentration in the shoots of tall and intermediate willows in comparison to suppressed willows, except

Table 3. Nitrogen concentration and percent dry matter digestibility (IVDOM) of willow shoots from suppressed, intermediate and tall willow stands on Yellowstone's Northern Winter Range, 1988–90. All species values were pooled at a site.

	Suppressed		Intermediate		Tall	
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
1988:						
% N	1.3	0.06 (46)^{a}	1.1	0.05 (32)^{b}[1/]	1.5	0.08 (41)^{b}
% DMD	50.2	1.3	52.9	0.4	52.4	0.9
1989:						
% N	1.4	0.05 (53)^{a}	1.5	1.0 (85)^{a}	1.5	0.06 (19)^{b}
% DMD	48.8	1.5	45.2	2.1	48.9	1.1
1990:						
% N	1.4	0.03 (75)^{a}	1.7	0.08 (53)^{b}	1.6	1.0 (21)^{a}
% DMD	49.3	1.1	48.6	1.3	53.8	0.9*

Different letters indicate a difference between intermediate or tall willows compared to suppressed willows within a year according to Mann–Whitney U tests ($P < 0.05$).

[1/] Includes low protein values from willow individuals that were drought stressed at the Lost Creek site and which later died. 1988 was the most severe summer drought since 1934 in Yellowstone National Park.

() = no. of samples.

for 1988, (a severe drought) when drought-stressed intermediate willow plants had low N values. Low water potentials of –5 to –9 bars were associated with the low N concentrations in drought stressed and dying willows.

Plant Level Measurements

Booth and Wolf willows from tall communities contained higher N concentrations than height-suppressed individuals of the same species (Mann–Whitney U tests, U = 21 and 30, respectively, $P < 0.001$), but no relationship was observed between height class and nitrogen concentration for Geyer willow (U = 78, $P = 0.64$). Nitrogen concentrations in intermediate height Booth and Wolf willows were also less than for individuals from tall communities (U = 13, 3, $P < 0.52$). Percent digestibility was higher in tall than suppressed Booth, Wolf and Geyer willow (U = 37, 56, 14, $P < 0.01$), and digestibility was higher in tall than in intermediate Wolf willow (U = 3, $P < 0.05$).

Significant differences in water potentials were found between browse-suppressed and adjacent protected willows (F = 30.33, $P < 0.0001$), and between locations (F = 7.60, P 0.0008), but interactions were significant (F = 6.94, $P = 0.001$). Unbrowsed Bebb and False Mountain willows showed a greater water stress (xylem pressure potential range = –2.4 ± 0.85 bars) compared to browsed plants (–1.71 ± 0.68 bars), ($P < 0.01$, 2-way ANOVA, Table 4).

Lower water potential were observed for intermediate height willows ($\bar{x} = 2.86 \pm 1.35$ negative bars) than for suppressed willows ($\bar{x}$ 1.71 ± 0.68 negative bars, $P = 0.01$, 1-way ANOVA). Tall and intermediate willows have a larger canopy and leaf surface area and, therefore, a larger demand for water than do suppressed willows. The effects of location (F = 25.74, $P < 0.0001$) and interactions (F = 14.38, $P < 0.0002$) were also significant. Lower water potential readings suggest Wolf and Bebb willows were more vulnerable to drought stress in 1988, which was consistent with observed deaths of these 2 species in 1988 and 1989. No individuals of the other willow species died in 1988 or 1989. Nine percent of the Wolf willow individuals at the Lost Creek site died in 1989, and by 1990, 30% were dead (n = 96). All 8 marked

Table 4. Species differences in negative water potentials (negative bars) between browsing suppressed and nearby protected willow plants (1-way ANOVA).

	Willow Species	
Exclosure Location	Bebb	False Mountain
Junction Butte:		
Suppressed-browsed	1.79 ± 0.4	1.04 ± 0.14***
Unbrowsed	3.38 ± 0.91	2.04 ± 0.45***
Mammoth:		
Suppressed-browsed	2.59 ± 0.38	1.73 ± 0.48***
Unbrowsed	2.5 ± 0.5	2.38 ± 0.53
Lamar:		
Suppressed-browsed	2.27 ± 0.47	0.96 ± 0.14***
Unbrowsed	2.08 ± 0.38	1.3 ± 0.45**

*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$

Bebb willows on a transect in the Lamar Valley died in 1989, the year after the severe drought.

For all willow species combined, height-suppressed willows produced significantly less condensed tannin ($\bar{x} = 39.9 \pm 20$ mg/g dw) compared to intermediate willows (ANOVA, $P < 0.05$, n = 64 tissue samples, 48.2 ± 17 mg/g dw). Since Wolf willow never grows beyond the reach of ungulates, and is chemically better protected (as is the determinant, and slow growing willows *S. lapponum* from Europe, Tahvanainen et al. 1985, an ecological equivalent of Wolf willow), and we excluded Wolf willow from the remaining analyses. *S. lapponum* is unpalatable to mountain hares in Europe and the species is chemically well defended (Tahvanainen et al. 1985). When all species were combined except for Wolf willow height-suppressed willows had lower tannin concentrations (42.7 ± 22 mg/g dw) compared to intermediate and tall willows (50.5 ± 16, 50.5 ± 23, respectively). Intermediate and tall willows were not significantly different from one another at 0.10).

Willow species inside (unbrowsed) the grazing exclosures were compared to willows outside (suppressed-browsed) the exclosures. Browse-suppressed willows produced significantly less condensed tannin (30.3 ± 13 mg/g dw, n = 78) than did protected willows inside the exclosure (38.1 13, ANOVA, $P < 0.05$, n = 23 tissue samples).

Discussion

Levels of large mammalian herbivory on Yellowstone's willows was moderate although ungulate herbivory clearly was the proximate factor in height suppression of willows. All plants (100%) were browsed each winter and about 37% of the current aboveground biomass of willows was removed from suppressed willows. By comparison, moose on Isle Royale browse less individual deciduous shrubs (36–76%) and remove only 3% of the current biomass (McInnes et al. 1992). Higher biomass removals similar to those we observed are sustained by willows and birches elsewhere (Danell et al. 1985, Fox and Bryant 1984).

As predicted by our second hypothesis, many browse-suppressed willows apparently grew on sites with lower growth potential than did tall or intermediate height willows, and thus they were more vulnerable to the effects of large herbivore browsing. Suppressed willows produced only about 28% the aboveground biomass of tall and 38% the biomass of intermediate height willows. Even after protection from ungulates for 31 years, formerly height-suppressed willows still produced only about 35% the aboveground biomass that tall-browsed willows did. We conclude that less-than-optimum growth conditions and lower biomass production coupled with less defense chemistry compounds were factors contributing to height suppression of willows. Willows are capable of rapid height growth, and vigorous willows can escape ungulate browsing in as little as 2–5 years following disturbances such as fire (Wolff 1978, MacCracken and Viereck 1990). Patten (1968) reached a similar conclusion for willows in the Gallatin drainage, Montana. Willows located further from a stream experienced greater mortality from elk browsing, while willows growing in the stream channel survived the same browse pressure (Patten 1968). In the absence of fires and beaver activity for nearly 70 years, competition from sedges and grasses likely has increased to the detriment of willow production.

Three possible explanations exist for the reduced productivity of some willow communities on Yellowstone's northern range. First, Yellowstone's northern winter range very slightly warmer (0.5–1.0° C warmer) and drier (1–2 mm less rainfall annually) this century than during the last century (Houston 1982). A 15-year drought period, 1919–1934, coincided with most of the reported willow declines (Jonas 1955, Houston 1982, Engstrom et al. 1991). Secondly, declines in beaver undoubtedly contributed to localized declines in water tables (Jonas 1955). Thirdly, increased competition from grasses and sedges growing in the abandoned beaver ponds also likely reduces the potential for seedling establishment of willows.

As we predicted, height suppressed willows possessed reduced concentrations of tannins, they were more highly preferred by ungulates, and off-take levels were higher than for taller willows. Browsing mammalian herbivores select forages primarily on the basis of lower concentrations of defense compounds (Bryant and Kuropat 1980, Bryant 1981, Picman et al. 1982, Cooper et al. 1985, Basey et al. 1988), as our data also indicated. Bryant et al. (1983) concluded that defense compounds influenced food selection by vertebrate herbivores more so than did plant nutrients or digestible energy concentrations. A number of studies suggest plant stress lowers defense chemistry and increases palatability of browse. Ruffed grouse (*Bonasa umbellus*), and Capercaille preferentially fed upon water- or injury-stressed woody browse (Guillion 1970, Pullanien 1970). Similar responses are observed with intense clipping or herbivory. Lower resins and lowered tannins were observed in intensely clipped or browsed birch and willow (Reichardt et al. 1984, Chapin et al. 1985, Suter 1991). A substantially larger proportion of height-suppressed compared to tall willows leaves are unshaded and exposed to strong sunlight. Sun leaves, those leaves exposed to strong sunlight, senesce more quickly, export N more quickly, and are preferred by herbivores more than are shade leaves (White 1984).

Lower secondary compound concentrations were apparently of overriding importance in the higher preference for suppressed willows than were nutrients or digestibility. We observed reduced N concentration and lower digestibility in height-suppressed willows on Yellowstone's northern range than for intermediate or tall willows. Ungulates clearly did not select willows based on forage quality. Either or both drought stress or intense browsing may explain the decreased values. Drought stress reduces the N content of grasses and woody browse (Tevini et al. 1983, Hayes 1985). Shoots from severely clipped birches had less N, Ca, Na, and more fiber than unclipped controls; N levels were reduced to only one-third to one-half the level of unclipped birches (Danell and Bergstrom 1987). Intense herbivory or clipping reduced aboveground production, heights, root biomass, dry matter digestibility and N concentrations in shoots of willows and birches (Åhlen 1975, Oldemeyer 1981, Wolfe et al. 1983, Neuvonen and Haukiohja 1984, Danell and Huss-Danell 1985, Danell and Bergstrom 1987).

Water stress per se is not currently a major factor in the height-suppression of willow communities on the northern winter range, and we can not infer that willow declines in the previous century were due to water stress alone. We observed only moderately low stomatal pressure (5 to 9 negative bars) in a number of intermediate-height willow individuals, some of which died following the drought of 1988. The death of many willows this century (Houston 1982, Chadde and Kay 1991), however, suggests that willows on most marginal sites on the northern winter range were likely eliminated well before our study. Additionally, height suppression of willows may alter root:shoot ratios to a more desirable relationship on marginal sites. Welker and Menke (1990) reported a similar situation when severely defoliated oak seedlings demonstrated higher water conductance and a longer growing season due to the removal of transpiring tissues and reduced shoot:root ratios. Georgiadis et al. (1989) also reported improved water status of grazed African grasses. Low biomass production in protected willows provides strong circumstantial evidence that some environmental factor (water stress, competition from sedges and grasses, etc.) has contributed to the height-suppression of willows.

Intermediate-height willows were apparently more vulnerable to water stress than suppressed willows. Significant willow mortality occurred at 2 intermediate stands following the drought of 1988, while no death was observed in height-suppressed willows that year. Intermediate willows are taller, and have more transpiring leaf tissue than suppressed willows, they likely have lower root:shoot ratios and, consequently, they may be more vulnerable during drought than shorter willows with higher root:shoot ratios. Height suppression may permit willows to cope with intense herbivory. Gradual height reduction, readjustments to more favorable root:shoot ratios, survival on wet subirrigated sites (most willows that died, 1920–1940, were probably on the driest sites), and the ability to root sprout might pre-adapt height-suppressed willows on the northern winter range to survival during drought.

Fire suppression this century on Yellowstone's northern range might have contributed to the declines. There is considerable evidence that the northern winter range and adjacent areas was subjected to high fire frequencies (as high as every 25 years), prior to extensive fire suppression about 1900 (Houston 1973, Barrett 1993). Fire stimulates willow production, vigor, and recruitment (Wolff 1978, Gruell 1980, MacCracken and Viereck 1990). More than a century of fire suppression on the northern range increased the distribution and density of conifers and big sagebrush adjacent to willow stands. These invading species might have increased transpiration rates, reduced local water tables and runoff patterns, and reduced soil moisture available to willows. Fire suppression, acting synergistically with fewer beaver ponds, increased competition from encroaching trees and shrubs, and locally reduced water tables, might explain the willow declines.

Height-suppression may permit willows to survive adverse environmental and herbivore influences in the short term (several decades), but severe reduction in heights results in the entire plants within the reach of browsing ungulates, and intense herbivory reduces seed production. Willow catkins are produced only on shoots that were unbrowsed the previous year; most willow seed from northern range willows is produced on unbrowsed crowns that grow above the reach of elk and moose. Reduced seed production, reduced recruitment, and little or no expansion of willow communities has been observed on Yellowstone's northern range over the past several decades (Chadde and Kay 1991). Willows of suppressed height are remarkably persistent and almost no deaths have been observed for the past 3 decades on a series of transects (Singer et al. 1995), but in the absence of recruitment, these stands will eventually disappear. Limited recruitment of willows does occur, even under existing conditions. Willows establish on new sites disturbed by floods (Houston 1982), tall willows that grow beyond the reach of ungulates, or shoots protected in the center of clumps (refugia) still produce seed, while root suckering due to ungulate browsing results in a larger number of smaller willows than in protected stands (Singer et al. 1994). However, willow declines of the magnitude observed this century on the northern range are suggested several times in the pollen record over the past 1,000 years (Engstrom et al. 1991). Extirpation of willows seems unlikely; sufficient willows will likely survive into the next wet and cold period to sustain yet another period of willow abundance.

Conclusions

We conclude that ungulate herbivory alone does not explain the declines and height reductions of willows on the northern winter range. Height suppression of willows was not correlated to wintering ungulate density, at least during our admittedly brief study period (5 years), while formerly height-suppressed willows produced far less aboveground growth and showed no community expansion even when protected from ungulates for 3 decades. Suppressed willows produced less defense compounds, resulting in a higher preference by ungulates and greater relative rates of offtake. Suppressed willows are so highly palatable that large elk reductions to 20–30% of ECC in the 1960's did not reduce percent leader use of suppressed willows (Singer et al. 1995). Willow deaths observed following the drought of 1988 were not correlated to intensity of ungulate browsing. One stand subjected to drought-related mortality was intensely browsed, but the other was not. Both stands were located on dry, marginal sites on higher stream terraces left behind by meandering streams. We speculate that a more xeric climate, lowered water tables, and/or changes in hydrological patterns contributed to the willow declines and changes in chemistry production on the northern winter range, but that the proximate factor in the declines has been intense herbivory by native ungulates. Well designed manipulative experiments might test the relative influences of herbivory, water stress, and burning.

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Differences Between Willow Communities Browsed by Elk and Communities Protected for 32 Years in Yellowstone National Park

Francis J. Singer

Research Division
Yellowstone National Park
Wyoming 82190

and

Natural Resource Ecology Laboratory
Colorado State University
Fort Collins, Colorado 80523

Abstract. Long-term (32-year) measurements of willow (*Salix* spp.) and associated shrubs, including heights, numbers of aboveground clumps, willow cover, and percent leader use of willows were made at four paired unbrowsed (exclosed) and browsed, low elevation willow communities. These stands were browsed mostly by elk (*Cervus elaphus*) during 1957–89 in Yellowstone National Park. These stands were classified as height suppressed, and they represent the most extreme case for browsing effects on the northern range. About one-half of the willow stands on the northern range are classified browsing-suppressed, while the remaining stands are 80–120 cm or taller (Singer et al. 1994). Elk were reduced by park management to <5,000 in the late 1960's, but following cessation of controls, elk increased to about 16,000–19,000 elk by the late 1980's under the park's natural regulation or hands-off management experiment. Willows were 200–400% taller inside exclosures, average individual crown areas were 200–500% larger and, due to much larger canopies and multiple canopy layers, unbrowsed willows produced 400% more biomass per square meter than did browsed willows. Notable trends in associated shrubs included three times more clumps of shrubby cinquefoil (*Potentilla cinquefoil*), a less palatable shrub for elk, were found on browsed sites versus protected sites. Only 45% as many aboveground shrub clumps of willows were tallied inside exclosures compared to adjacent browsed stands ($P < 0.05$), probably because of extensive root suckering in browsed stands caused by the elk herbivory. No willow recruitment occurred within the exclosures, probably because of the extensive shading effects. Numbers of aboveground willow clumps declined at two browsed sites and increased at two other browsed sites, 1957–89. Both willow heights and willow cover increased on browsed transects during the period 1957–89 (11% increase in height; $P < 0.05$), but the height increase (only 6 cm) was probably not biologically important. Percent leader use of willows averaged 65% each winter, biomass removed averaged 31% of annual aboveground production, and most of the willows were suppressed in height by browsing to ≤80 cm. Percent leader use of willows was not statistically different during the 1960's following elk population reductions and in the 1980's when elk numbers tripled following cessation of controls ($P > 0.05$). Bite size averaged 5.7 ± 0.9 cm of twig removed each winter, or about 48% of the average unbrowsed shoot length of 11.8 ± 1.5 cm. Bite size was not recorded in the 1960's, thus hampering direct comparisons of biomass removed. Elk herbivory levels on browsed-suppressed willows near upland exclosures on Yellowstone National Park's northern winter range did not change for the spectrum of elk densities observed. Willows were so rare (<0.1% of the elk diet) during the study period, that no obvious feedback occurred between elk and willows—this relationship was likely different when willows were more abundant and made up a larger portion of the elk diet. Our data suggest that willow can persist for three decades as a height-suppressed member of the vegetation understory subjected to intensive browsing pressure by elk. The continued persistence of height-suppressed willows is problematic, however, because average heights of willows decreased slightly (11%) over the study period ($P < 0.05$), numbers of willow clumps declined at two of four browsed sites over the 32-year period, many other stands have disappeared, and a general lack of seed production and new seedling establishment exists across most of the northern Yellowstone winter range.

Key words: Community structure, elk browsing, willow species composition.

Willow (*Salix* spp.) communities declined by about 50% on Yellowstone's northern winter range this century (Houston 1982). The large size of the northern Yellowstone elk (*Cervus elaphus*) herd has been cited as the cause for declining numbers and biomass of willows and beavers (*Castor canadensis*) and for the reduced heights of willows (Wright 1934; Cahalane 1943; Beetle 1974; Chase 1986; Chadde and Kay 1991). The northern Yellowstone elk herd was culled inside park boundaries, particularly during 1942–67, to benefit winter range conditions, especially willow status (Kittams 1959; Houston 1982). In 1968, the administration of Yellowstone National Park (YNP) implemented a policy of natural regulation of ungulates (Cole 1971; Houston 1976, 1982) and, following cessation of controls, elk numbers increased from less than 5,000 in 1968 to 16,000–19,000 in the late 1980's (Houston 1982; Singer 1991). Elk on Yel- lowstone's northern range consume mostly grasses (73% of diets) during winter, while willows constitute less than 0.1% of the elk diet (Barmore 1980; Singer and Norland 1995). Kay (1990) and Chadde and Kay (1991), however, argued that the lack of tall willows and the near absence of establishment of new willow plants on Yellowstone's northern winter range is a failure of the natural regulation paradigm, although Boyce (1993) countered changes in some rare plant communities are acceptable under natural regulation. The large perturbations in northern Yellowstone elk numbers during the 1950's–90's provide the oppor- tunity to study any correlations between elk densities observed and changes in heights and browse utilization of willows.

Two main hypotheses exist for the large declines in willows on Yellowstone's northern winter range:

1. Elk are overabundant in the park because of elimination of a significant predator (the wolf, *Canis lupus*), human disrupted elk migrations, and more elk concentrating within the park during winter than during historic times—consequently, elk are overbrowsing willows (Chase 1986; Kay 1987; Chadde and Kay 1991).
2. Yellowstone's climate is drier and warmer this century (Balling et al. 1992), and beaver (*Castor canadensis*) declined drastically since the 1920's —consequently, streams are downcuting, local water tables are thus reduced, willow establishment sites are reduced, and willows are less able to sustain high levels of elk herbivory (Houston 1982; Singer et al. 1994).

We examined the long-term trends in elk numbers, willow abundance, and browsing intensity of the northern winter range. Our objectives were to compare browse intensity, height stature, and biomass production of height-suppressed willows protected for 27–31 years and adjacent willows browsed by ungulates. We report on long-term trends in willows during a period when elk densities varied about threefold (from 5/km^2 to 16–19/km^2) across the northern range.

We sampled paired browsed–unbrowsed transects to answer the following questions:

1. Did the reduction to 5,000 elk reduce elk enough to allow browse-suppressed willows to grow taller on the study sites?
2. Does some correlation or feedback between willow use and elk density occur on the study areas?
3. Are any of the vegetation changes proposed by Houston (1976) as evidence for rejection of the natural regulation of ungulates in Yellowstone observed, including
   a. Has shrub species composition been altered to favor less palatable species—that is, has retrogressive succession occurred?
   b. Have willows declined on the study sites? Are willows dying?
   c. Has ungulate herbivory reduced densities of forage plants to low values? Has biomass production or forage quality of willows declined and thereby depleted ungulate food supply?

Study Area

Ungulate exclosures, 2 ha in size, were erected in 1957 and in 1962 within height-suppressed upland willow stands at Mammoth Hot Springs (1 exclosure), Junction Butte (1), and the Lamar Valley (2). Browse-suppressed willows were defined as stands where nearly all plants were 80 cm tall or less (Singer et al. 1994). Roughly 47% of the willow stands on the northern winter range were suppressed in height (Singer et al. 1994). Our study sites represent the extreme case for ungulate herbivory because all of our plots were in height-suppressed willows, and they occur at lower elevations on the northern range where conditions are drier and willows are more exposed to ungulate herbivory because of shallow snows. Permanently-marked belt transects were established in both protected and browsed willow communities in 1958 or 1962.

Annual precipitation at the study sites ranged from 30 to 55 cm (Houston 1982; Despain 1991) and snowfall typically accumulates to depths of 40–60 cm. Elevations of the study sites range from 1,890 to

2,006 m. Nearly all the ungulate activity at the study sites was by elk during the 1957–91 study period (Barmore 1980; Houston 1982; Singer 1991). Densities near the study exclosures during the late 1980's were 16–19 elk/km^2, <0.6 bison/km^2, and <0.1 moose/km^2 (Meagher 1989; Singer 1991; Singer and Norland 1995).

Riparian areas are only 0.4% of the northern winter range (Houston 1982). Most of the northern range is grasslands (mostly *Festuca idahoensis*, *Pseudoroegnaria spicata*, *Koeleria cristata*, and *Poa compressa*) or big sagebrush (*Artemesia tridentata*) —grasslands (55% of the area) and coniferous forests (*Pseudotsuga menziesii* and *Pinus contorta*; 41% of the area). Willow communities are restricted on upland sites to wet springs and seeps, and to streamside areas along rivers and tributaries.

Study sites are dominated by false mountain willow (*Salix pseudomonticola*), Bebb willow (*Salix bebbiana*), Geyer willow (*S. geyeriana*), Booth willow (*S. boothii*), and wolf willow (*S. wolfii*; Dorn 1977). Other shrubs in willow stands are water birch (*Betula occidentalis*), rose (*Rosa* spp.), currant (*Ribes* spp.), shrubby cinquefoil (*Potentilla fruticosa*), and bog birch (*B. glandulosa*). A variety of sedges (*Carex* spp.) and mesic grasses (*Deschampsia caespitosa*) dominate the understories of the willow stands.

Methods

Belt Transect Measurements, 1958–89

Four paired willow belt transects were selected in 1957 or 1962 as nearly similar as possible with respect to pre-treatment site conditions and vegetation (Barmore 1980). One belt transect (1.3 × 25.6 m) was permanently located inside and one outside each of four ungulate exclosures erected in 1957 (three willow exclosures) or 1962 (one willow exclosure). In 1958, after one winter of exclosure, the canopy cover of each aboveground clump of each willow and other shrub species were mapped on graph paper at three sites and mapped at the fourth site in 1962; similar measurements were made at approximately 4-year intervals thereafter (1958, 1962, 1967, 1974, 1981, 1986, and 1989). The experimental treatment was sites (4) × browsing (2) × year (7). The cover of willows and all other shrubs was later estimated by species using the grid method. Aboveground willow clumps were subjectively defined as each cluster of rooted stems separated by ≥0.5 m from one another, although some of these clumps might be connected by root systems. From 1958 to 1967, only willow clumps were recorded, but from 1974 to 1989, the height and species of each aboveground willow clump were also recorded. Pre-treatment differences in the willow communities could be evaluated for the 1962 exclosures because shrubs were sampled at the time of fence construction, but measurements were not taken until the next growing season (1958) for exclosures erected in 1957, therefore, one winter of treatment effects was missed for the 1957 exclosures.

ANOVA was inappropriate for the permanently-marked belt shrub transects, because they were not randomly placed in 1957 or 1962. However, these belt transects represent a potentially valuable data set, because they were consistently sampled during such a lengthy period (32 years). Repeated measures analysis (Potvin et al. 1990; Eberhardt and Thomas 1991) was conducted on data gathered from these transects. Data were logarithmically transformed as suggested by Eberhardt and Thomas (1991). We proceeded with the Multivariate Pillai's trace test for cover and heights, because it is less stringent for small sample sizes (Potvin et al. 1990).

Percent leader use of all willows by elk on the same permanently marked browsed belt transects was recorded annually during both summer and late winter periods 1963–1969 (YNP files, Mammoth, Wyoming 82190) and during 1987–91 (n = 5 years). Percent leader use was obtained by counting the number of browsed shoots or leaders (n_1) ÷ the number of unbrowsed shoots (n_2) and multiplying their quotient by 100 ($n_1/n_2 \times 100$). Height (cm) of the tallest live shoot in each clump was recorded. All measurements used in the analysis were taken at the end of the winter (late April–early May) and before leaf emergence summed the previous summer's and winter's browsing. One browsed belt transect could not be relocated in the 1980's. Mann-Whitney U-tests were used to compare percent leader use rates and willow heights between the two periods, 1963–69 versus 1987–92. Ungulate densities were estimated annually using fixed-wing aircraft (Super Cub) surveys each winter in each of 66 count units on the northern winter range as described in Singer et al. (1989) and Singer (1991). The ungulate count units surrounding each willow site were 30–50 km^2 . Two or three aerial surveys of the entire northern winter range were conducted each early winter (December– January) during 1986–91. Minimum elk densities based on actual counts, which likely underestimate elk (Singer et al. 1989), were calculated for each count unit surrounding each willow site because elk visibility corrections were not available for the 1960's period.

Biomass and Willow Measurements From Circular 9.3-m Plots, 1986–90

Willow species abundance and production were measured during late summer 1986 at the same paired browsed and unbrowsed sites but using a different sample design. Randomness of plot location and replication ($n = 15$) of plots within each treatment at each location were incorporated into this design. In each 9.3-m^2 macroplot, the species of each shrub clump, the height of the tallest live leader, the widest shrub crown diameter, and the perpendicular shrub diameter were recorded. Percentage dead portion of each willow was estimated. On every fourth shrub of each species, the number of rooted stems, the number of shoots per stem, the length, height, the basal diameter of current annual growth (CAG), and the diameter at the tip or browse point of 10 randomly selected shoots were recorded. Measurements of shoots were gathered on the same stands in 1987–90.

The tallest leader (cm), the widest crown diameter, the perpendicular crown diameter, and percent dead for each aboveground shrub clump within each plot were measured. We recorded any beaver dams or cuttings and any snowshoe hare (*Lepus americanus*) or cottontail (*Sylvilagus nuttalli*) browsing activity. None were observed on the study plots.

Willow height, cover, crown area, and percentage of dead willows were compared with a 2-way ANOVA (browsing and location) from the 1986 plots. Tukey's multiple range tests are reported for paired sites for those cases with a significant main effect. Data from each 9.3-m^2 plot at each location ($n = 4$) were treated as samples ($n = 15$) of the treatments (browsing) for each location. Data from the two Lamar Valley study sites did not differ and are pooled. Plots were 5–15 m from each other, and because excavated rhizome systems averaged 0.3– 1.3 m, we concluded each sample plot likely included different willow individuals from individuals on all other 9.3-m^2 plots. Plots therefore represented a degree of independence (but recognizing that within each 9.3-m^2 plot some clumps were from the same willow individual(s)).

Bite size by ungulates was estimated for browsed twigs following the method of Pitt and Schwab (1990). Bite size in winter and summer was calculated with the formula

$$BS = \frac{100(Dp - Dt)}{Db - Dt}$$

where BS = bite size, Dp = twig diameter at the point of browsing, Db = basal diameter of browsed twig, and Dt = mean diameter of a representative sample of unbrowsed twig tips (Pitt and Schwabb 1990). This equation differed from bite size determined by twig length differences by only 4–6% (Jensen and Urness 1981) and it accurately predicted bite size for 4 of 6 shrub species (Pitt and Schwab 1990). Bite size was not recorded 1963–69 (Barmore 1980 op. cit; YNP files) and, therefore, we could not compare bite size between the two study periods.

Forage quality was sampled from Booth, Bebb, and False Mountain willow from the same paired browsed and unbrowsed willows during August 1991. At each browsed and unbrowsed location, a minimum of 5 g of stem and leaf sample were taken from six randomly selected shrubs. Twigs were gathered from the primary browse zone about 1 m aboveground on all shrubs. Samples were oven-dried for 48 h at 50–60° C. Percent crude protein (Association of Official Analytical Chemists 1970) and in vitro digestibility (Tilley and Terry 1963) were analyzed at the Nutritional Analysis Laboratory, Colorado State University.

Production estimates were calculated for each willow species in each treatment at each willow location using the methods of MacCracken and Viereck (1990) following Telfer (1969) and Oldemeyer (1983). Average twig weight was calculated from linear regressions of dry weight (dependent variable) against twig length and basal green twig diameters at the base of the current annual growth (independent variables, MacCracken and Viereck 1990). Log–log prediction regressions were calculated only for the four common willows. Separate regressions were calculated for each willow species each year and each season (winter, summer) because the regressions varied between seasons and years. The R values were high for the predictive equations (range $R = 0.78–0.97$; $R, \bar{x} = 0.87$, SE = 0.13; $n = 19$) and the plots of the residuals followed a normal distribution. The biomass of each willow species was estimated from the predicted twig weight using the regressions × average number of twigs per plant × the number of shrubs per plot. Leaves were included in the summer twig weights; the presence of leaves likely accounted for the summer–winter differences in the regressions.

Results

Elk Density Compared to Leader Use on Willows

Winter elk rangewide populations averaged about 7,000 (i.e., 7/km^2) during the 1963–69 sampling period and 16,000–19,000 (16–19/km^2) during the

1987–89 study period (Houston 1982; Singer 1991), an increase of about 240% after elk reductions were discontinued (Fig. 1).

Elk densities in count units that included the riparian study sites averaged 36/km^2 (1986–91) or about double the average density for the entire northern range (16–19/km^2). The willow study sites were in the broad, valley bottoms where elk found lesser snow depths in winter. No moose were observed in the study count units during the winter flights. We observed no moose or bison browsing of the study sites during a 6-year period, 1986–1991, although both ungulates browse willows elsewhere on the northern winter range.

Percent leader use of height-suppressed willows did not vary between sampling locations ($P > 0.05$) and locations were pooled in subsequent analysis. Percent leader use averaged 67.1 ± 4.4 ($\bar{x}$ ± SE) in the 1960's and 64.4 ± 2.1 during the 1980's; these differences were not significant (Mann-Whitney U-test, U = 107, $P > 0.05$). Leader use was consis- tently high, ranging from 50–89% over all years on browsed transects. Heights of willow clumps located on these transects were 11% shorter in the 1980's ($\bar{x} = 45.2 \pm 1.8$ cm; $\bar{x}$ ± SE) than during the 1960's ($\bar{x} = 50.5 \pm 2.3$ cm, $n = 250$ individuals per year, U = 187, $P < 0.05$).

Bite sizes during winters 1987–1991, (5.7 ± 0.9 cm) averaged about 48% of the average unbrowsed shoot length (11.8 ± 1.5 cm). Bite size did not vary among the 3 winters, 1987–90 ($P > 0.05$). Approximately 31% of the annual biomass produced was removed by elk each winter during the late 1980's. Bite size was not measured during the 1963–69 period, making comparisons of biomass removed impossible between the two periods.

Long-Term Willow Trends, 1958–89

Density of aboveground willow clumps increased about 80% on the Mammoth browsed transect by 1965 due to root suckering, but then density declined by 1974 to levels recorded in 1958. There were 32% fewer willows on browsed transects at Mammoth and 42% fewer at Lamar at the end of the study period, but there were 31% more at Junction Butte. Numbers of aboveground willow clumps declined an average of 25% (all 4 sites pooled) on unbrowsed sites between 1958 and 1989, whereas heights of willows increased about 620% on unbrowsed transects during 1958–89. Maximum willow heights were apparently reached about 1981 on unbrowsed transects. Shading by adjacent willows increased greatly inside exclosures during the 32 years of protec- tion, due to the large increases in willow heights and canopy sizes.

Willow cover increased 130% on unbrowsed sites during the 27–31-year period, but willow cover also increased 220% on browsed sites during the same period (Fig. 2). Height and cover differed significantly on the belt transects due to browsing (Pillai's trace, $F = 25.9, 34.1$, $P < 0.001$) and year ($F = 52.6$, $P < 0.001$), but location was not significant ($F = 1.4$, $P = 0.24$). There were no interactions ($P = 0.10$).

Willows were not equivalent in size at the time of the first readings. Willows on sites selected for browsing treatment were less abundant, and had less cover than exclosed willows at the time of exclosure at Junction Butte (Fig. 2). Fewer willow clumps, and shorter willows occurred in the Lamar and Mammoth browsed sites than paired protected sites at the time of the first readings, but these differences might have been due to one winter of exclosure (1957–58) before the

Table 1. Number of aboveground clumps of willows per 9.3-m^2 plot on browsed and nearby unbrowsed sites on Yellowstone's northern winter range ($\bar{x}$ ± SE) in 1986. Differences due to browsing and location were tested using a 2-way ANOVA. Data from the two exclosures at the Lamar Valley location are pooled in the presentations.

	Mammoth				Junction Butte				Lamar			
	Unbrowsed		Browsed		Unbrowsed		Browsed		Unbrowsed		Browsed	
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Bebb willow	2.7	0.3	5.9	0.8**	3.5	0.5	9.1	1.0**	1.3	0.3	7.6	2.1*
False Mountain willow	0.4	0.2	2.9	0.7	5.5	0.5	3.2	1.0*				
Geyer willow					1.1	0.3	0.6	0.3	0.8	0.4	1.4	0.8
Booth willow									0.8	0.4	2.2	1.6
Shrubby cinquefoil					4.1	0.7	7.7	1.1**	0.6	0.3	2.7	0.7**
Rose									1.8	0.8	2.5	0.9

$^*P < 0.05$, $^{**}P < 0.01$ indicates a difference due to grazing.

Sample size was insufficient for statistical analyses for *Betula occidentalis*, *B. glandulosa*, *Ribes* spp. and *S. wolfii* at any site, and shrubby cinquefoil at the Mammoth location.

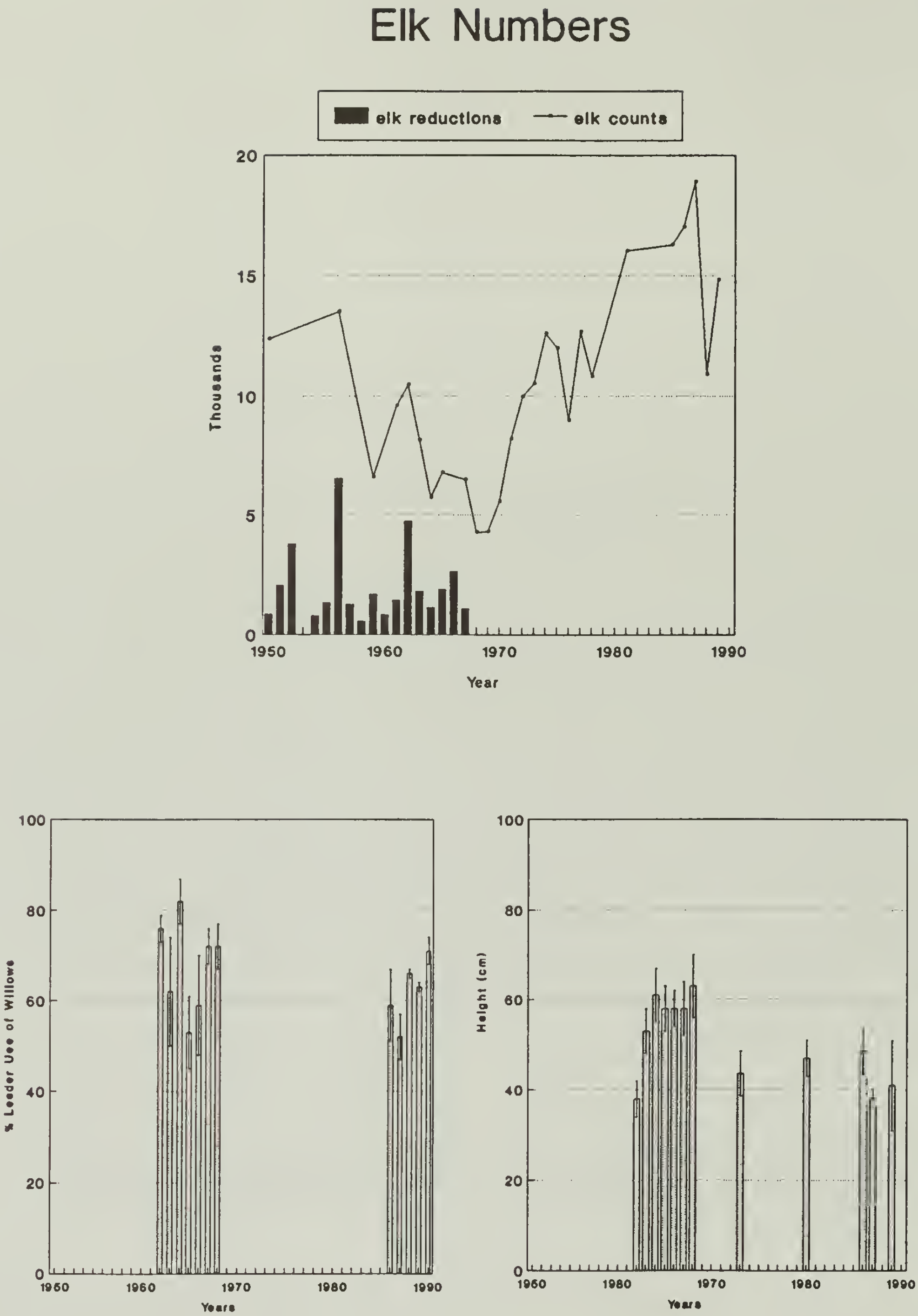


Fig. 1. Elk counts, numbers of elk harvested, and percent leader use of willows and willow heights ($\bar{x} \pm$ SE) on five permanently marked 46.5-m^2 transects on Yellowstone's northern winter range, 1950–1991. No willow-use data were gathered before 1961 or between 1969 and 1985.

first readings were made in 1958. Cover values were nearly equivalent at the time of first readings at Lamar and Mammoth.

Effects of Browsing on Willow Communities
Structure and Composition

Browsing and location treatments significantly influenced total numbers of Bebb willow at all exclosures, with a significant interaction effect (F = 42.8, 15.4, 4.9, for the 3 willows, interactions F = 3.3, 6.2, $P < 0.01$; Table 1). Fewer aboveground Bebb willow clumps ($\bar{x} = 2.5$) were sampled on unbrowsed plots than on browsed plots ($\bar{x} = 7.5$; $P < 0.001$). Browsing, however, did not influence the numbers of false mountain willow, Geyer willow, or Booth willow clumps ($P > 0.05$). Approximately 66% fewer shrubby cinquefoil clumps (suspect to represent individuals) were found on unbrowsed than browsed sites ($P < 0.01$).

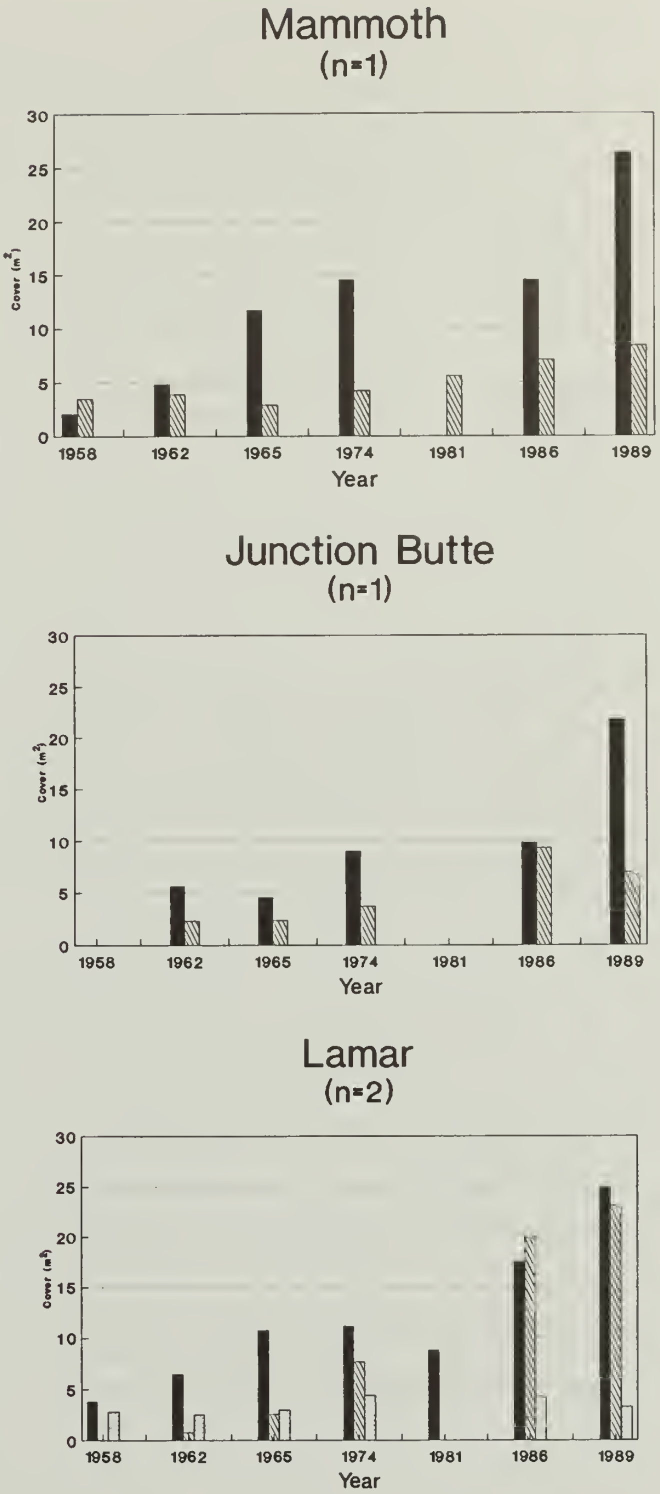
Shrub species diversity was not influenced by browsing. An average of 3.3 shrub species was found on each plot in both browsed and unbrowsed willow communities ($P > 0.05$).

Willows were 200–400% taller on unbrowsed compared to browsed sites ($P < 0.01$). Bebb and Geyer willows were taller on both browsed and unbrowsed plots at the Lamar exclosure site where elevation was higher and precipitation was greater, but false mountain willow followed the opposite trend and was taller at the lowest elevation exclosure site located at Mammoth ($P < 0.05$). Ungulate herbivory did not influence the heights of shrubby cinquefoil or roses, and location did not influence the heights of roses ($P > 0.05$).

Crown areas of individual clumps of willows and roses were 200–500% larger in protected stands ($F = 38.0, 31.6, 7.8, 26.9$, and 9.4 for Bebb, False Mountain, Geyer and Booth willow, respectively, all were $P < 0.001$), but browsing did not influence crown areas of shrubby cinquefoil ($F = 2.3$, $P = 0.13$). Because some willow clumps within a plot were one individual, we pooled percent cover for each species within each 9.3-m^2 plot. Following pooling, total canopy area averaged 390% more on unbrowsed than on browsed sites for False Mountain willow, 510% more for Geyer willow, 220% more for Bebb willow, and 610% more for Booth willow. Aerial canopy area does not adequately compare browsed and unbrowsed willows since the much taller unbrowsed willows had multiple canopy layers; biomass production better compares the two treatments for willows.

Ungulate herbivory stimulated shoot sizes on the study plots. Browsed shoots were 8% larger in diameter, 74% longer, and 265% heavier than unbrowsed shoots (Table 2). In spite of larger shoots, suppressed-browsed willow stands produced only about 24% ($\bar{x} = 213$ g/m^2) as much biomass as did unbrowsed stands (876 g/m^2), reflecting the much taller and larger canopies and greater number of shoots on unbrowsed willows.

Frequency distributions by heights differed between browsed and unbrowsed willow communities for Bebb, False Mountain, and Geyer willows (Kolmogorov-Smirnov test, $D = 0.63, 0.45, 0.38$, respectively, all $P < 0.01$). More individuals occurred in the shortest class (0–50 cm) on browsed sites, and more individuals occurred in the three tallest classes on unbrowsed sites. More shrubby cinquefoil occurred in the shortest classes (0–40 cm) and in the tallest height class (>81 cm) on browsed sites versus unbrowsed sites.


Mammoth
(n=1)

Junction Butte
(n=1)

Lamar
(n=2)

Fig. 2. Total cover (m^2 of cover per 46.5-m^2 transect) on permanently marked belt transects at four exclosure locations on Yellowstone's northern winter range, 1958–1989. *Blanks* indicate that no data were gathered that year or that the transect was not yet in place. Key: ■ = browsed; ▨ and ⊡ = protected.

Table 2. Twig measurements and estimated biomass produced in browsed and unbrowsed shrubs on Yellowstone's northern winter range in 1987. Biomass per 9.3-m^2 plot was estimated from methods following MacCracken and Viereck (1990), and was calculated with the formula: twig weight (from regression of diameter and length) × twigs per plant × plants per 9.3-m^2 plot ($n = 15$ plots/site).

	Twig diameter (cm)				Twig length (cm)				Twig weight (g)				Estimated biomass (g/m)	
Exclosure location	Unbrowsed		Browsed		Unbrowsed		Browsed		Unbrowsed		Browsed			
Plant species	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	Unbrowsed	Browsed
Mammoth														
Bebb willow	0.15	0.01	0.15	0.01	6.1	0.6	9.2	0.9**	0.19	0.02	0.31	0.04**	506	102
False Mountain willow	0.14	0.01	0.17	0.01	14.0	0.8	16.9	0.7	0.61	0.06	0.40	0.05	437	44
Water birch	0.18	0.01	0.19	0.01	10.4	1.3	6.9	0.7	0.29	0.04	0.23	0.02	97	6
Junction Butte														
Shrubby cinquefoil									0.09	0.02	0.08	0.01	10	20
Bebb willow	0.18	0.01	0.1	0.01	9.9	1.3	7.9	0.9	0.24	0.03	0.20	0.03	371	61
False Mountain willow	0.14	0.01	0.1	0.01	4.7	1.3	15.9	1.4**	0.18	0.01	0.41	0.05**	252	47
Geyer willow	0.16	0.01	0.1	0.01	9.29	1.0	11.8	1.1	0.18	0.03	0.25	0.03**	96	10
Lamar														
Shrubby cinquefoil	0.11	0.01	0.11	0.003	5.1	0.9	6.7	0.5	0.14	0.03	0.16	0.02	10	45
Bebb willow	0.08	0.03	0.20	0.09**	2.3	0.4	18.8	1.0**	0.10	0.09	0.78	0.08**	634	92
False Mountain willow	0.20	0.04	0.23	0.01	9.4	1.1	19.1	1.3**	0.19	0.02	1.09	0.11**	23	184
Geyer willow	0.19	0.05	0.22	0.01**	6.6	1.1	22.6	1.4**	0.13	0.09	0.65	0.07**	100	13
Booth willow	0.13	0.02	0.22	0.01**	12.1	3.5	21.2	14.3**	0.11	0.01	1.94	0.24**	91	16

*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$ difference between control and browsed willows according to 1-way ANOVA's.

Forage Quality of Browsed and Unbrowsed Willows

Ungulate herbivory significantly reduced protein and digestibility concentrations in two species of willows but increased forage quality in a third species. Percent protein concentration was 9% less in browsed False Mountain and 10% less in browsed Booth but 15% greater in browsed Bebb willow compared with unbrowsed plants (Table 3). Digestibility was 7% less in browsed False Mountain and 8% less in browsed Booth but 11% greater in browsed Bebb willow compared to unbrowsed plants.

Discussion

Browse-suppressed willows were only slightly taller (11 cm) during the period of elk reductions, but there was no difference in percent leader use when compared to the 1980's when elk densities were higher. During the latter period, elk consumed about 31% of the annual aboveground biomass of height-suppressed willows on Yellowstone's northern range. Biomass removed could not be estimated from the 1960's data since bite sizes were not measured then. We suspect bite sizes did not differ dramatically since mean heights of willows differed by only 11 cm between the two periods.

Several possible explanations might account for a lack of correlation between elk densities and willow percent leader use during the two periods: (a) Willows were already reduced to such a rare community type by the beginning of the study (1957), that no feedback between elk densities and willows could be observed, (b) elk habitat use and habitat preferences might not be linear with elk densities, (c) elk might have increased their use of willows, aspen and other riparian areas as hiding cover during the reductions to avoid humans, and (d) elk were not reduced sufficiently during the 1960's to reach some threshold value that would have allowed willows to grow taller.

Numbers of long-term willow transects were inadequate to determine trends for willows on the

Table 3. Percent protein and digestibility for current year's willow shoots compared between browsed willows and willows protected for 28–32 years. Differences were tested with a 2-way ANOVA (browsing × location), $*P < 0.05$. No interactions were significant.

Nutritional constituent value	Willow Species		
	Bebb	Booth	False Mountain
% Protein			
r^2	0.38	0.19	0.55
Area effect			
$F =$	0.13	0.07	15.25
$P =$	0.87	0.93	0.0001*
Browsing effect			
$F =$	14.12	4.73	4.91
$P =$	0.0007*	0.04*	0.03
$\bar{x}$ Browsed	9.93	8.77	9.36
$\bar{x}$ Protected	8.63	9.78	10.28
DMD			
r^2	0.58	0.41	0.75
Area effect			
$F =$	9.08	1.63	40.21
$P =$	0.0008*	0.22	0.0001*
Browsing effect			
$F =$	15.73	11.21	8.25
$P =$	0.0004*	0.0038	0.007*
$\bar{x}$ Browsed	49.86	43.81	46.79
$\bar{x}$ Protected	45.09	47.71	50.27

northern range since 1958, although large scale declines in willows before 1950 are well documented (Houston 1982; Kay 1990). The data from four study sites were inconsistent; density of aboveground willow clumps increases on two transects but declined on two other transects. Average heights of willow clumps declined 6 cm on the average, suggesting a slow decline in stature. Willow cover increased on browsed transects 220% over the time period, primarily due to root suckering of browsed clumps, but the browsed clumps were very small aboveground clumps. Little or no willow seed was produced on these browsed clumps. As expected, heights and canopy sizes of willows increased dramatically in unbrowsed sites over the time period, but the numbers of individuals declined due to increased competition for light and self-thinning. Browsed willows produced larger shoots, as Bergström (1983) also observed, but this did not compensate for much larger canopy sizes, multiple canopies, and many more shoots inside exclosures. Consequently, browsed stands produced only about one-quarter the aboveground biomass per unit area of unbrowsed stands. Willows unbrowsed for 32 years inside the exclosures also produced abundant seed (Kay 1990). The criteria of Houston (1982:5) for substantial changes in willow communities because of elk herbivory were met; biomass production of height-suppressed willows was severely curtailed—although production of taller browsed stands on the northern range is not (Singer et al. 1994).

Willow species composition differed little between browsed and unbrowsed sites, but shrubby cinquefoil individuals were 300% more abundant on browsed sites. Shrubby cinquefoil is less preferred by ungulates than willows on the study area (Singer and Norland 1995). An increase of shrubby cinquefoil may indicate, as originally hypothesized, an increase in less palatable species. Shrubby cinquefoil is shade intolerant, however, and its increase on browsed sites may also be explained by less competition for light from height-suppressed willows on browsed sites.

Suppressed willows of the northern winter range may exist on sites of inherent low productivity; willows protected for 28 to 32 years still produced only one-third the biomass of taller, browsed willows located elsewhere (most at higher, more mesic locations) on the northern range (Singer et al. 1994). Moose herbivory equivalent to or greater than that observed on the plots are sustained by willows and birches in Alaska and Sweden with no documented short-term effects (Danell et al. 1985; Fox and Bryant 1984). Also, slightly warmer (0.5–1.0° C) and drier (1–2 cm less rain) conditions on the northern Yellowstone winter range this century may have contributed to the willow declines (Houston 1982). Summer temperatures were warmer, and January–June precipitation less this century than last in Yellowstone National Park (Balling et al. 1992).

Nutritive values were lower in browsed than unbrowsed willows in our study area, an observation supported by Neuvonen and Haukioja (1984) and Danell et al. (1985). Digestibility of browsed willows in Yellowstone were similar to (about 47%) and protein concentrations were higher (9.4% versus 5.2%) than willows sampled by Hjeljord et al. (1982), however, suggesting browsing suppressed willows of Yellowstone's northern range should still be highly palatable to ungulates.

Everywhere in North America where willows are protected by exclosures on ungulate winter ranges, the protected willows are substantially taller than their browsed counterparts (Bédard et al. 1978; Chadde and Kay 1988; Schulz and Leininger 1990); that is, shrubs inside exclosures do not represent the natural appearance of shrub communities (Gruell 1980). A suppressed growth form of willows due to persistent browsing was regarded as the historic norm in Jackson Hole, Wyoming (Gruell 1980). Although willow abundance and stature were maintained on some of our study sites between 1958 and 1989, reduced willow seed production (Kay 1990), limited new seedling recruitment, and little new willow establishment has been observed on the study sites (Houston 1982; Chadde and Kay 1991). Our data indicate browsing-suppressed willows can maintain height, cover, and numerical abundance on some sites even over three decades of intense ungulate herbivory. Willow stands have disappeared from many sites on the northern winter range, however, and the continued existence of height-suppressed willows in the study area is a problem because of the near absence of recruitment.

Considerable evidence exists to support both of the stated hypotheses for the declines in willows. We were unable, however, to gather evidence to reject one hypothesis in favor of the other. Considerable evidence exists that the northern Yellowstone winter range is warmer and drier this century (Balling et al. 1992). Localized beaver declines were dramatic (Warren 1926; Jonas 1955) in the early part of this century—a period that corresponds to most of the disappearance of willow stands (Houston 1982; Engstrom et al. 1991). Elk also increased dramatically several times this century, and elk concentrated within the park boundaries because of hunting (the boundary line fence effect) and human developments outside the park (Houston 1982). Suppression of the elk population resulted from unrestricted overharvesting for market hunting in the late 1800's, but elk subsequently increased during 1919–1930's following complete protection within the park and the elimination of wolves. Elk numbers then declined with artificial culling (1936–67), then increased dramatically following cessation of artificial controls (1968–1988—prefire; Houston 1982; Singer 1991).

The first period of elk increase coincided nearly exactly with a period of extended drought (1919–36) and beaver declines (1920's–40's) making it impossible to separate the relative effects of elk herbivory, climate, and water tables on willow status. Interpretation of the data sets was confounded because elk were both under- and overpopulated in relation to estimated environmental capacity. Elk were underpopulated at densities below computer model estimates of ecological carrying capacity (Houston 1982; Garton et al. 1990; Boyce 1993) twice during the past century (1880's–1910's, 1936–67) because of human controls and were likely overpopulated during the 1980's study period because of absence of human controls. Computer models suggest there would have been 8–25% fewer elk during the 1980's if wolves were fully recovered into the area (Garton et al. 1990; Boyce 1993; Mack and Singer 1993). No similar large park ecosystem occurs at the same latitude with wolves for comparison. The reintroduction of wolves to the northern Yellowstone winter range is currently under way (April 1995), which will provide a test of the elk density hypothesis (Peek 1980). Without similar unhunted, control park ecosystems (with wolves and no climate change), or without purposeful, well-designed experiments, the Yellowstone ungulate management experiment remains largely untestable as Kay (1990) and Chadde and Kay (1991) have pointed out.

My data suggest a third, related hypothesis— the secondary, defense chemistry hypothesis. I propose that height-suppressed willows will always be heavily browsed across a fairly wide range of elk densities because of reduced defense chemistry and a reduced biomass potential under existing climate conditions. In support of this hypothesis, I observed consistently higher ranges of ungulate browsing of height-suppressed willows, across a wide range of elk densities. In addition, lower tannin and phenolic concentrations were observed in height-suppressed versus both tall–browsed and tall–unbrowsed willows (Singer et al. 1994), and reduced biomass potential in height-suppressed willows occurred under existing conditions. Height-suppressed willows produced only one-quarter the aboveground biomass production of protected willows and only one-third the biomass of tall-browsed willows, thereby reducing their ability to recover tissues following ungulate herbivory. The proximate factor in the reduction of the stature of many willows is clearly high levels of herbivory by elk of northern Yellowstone (Houston 1982). If wolves had dampened the more extreme population fluctuations of elk in Yellowstone (Gasaway et al. 1986; Boyce 1993), willows might not have been subjected to periodically high impacts from elk in historic times.

Management Implications

The largest changes in willow abundance (≥50% decline) on the Yellowstone northern winter range occurred before the study period (Houston 1982). My observations should be qualified, in that willows were already reduced to a rare plant type (<0.1% of the elk diet) by the time of my study. I could find no correlation between percent leader use or status of height-suppressed willows and rangewide elk densities, during the study period, 1957–89, except average heights of browsed willows were slightly taller (6 cm) during the period of reductions. Perhaps elk numbers were not reduced low enough or long enough to result in a willow response.

No obvious change in species composition of the willow stands were observed during the study period, 1957–89, with the single exception that shrubby cinquefoil increased dramatically on browsed sites. This might be a browsing response (shrubby cinquefoil is relatively less palatable to elk), but also the species is shade intolerant, and may increase where willows are short.

I could not conclude willows trends from the browsed study plots, since the trends were not consistent. Willows increased on two browsed transects but declined on two other transects. However, the disappearance of many other stands, the lack of seed production, and the lack of new willow establishment, suggest that willows have continued to decline on the study area.

Two hypotheses for the decline in willows, the overabundant elk hypothesis and the warmer–drier climate hypothesis, are both well-supported. I was unable to reject one in favor of the other. No similar park ecosystem exists as a control (with wolves but no climate change), and no well-designed experiments (reintroduce wolves, manipulate water tables) have yet been conducted. I suggest that reduced chemical defenses in height-suppressed willows combined with a reduced biomass potential, both due to climate and water table reductions, act to keep willows in a heavily browsed and height-suppressed condition across a wide range in elk densities. I am conducting water level and clipping experiments (with R. Cates) to test the latter hypothesis.

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Physiological Assessment of Winter Nutritional Deprivation in Elk of Yellowstone National Park

GLENN D. DELGIUDICE,[1] U.S. Veterans Affairs Medical Center, Research Service, Minneapolis, MN 55417, and Department of Fisheries and Wildlife, University of Minnesota, St. Paul, MN 55108
FRANCIS J. SINGER, U.S. National Park Service, Yellowstone National Park, WY 82190
ULYSSES S. SEAL, U.S. National Veterans Affairs Medical Center, Research Service, Minneapolis, MN 55417, and Departments of Biochemistry and Fisheries and Wildlife, University of Minnesota, St. Paul, MN 55108

Abstract: During 13 January–29 March 1988, we assessed the extent of nutritional deprivation in cow elk (*Cervus elaphus nelsoni*) groups on the lower, middle, and upper Northern Range and at Madison–Firehole Range in Yellowstone National Park by 4 sequential collections and chemical analyses of urine excreted in snow (snow-urine). Associated changes in elk density and calf:cow ratios also were estimated during early and late winter or spring. Decreasing ($P = 0.0001$) potassium:creatinine (K:C) ratios throughout winter and increased ($P = 0.0001$) urea nitrogen (U:C) on all 4 areas indicated progressive nutritional deprivation and increasing net catabolism of lean body tissue, respectively. These ratios also varied among the 4 sampling areas during early ($P = 0.0001$) and late winter ($P < 0.005$). Low sodium:creatinine (Na:C) indicated low sodium availability on the Northern and Madison–Firehole Ranges throughout winter. Comparison of U:C and K:C data to those of supplementally fed captive elk and winter-killed elk permitted classification of the physiological status of Yellowstone elk relative to nutritional deprivation. Nutritional deprivation across the Northern Range and at Madison–Firehole was associated with significant ($P < 0.05$) declines in calf:cow ratios from early to late winter. Throughout winter, snow-urine samples with metabolite profiles indicative of severe energy deprivation and accelerated degradation of lean body tissue were most apparent in areas associated with increased elk density and/or deeper snow cover.

Elk are the most abundant ungulate in Yellowstone National Park (NP) and are a principal tourist attraction. During winter, 2 principal herds include 17,000–22,000 elk on the Northern Range (Houston 1982, Singer 1991) and an additional 800 elk on the Madison–Firehole Range in the interior of the Park (Cole 1983).

Management of the Park's elk herds has remained controversial throughout this century (Skinner 1928, Kittams 1959, Chase 1986). Park policy included winter feeding until 1945. Herd reductions were conducted as a means of regulating population size, but this practice was discontinued in 1968 (Houston 1982). The Park Service adopted an experimental "hands-off" or natural regulation management program in 1968 (Cole 1971) and it has been controversial since its inception (Cayot et al. 1979, Chase 1986).

Houston (1982) reported that the Northern Yellowstone elk herd was regulated primarily by calf mortality as directly affected by winter severity and population density. The Madison–Firehole elk, a nonmigratory herd, also appeared to be naturally regulated by density-influenced competition for food and by the related influence of severe winters (Cole 1983).

A primary objective of the Park Service's "hands-off" management policy, to minimize disturbance of the elk, has precluded the use of conventional techniques to assess their nutritional condition. Studies of the winter condition of

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[1] Present address: Forest Wildlife Populations & Research Group, Minnesota Department of Natural Resources, 1201 E. Highway 2, Grand Rapids, MN 55744.

Yellowstone elk have been limited to counting carcasses, measuring fat indices during late winter and early spring, and assessing mortality by sex and age (Craighead et al. 1973, Houston 1982, Cole 1983). Houston (1982) asserted that undernutrition is the ultimate cause of winter mortality of elk.

Analysis of urine for various metabolites and chemistries provides assessments of physiological status in elk and other ungulates (Mould and Robbins 1981, DelGiudice et al. 1987a, 1990, 1991; Saltz and White 1991a,b). Collection and chemical analysis of urine in snow permits sequential physiological data collection without capture and with minimal disturbance to animals (DelGiudice et al. 1988, 1989a).

Using collections of urine in snow, we assessed and compared the extent of nutritional deprivation in elk on the Lower, Middle, and Upper portions of the Northern Range, and on the Madison–Firehole Range; we related these urine measurements to differences in snow cover, herd composition, and elk distribution.

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STUDY AREA

Northern Elk Winter Range

The Northern Range encompasses 100,000 ha; 83% of this range occurs within Yellowstone NP, and the remaining 17% within the Gallatin National Forest or on private lands (Houston 1982). Our sampling was restricted to within the Park (Fig. 1). Elevations range primarily from 1,500 to 2,400 m with only 13% of the area above 2,400 m. Soils on the Northern Range have higher water-holding capacities and plant nutrient levels than soils in the Madison–Firehole area (Despain 1991).

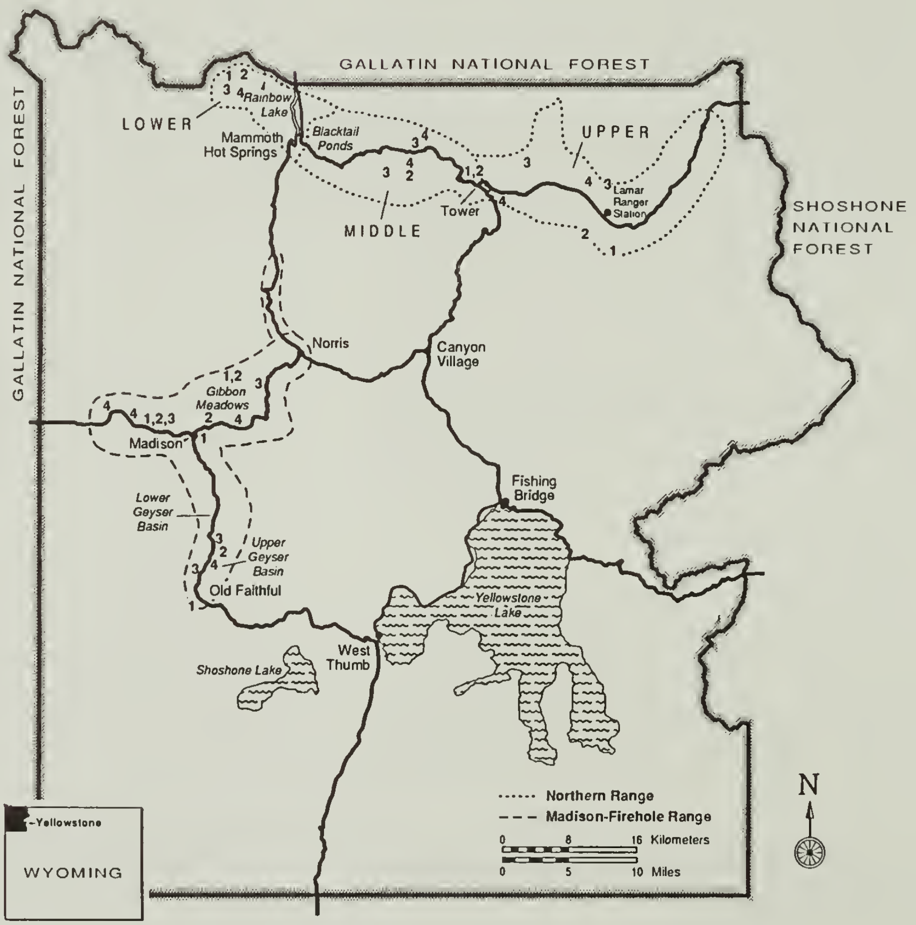

Fig. 1. Locations of 4 collections of urine excreted in snow by elk on winter ranges of Yellowstone National Park, Wyoming, 13 January–29 March 1988.

Annual precipitation is ≤75 cm for most of the Northern Range; however, it may vary from 35 cm near Gardiner, Montana, to 55 cm at Lamar Ranger Station (Fig. 1) (Houston 1982). Total snowfall from November 1987 to April 1988 was 109 and 150 cm at Mammoth and Tower Falls, respectively. The greatest monthly snow depths at Mammoth occurred in February 1988 (18.5 cm) and at Tower Falls in December 1987 (43.2 cm) (Fig. 2) (Natl. Oceanic and Atmos. Adm. 1987, 1988). Mean monthly maximum and minimum temperatures were lowest (-3.4 and-14.2 C) in January and highest (10.9 and -1.8 C) during April 1988 at Mammoth and were lowest (-3.3 and -21.2 C) in January and highest (12.6 and -7.6 C) in April at Tower Falls (Fig. 1) (Nat. Oceanic and Atmos. Adm. 1987, 1988).

Vegetation is shrub steppe interspersed with conifers (Houston 1982). About 41% of the range was forested by Douglas-fir (*Pseudotsuga menziesii*) and lodgepole pine (*Pinus contorta*); trembling aspen (*Populus tremuloides*) covered an additional 2–3% (Houston 1982, Despain 1991). Shrub-grasslands composed of Idaho fescue (*Festuca idahoensis*), bearded wheatgrass (*Agropyron caninum*), and big sagebrush (*Artemisia tridentata*) covered 53% of the range.

Mule deer (*Odocoileus hemionus*), bison (*Bison bison*), pronghorn antelope (*Antilocapra americana*), bighorn sheep (*Ovis canadensis*), and moose (*Alces alces*) inhabit portions of this range during winter (Houston 1982, Singer 1991).

Madison–Firehole Elk Winter Range

The Madison–Firehole area constitutes about 16,200 ha of winter range for elk in the westcentral portion of the Park (Fig. 1) (Cole 1983). Elevation ranges between 2,000 and 2,300 m.

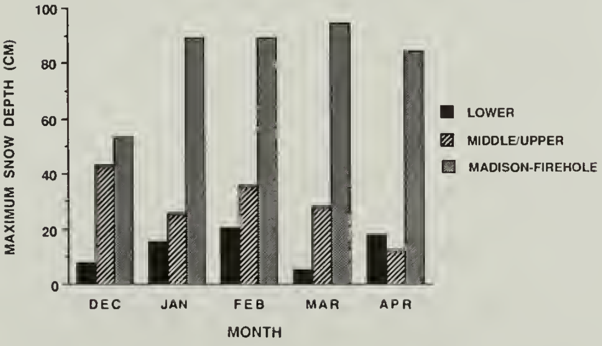

Fig. 2. Maximum monthly snow depths on the Lower (Mammoth) and Middle/Upper (Tower Falls) sampling areas of the Northern Range and on the Madison–Firehole Range (Old Faithful), Yellowstone National Park, Wyoming 1987–1988.

Mean annual precipitation on this range is 58 cm and occurs mostly as snow. Total snowfall from November 1987 to April 1988 was 440 cm at Old Faithful, and maximum snow depth ranged from a low in November to a high in March (Fig. 2). Mean monthly maximum and minimum temperatures were lowest (–1.1 and –21.2 C) in January and highest (9.2 and –6.4 C) in April 1988 (Natl. Oceanic and Atmos. Adm. 1987, 1988).

About 75% of this winter range was forested. Lodgepole pine, Engelmann spruce (*Picea engelmannii*), and whitebark pine (*P. albicaulis*) predominate (Craighead et al. 1973, Cole 1983). Mesic meadows along waterways, scattered parks, and geothermal areas interspersed these forests and comprised the remaining area. Bearded wheatgrass, sedges (*Carex* spp.), and marsh reedgrass (*Calamagrostis* spp.) occurred on mesic meadows. Idaho fescue and bluegrass (*Poa* spp.) dominated drier sites (Craighead et al. 1973).

Elk inhabiting this range were nonmigratory (Craighead et al. 1973). Small portions of the Northern and Gallatin elk herds also summered in this area (D. Vales, Univ. Idaho, pers. commun.). A few moose and mule deer and about 1,400–1,700 bison also wintered on this elk range and on ranges immediately to the east (Cole 1983).

METHODS

Collections.—We divided the Northern Range into Lower, Middle, and Upper sampling areas for snow-urine collections (Fig. 1). This facilitated examination of potential location and snow depth effects on physiological status of elk. We treated the Madison–Firehole Range as 1 sampling area. We made 4 sample collections in each area between 13 January and 29 March 1988 and allowed ≥2 weeks between consecutive collections within sampling areas.

We limited sampling to cow groups in all areas (Table 1). Our objective in the field was to collect approximately 60 snow-urine samples from each of the 4 sampling areas during each of 4 collections. Field procedures included locating a cow group in each area; recording herd composition (i.e., total no., calf:cow ratio) and snow depth; determining location (UTM); and collecting snow-urine samples from the area occupied by the group. To minimize the risk of repeated sampling of an individual in a group, we kept the number of samples collected from a group to

Table 1. Mean size (*N*) and calf:cow ratios of elk groups sampled for urine in snow, Yellowstone National Park, Wyoming, 13 January-29 March 1988.

	Northern Range											
	Lower			Middle			Upper			Madison–Firehole		
Collection	$\bar{x}$	SE	n[a]	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE	n
Group Size	72	6	10	104	20	8	382[b]	5	7	28	4	3
Calves:100 cows	36	3	10	34	1	8	34	4	6	39	3	23

[a] Sample size is the number of elk groups sampled.

[b] Represents mean minimum group size. During collection 1, all samples were collected from a group estimated at >2,000 animals; the entire group was not counted, and thus, was excluded from this calculation.

≤33% of the total number of individuals in the group. We recorded the number of yearling and subadult bulls that occasionally occurred in the cow-calf groups.

We collected the most concentrated portion of each snow-urine sample into a plastic bag, while avoiding contamination by skin contact (DelGiudice et al. 1988, 1989a). Samples were kept frozen in the field. In the laboratory, samples were handled as described by DelGiudice et al. (1989a) and stored at –20 C. Thawed samples were chemically assayed for urea nitrogen, creatinine, and phosphorus (P) by spectrophotometry; Na and K concentrations were measured by flame photometry (DelGiudice et al. 1987a, 1988).

We collected snow-urine samples from captive elk (6 cows, 5 calves) at Livingston, Montana, (68 km from Yellowstone NP) on 22 March 1988 to serve as nutritional controls during the final sample collection. These elk were pasture-grazed but supplementally-fed an alfalfa (25%) and brome (75%) hay (13.6 kg/elk/day), with crude protein contents of 15.9 and 11.8%, respectively. They were also fed a protein supplement that was 18% crude protein.

Chemical Analyses.—Concentrations of urinary chemistries were compared as units excreted per mg creatinine excreted to control extraneous variability associated with single, random urinations and different hydration states in animals and to correct for dilution by snow (DelGiudice et al. 1988). Detailed studies of the constancy of 24-hour urinary excretion of creatinine in cervids have not been conducted; however, the following characteristics of creatinine lend support to its use in comparing metabolite data: (1) daily creatinine production is reasonably constant at 2% of the total creatine pool; (2) there is a good correlation between muscle mass and creatinine output; (3) the creatine pool and creatinine excretion are not affected by vegetative diets; (4) because creatinine is completely filtered by the glomerulus and is not reabsorbed in the renal tubules, it reflects glomerular filtration (Forbes and Bruining 1976, Kopple 1988). Sodium:C and K:C ratios were multiplied by 100 and P:C by 1,000 to facilitate comparing our data with other studies (DelGiudice et al. 1989a, 1990, 1991). We used U:C ratios ≥3.8 as indicators of severe nutritional deprivation or energy restriction, based upon values observed in control and winter-killed elk and upon values observed in white-tailed deer (*Odocoileus virginianus*) fasted for 4 weeks (DelGiudice et al. 1987a,b, 1991).

Counts.—We conducted an early winter count of elk on the Northern Range on 18 January 1988 with 4 fixed-wing aircraft surveying simultaneously. We counted elk again during 26–28 February 1988. We used both helicopter and ground surveys to estimate calf:cow ratios during December 1987, and we obtained estimates from a helicopter during 26–28 February 1988.

We counted Madison–Firehole elk from a fixed-wing aircraft on 29 February and 13 May 1988. We determined calf:cow ratios by ground survey during October–November 1987 and by fixed-wing aircraft on 29 February 1988.

Statistical Analyses.—We log$_e$-transformed urine metabolite data to stabilize the variance prior to analysis by 1- and 2-way ANOVA's. We used the least squares means test to make multiple comparisons among the 4 sampling areas and collections. We made comparisons of mean minimum elk densities (based on uncorrected data) and calf:cow ratios during early and late winter by Mann-Whitney *U*-tests and the Friedman test, respectively, at $P < 0.05$.

RESULTS

Physiological Assessment

Temporal Trends.—Parkwide, urinary U:C, K:C, Na:C ($P = 0.0001$), and P:C ($P = 0.01$) varied from collections 1 to 4. There were significant ($P = 0.0001$) interacts between collection and sampling area for all of these ratios. Analysis of U, K, and C concentrations showed that they varied ($P = 0.0001$) temporally

(Fig. 3). Urea nitrogen and K exhibited similar trends as U:C and K:C, respectively (Fig. 3). Creatinine concentrations remained stable from collections 2 to 4 (Fig. 3).

Mean urinary U:C, Na:C, K:C ($P = 0.0001$), and P:C ($P = 0.05$) varied on Lower range throughout winter (Fig. 4, Table 2). Mean U:C steadily increased from collections 1 to 3 and remained elevated through collection 4 (late Mar). Potassium:C decreased from collections 1 to 4. Urinary Na:C was low throughout winter, but exhibited an increase ($P = 0.0001$) during collection 2. Mean P:C increased ($P = 0.01$) by collection 3.

Mean urinary U:C, K:C, and P:C ratios varied ($P = 0.0001$) on Middle and Upper ranges as winter progressed (Fig. 4, Table 2). On Middle range, U:C increased ($P = 0.0001$) from collection 2 to its maximum winter value during collection 3. Maximum U:C on the Upper range was observed during collection 1. Mean U:C increased ($P = 0.01$) from collections 2 to 3 and remained elevated through collection 4 on Upper range. Similar to Lower range, urinary K:C on Middle range declined from collections 1 to 4. On Upper range, K:C was low, but stable until collection 4, when it decreased ($P = 0.0001$) further. Urinary Na:C remained low and unchanged from collections 1 to 4 on Middle and Upper ranges.

Mean P:C of elk on Middle range declined ($P = 0.0001$) from collections 1 to 2, then was unaltered through collection 4. On Upper range, this ratio did not decrease ($P = 0.0001$) until collection 3 and remained similarly low during collection 4.

Urinary U:C, K:C, Na:C, and P:C differed ($P = 0.0001$) in Madison–Firehole elk as winter progressed (Fig. 4, Table 2). Urea nitrogen:C increased ($P = 0.0001$) from collection 2 to 3 and remained elevated during collection 4. Mean K:C was greatest during collection 1 and lowest during collection 4. Greatest Na:C occurred during collection 2. Phosphorous:C fluctuated over the 4 collections; lowest values occurred during collection 1 and greatest values during collections 2 and 4.

Spatial Differences.—During early winter (collection 1), C ratios of U, K, Na, and P differed ($P = 0.0001$) among the 4 sampling areas (Fig. 4, Table 2). Urinary U:C was greatest and K:C was lowest on Upper range. Mean U:C was lowest in elk on Lower range, and K:C was highest on Lower and Middle ranges. Phosphorous:C also was highest on Middle range and lowest in Madison–Firehole elk. Sodium:C was lowest and similar on Middle and Upper ranges and highest and similar in elk on Lower and Madison–Firehole ranges.

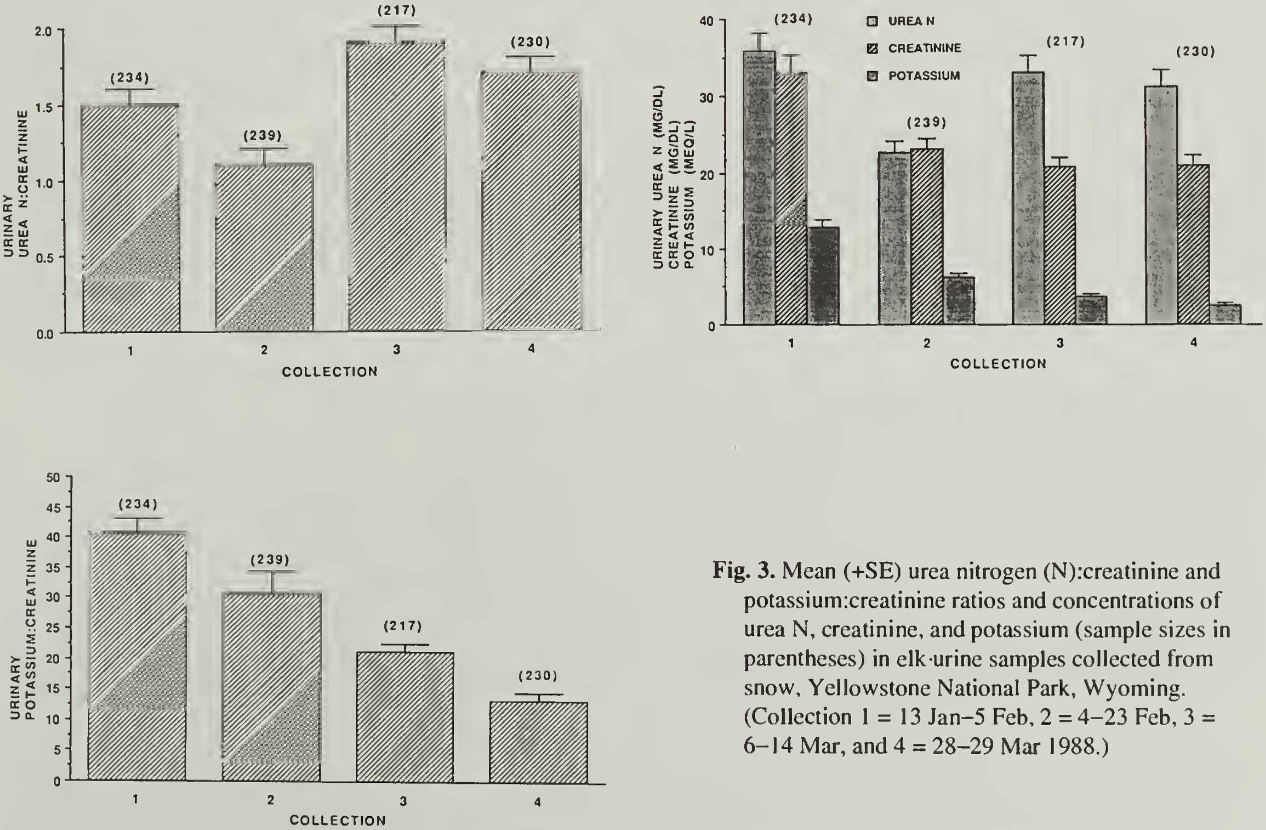

Fig. 3. Mean (+SE) urea nitrogen (N):creatinine and potassium:creatinine ratios and concentrations of urea N, creatinine, and potassium (sample sizes in parentheses) in elk urine samples collected from snow, Yellowstone National Park, Wyoming. (Collection 1 = 13 Jan–5 Feb, 2 = 4–23 Feb, 3 = 6–14 Mar, and 4 = 28–29 Mar 1988.)

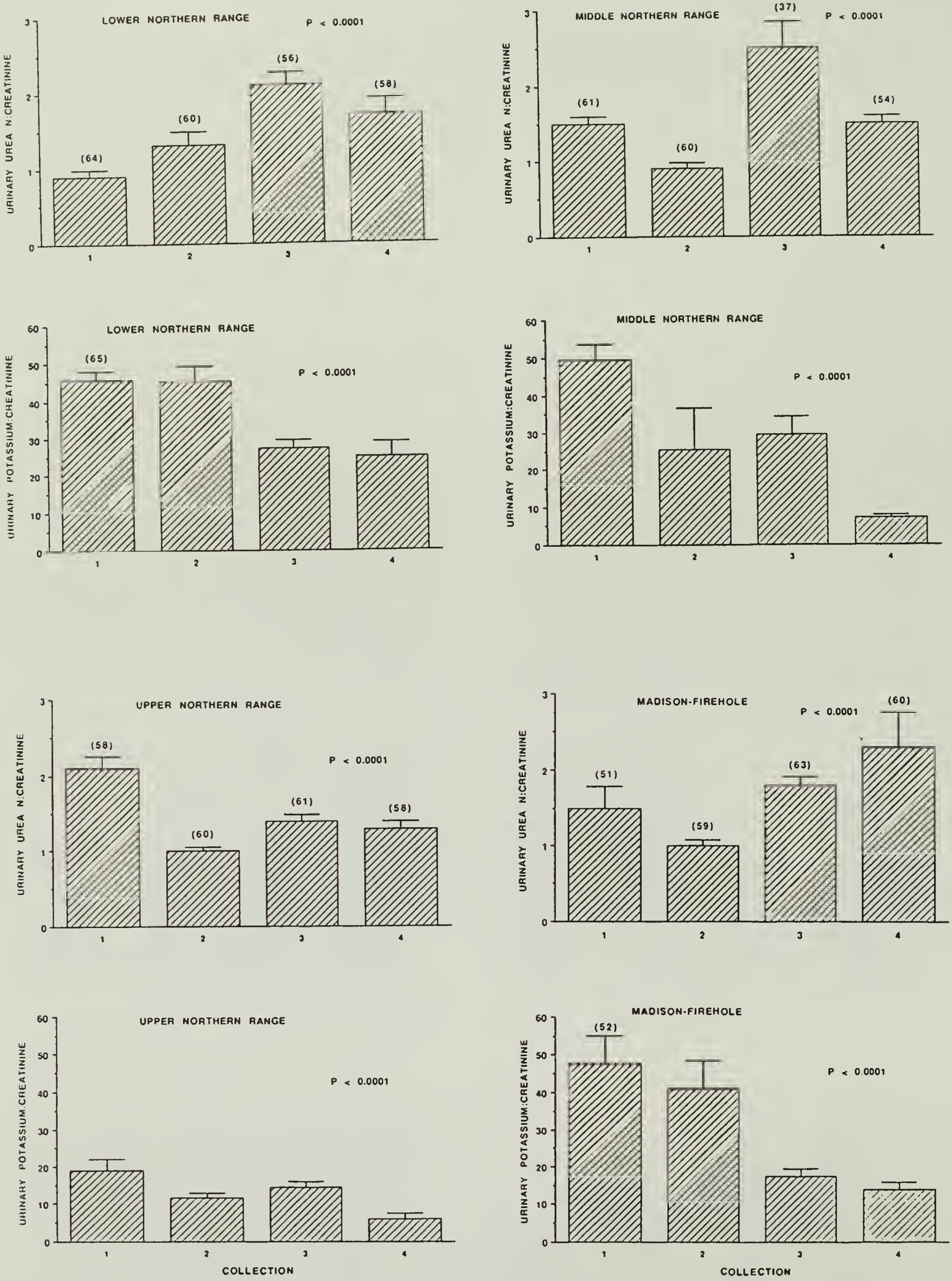

Fig. 4. Mean (+SE) urea nitrogen (N):creatinine and potassium:creatinine ratios (sample sizes in parentheses) in elk urine collected from snow on the Lower, Middle, and Upper Northern Range and on the Madison–Firehole Range, Yellowstone National Park, Wyoming. (Collection 1 = 13 Jan–5 Feb, 2 = 4–23 Feb, 3 = 6–14 Mar, and 4 = 28–29 Mar 1988.)

During late winter (collection 4), urinary U:C ($P = 0.002$), K:C, and Na:C ($P = 0.0001$) continued to differ spatially (Fig. 4, Table 2). Urea nitrogen:C was lower ($P = 0.04$) on Upper range than on Lower range, but Na:C was similar across the Northern Range. Urea nitrogen:C ratios were higher in Madison–Firehole elk than in elk on Upper ($P = 0.0001$) and middle ($P = 0.03$) ranges, and Na:C values were greater in Madison–Firehole elk than in all Northern Range elk. Potassium:C was highest on Lower range and lowest on Upper Range. Phosphorous:C was similar among sampling areas.

During collections 1–4, 4.3, 0.4, 6.0, and 3.9%, respectively, of Yellowstone elk exhibited U:C ratios (3.8) indicative of severe energy deprivation. These percentages were 3.8, 0.6, 7.1, and 2.9% for elk on the Northern Range during the 4 collections. Proportions of elk on the 4 sampling areas experiencing accelerated net catabolism of protein during the 4 collections are presented in Figure 5.

Comparison of Reference Values.—A comparison of U:C and K:C ratios among captive controls, free-ranging elk with U:C values indicative of severe energy deprivation, and winter-killed elk of Yellowstone NP that had % femur marrow fat (DelGiudice et al. 1991) showed that mean U:C in control elk was less ($P < 0.005$) than in winter-killed individuals and in free-ranging elk experiencing severe energy deprivation; values were highest ($P < 0.005$) in the latter (Fig. 6). Urinary K:C was lower in elk with U:C ratios indicating severe energy deprivation compared to controls ($P = 0.05$) and winter-killed elk ($P < 0.005$). Urinary K excretion was similar in control and winter-killed elk.

Population Characteristics

Elk density declined 59% and increased 64% from early to late winter on Upper and Middle ranges, respectively (Table 3). Mean densities remained unchanged on Lower range and at Madison–Firehole. Calf:cow ratios on Lower, Middle, and Upper ranges decreased 35, 48, and 50%, respectively; ratios declined 44% at Madison–Firehole (Table 3).

DISCUSSION

Progressive Nutritional Deprivation

Justification for Creatinine Ratios.—Ratios of K and U to C were the most useful urinary characteristics for monitoring progressive nutritional deprivation of Yellowstone elk because temporal changes of these ratios were attributable to alterations of numerators, not changes in urinary C concentrations (Fig. 3). Furthermore, urinary U, K, and C are similarly diluted by snow (DelGiudice et al. 1988). These things support the validity and accuracy of the physiological interpretation of C ratios. Although urinary excretion of C may decrease

Table 2. Comparison of chemistries in elk urine collected from snow on the Northern and Madison–Firehole Ranges, Yellowstone National Park, Wyoming, 13 January–29 March 1988.

		Collection[a]											
		1			2			3			4		
Snow-urine characteristic[b]	Sampling area	$\bar{x}$[c]	SE	*n*	$\bar{x}$	SE	*n*	$\bar{x}$	SE	*n*	$\bar{x}$	SE	*n*
Na:C × 100													
	Northern Range												
	Lower	0.9A[d]a[e]	0.22	65	4.3Ba	1.02	60	0.9Aa	0.35	56	1.0Aa	0.49	58
	Middle	0.1b	0.02	60	2.9b	2.81	60	0.1a	0.03	36	0.2a	0.04	53
	Upper	0.1b	0.04	58	0.3b	0.05	60	0.2a	0.08	61	3.0a	2.65	58
	Madison–Firehole	0.8Aa	0.26	52	8.6 ba	3.77	59	7.1 Cb	3.22	62	3.7Bb	0.98	60
P:C × 1,000													
	Northern Range												
	Lower	11.7Aa	0.4	65	14.8ABa	1.3	60	17.8Ba	1.6	56	22.8B	4.4	58
	Middle	30.1Ab	1.8	61	20.8Bab	5.1	60	21.9Ba	2.3	37	17.1B	1.3	54
	Upper	24.6Ac	1.6	58	20.6Ab	1.3	60	12.9Bb	0.8	61	20.8B	6.3	58
	Madison–Firehole	9.7Ad	0.9	52	25.9Bb	7.8	59	12.3Cb	0.9	63	46.3B	26.8	60

[a] Collections: 1 = 13 Jan–5 Feb; 2 = 4–23 Feb; 3 = 6–14 Mar; 4 = 28–29 Mar.

[b] Na:C = sodium:creatinine and P:C = phosphorous:creatinine.

[c] Comparisons were made by Duncan's multiple-range test after data were $\log_e$ transformed to stabilize variance; however, original means and standard errors are presented.

[d] Mean values in a row with the same upper case letter are not different ($P > 0.05$).

[e] Mean values of a particular urine characteristic within a column with the same lower case letter are not different ($P > 0.05$).

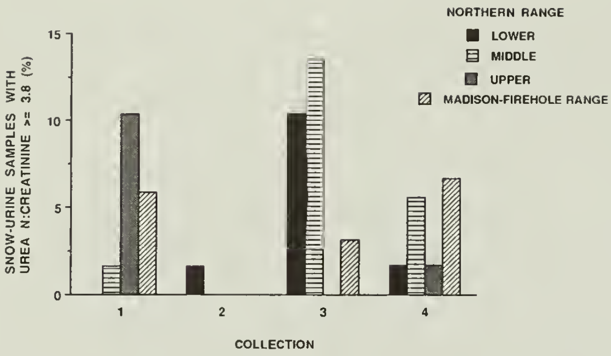

Fig. 5. Distribution of the proportion of elk snow-urine (urine collected from snow) samples with urinary urea nitrogen (N):creatinine ratios ≥3.8 among 4 collections on the Lower, Middle, and Upper Northern Range and on the Madison–Firehole Range, Yellowstone National Park, Wyoming, 13 January–29 March 1988.

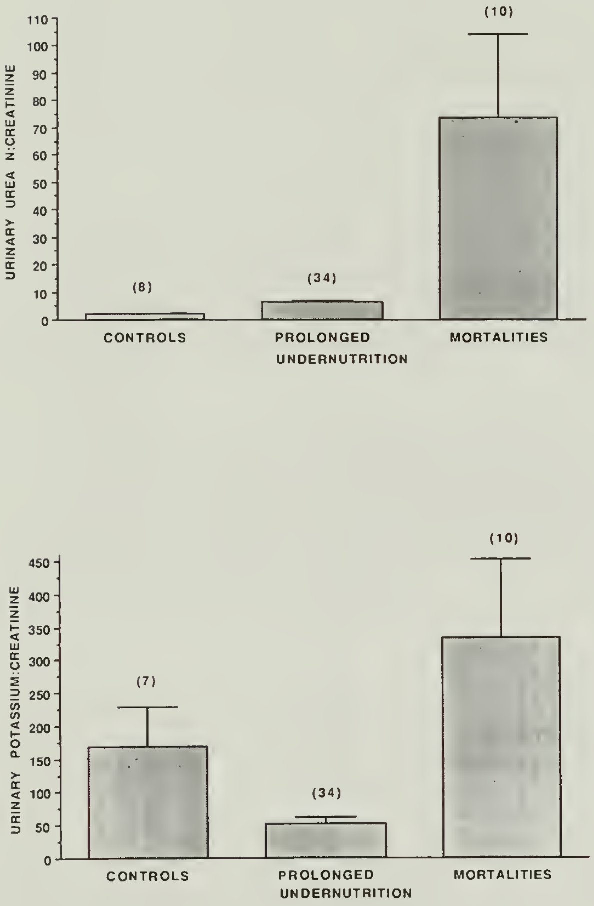

Fig. 6. Mean (+SE) urea nitrogen (N):creatinine and potassium:creatinine ratios of pasture-grazed captive elk supplementally fed a high quality diet, elk experiencing severe energy deprivation, and winter-killed elk with <10% femur marrow fat (DelGiudice et al. 1991), Yellowstone National Park, Wyoming, 13 January–29 March 1988.

with undernutrition and mass loss in ruminants, the changes tend to be slight compared to U loss (Blaxter and Wood 1951, Hovell et al. 1987). Finally, it is the close correlation of urinary C with muscle mass that permits meaningful comparisons of ratios of metabolites among animals of different and changing masses.

Temporal Trends.—Mean urinary P:C values of elk were similar to ratios in free-ranging white-tailed deer during winter (DelGiudice et al. 1989a); however, inconsistency of the temporal trends of this characteristic in elk on the 4 sampling areas limits our ability to interpret results. It is likely that this inconsistency is partially ascribable to complex interactions between dietary P and calcium that affect intestinal absorption, "obligatory interactions" between these minerals in bone (Robbins 1983:32, Avioli 1988), and interactions between the 2 sources of these elements during a season of nutritional deprivation and mass loss.

The decreasing trends of K:C indicated progressive nutritional deprivation from early January to late March in elk on the 4 sampling areas. This deprivation is attributable to depressed forage availability and quality and to reduced feeding activity (Pollack 1974, Hobbs et al. 1979). The K content of plants is high, generally occurring in excess of animal requirements (Charley 1977, Robbins 1983:48), and urinary excretion of this electrolyte is directly related to intake (Keynes and Harrison 1967, Kopple 1988). DelGiudice et al. (1987a) have shown that urinary K:C is directly related to food intake in white-tailed deer. A similar declining trend of urinary K:C was observed in free-ranging white-tailed deer in northeastern Minnesota where deep snow cover (>30 cm) occurred through late March (DelGiudice et al. 1989a,b); however, deer (primarily browsers) at lower elevations where snow was patchy by late March, exhibited a dramatic increase (250%) in K:C associated with increased mobility and feeding activity. However, by late March during our present study, there was no evidence of such an initiation of nutritional recovery in our Yellowstone elk.

During late March, the higher K:C ratios of our captive elk compared to free-ranging elk, reflected their access to an artificial, high quality diet all winter. Higher K:C ratios have also been noted in deer confronted with prolonged deep snow, but supplementally fed commercial diets, compared to deer not supplementally fed (DelGiudice et al. 1989a).

The increasing urinary U:C values that accompanied the declining K:C trend from February to late March indicated progressive energy restriction and accelerated net catabolism of protein (Mould and

Table 3. Elk density (*N*/km) and calf:cow ratios on the Northern and Madison–Firehole winter ranges, Yellowstone National Park, Wyoming, winter 1987–88.

		Elk density in winter				Calves:100 cows in winter			
		Early		Late		Early		Late	
Winter range	No. 30-km count units	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Northern									
Lower	7	21A[a]	7	24A	2	48A	18	31B	11
Middle	12	11A	4	18B	3	40A	7	21B	4
Upper	8	34A	10	14B	1	32A	9	16B	4
Madison–Firehole	4	3A	1	3A	1	32A	9	18B	5

[a] Means with the same letter within a row were not different ($P > 0.05$).

Robbins 1981; DelGiudice et al. 1987a, 1990, 1991; Saltz and White 1991a). Saltz and White (1991b) reported a similar pattern of U:C ratios of yearling mule deer occurring at high densities on a pasture. Furthermore, these authors reported midwinter increases in U:C ratios of fawns, accompanied by elevated cortisol:C ratios, as evidence of increased catabolism of lean body mass.

As noted in earlier studies (Craighead 1973, Houston 1982), declines in calf:cow ratios across the Northern Range suggested that calves were more vulnerable to nutritional deprivation than cows. Loss of endogenous protein and fat occur simultaneously in undernourished deer (Torbit et al. 1985, DelGiudice et al. 1990). When digestible energy intake is adequate for maintenance of positive nitrogen balance, decreased protein intake results in increased urea recycling and decreased urinary U in elk (Mould and Robbins 1981). However, as nutritional deprivation progresses, energy becomes more limiting, animals continue to lose mass, and their location along a gradient of body fat and protein catabolism moves to a detrimental extreme (Robbins 1983:6–7; Torbit et al. 1985; DelGiudice et al. 1990, 1991). Urea from endogenous protein catabolism constitutes an increasingly high proportion of the urea pool (Mould and Robbins 1981), renal filtration of urea eventually increases, and U:C ratios become elevated (DelGiudice et al. 1987a,b, 1991; Saltz and White 1991a,b). Increased net catabolism might also be attributable to diminished substrate availability for protein synthesis (Waterlow et al. 1977).

Phases of Nutritional Deprivation.—Mean U:C ratios in winter-killed elk with <10% femur marrow fat represent the detrimental extreme on the tissue catabolism gradient or nutritional continuum, and captive elk represented the optimal, albeit unnatural, extreme of the continuum. Although the mean ratio of captive elk in this study was 23 O.2 (SE), we have reported values as high as 4.4 0.3 for captive elk supplementally fed artificial high quality diets (DelGiudice et al. 1991). Data representing both extremes of the continuum were critical to an accurate interpretation of these ratios from living, free-ranging elk. However, it is essential to an accurate interpretation to know that sampled Yellowstone NP elk did not have access to artificial diets. Thus, increasing U:C ratios that approached or exceeded levels observed in captive elk did not indicate high crude protein intake equivalent to that derived from artificial diets, but reflected accelerated net catabolism of body protein.

We propose that the relative phases of nutritional deprivation of free-ranging Yellowstone elk indicated by U:C and K:C ratios as follows: (1) low K:C and U:C ratios reflected diminished food intake, but high efficiency of urea recycling; (2) continued low K:C and increasing U:C indicated continued low food intake and increasing net catabolism of protein; and (3) high K:C and U:C (≥4) (DelGiudice et al. 1991), reflected extensive proteolysis and muscle cell breakdown accompanied by increased loss of endogenous K (Tepperman 1980:253).

Sodium Deprivation.—Dietary restriction of Na was indicated by diminished Na:C ratios in elk throughout winter. Lower C ratios of Na than K throughout winter were attributable to the lower Na content of plants than K content (Short et al. 1966, Charley 1977) and the highly efficient renal reabsorption capacity of mammals for Na (>99%) (Gans and Mercer 1984, Kopple 1988). The Na content of plants is lowest during winter (Short et al. 1966), therefore, renal conservation of this electrolyte is maximized throughout winter, accounting for trends of Na:C that were not useful for monitoring progressive nutritional deprivation. Dramatic decreases in urinary Na:C values have been observed in captive deer fasted during winter (DelGiudice et al. 1987a), and low Na:C values, similar to ratios of Yellowstone elk, have been reported for free-ranging deer during winter (DelGiudice et al. 1989a). The relatively higher Na:C ratios of Madison–Firehole elk throughout winter may have been attributable to the high Na content of aquatic vegetation consumed along streams influenced by the thermal areas (Botkin et al. 1973, Craighead et al. 1973).

Spatial Differences in Physiological Status.— Urea nitrogen:C and K:C ratios also provided the most meaningful physiological differences among elk of the 4 sampling areas. Lowest K:C and highest U:C ratios in Upper elk during early winter suggested that they entered winter experiencing the greatest dietary energy deficiency. Lower, Middle, and Madison–Firehole elk exhibited U:C and K:C values more comparable to deer in northeastern Minnesota (DelGiudice et al. 1989a). Upper elk contended with snow depths most similar to those occurring in Minnesota; however, much of the deer's primarily browse diet was available above snow cover (Rogers et al. 1981, DelGiudice et al. 1989b). Yellowstone elk are primarily grazers, and grasses constitute >80% of their diet (W. J. Barmore, unpubl. rep., F. J. Singer, unpubl. data). Grasses tend to be lower in crude protein than browse (Hobbs et al. 1979, Houston 1982) and are rendered less available by snow cover (Wickstrom et al. 1984). Additionally, snow depth and density contribute directly to nutritional deprivation by the combined effect of increasing energy expenditure by ungulates (Parker et al. 1984). As early as December, snow cover was notably deeper on Upper range compared to lower elevations; Madison–Firehole elk had adapted to deeper snow by using snow-free thermal areas that provided improved access to forage (Craighead et al. 1973). The high proportion (10.3%) of snow-urine samples of Upper elk with U:C ratios indicative of severe energy deprivation (≥3.8) was additional evidence of their poor nutrition. Winter-killed elk with <10% femur marrow fat had a 95% confidence interval for U:C of 4.4–142 (DelGiudice et al. 1991). Relative to Upper elk, greater food intake (i.e., energy) and a more "sparing" rate of protein catabolism in Lower elk were indicated by higher K:C and lowest U:C values.

By early March (collection 3) on the Northern Range, Middle and Lower elk appeared to be experiencing the greatest nutritional deprivation, as evidenced by continued low K:C ratios, highest U:C values, and the high proportion (10.3–13.5%) of snow-urine samples with U:C ratios indicative of severe energy restriction and accelerated catabolism. This shift in abundance of snow-urine samples indicative of a more deteriorating physiological status from the Upper to the Middle and Lower ranges paralleled a migration of Northern Range elk in the same direction (F. J. Singer, unpubl. data) and was associated with the 59 and 50% declines in Upper elk density and calf:cow ratios, respectively. Conceivably, Lower and Middle areas were recipients of elk in poorer condition and/or higher elk densities on these areas during late winter exacerbated nutritional deprivation. Elk numbers on the Northern Range had been increasing steadily since the mid-1970's and peaked during the winter of our study (Mack and Singer 1991). Merrill and Boyce (1991) contend that the population was near or at carrying capacity. Harsh environmental conditions modify Yellowstone elk's normal affinities for portions of their range, and during severe winters over 50% of the Northern Range population has been known to migrate to lower elevations beyond the northern Park boundary (Houston 1982). However, winter during our study was considered mild, evidenced by only 5% of the herd being counted beyond the northern Park boundary (F. J. Singer, unpubl. data).

During late March, similar mean U:C ratios in Lower, Middle, and Upper elk suggested similar overall rates of urea recycling (Mould and Robbins 1981). However, as indicated by the proportion of snow-urine samples with U:C ratios ≥3.8, >3 times as many Middle elk were still experiencing severe energy deprivation and accelerated catabolism. Prolonged deep snow (>90 cm) was associated with a continued decline in the physiological status of Madison–Firehole elk, reflected by a doubling of the proportion of animals from early to late March yielding U:C values indicative of extreme energy restriction. However, during March, only 1 sample from Madison–Firehole exhibited an U:C ratio (28.2) reflective of the severe muscle-wasting apparent in winter-killed elk and other ungulates (DelGiudice et al. 1987a, 1991; Saltz and White 1991a,b).

MANAGEMENT IMPLICATIONS

Our study demonstrated that sequential collection and chemical analysis of snow-urine permits direct, quantitative monitoring of the physiological response of elk distributed over vast winter ranges in Yellowstone NP to nutritional deprivation. Large sample sizes can be obtained with minimal apparent animal disturbance, and in contrast to past assessments, evaluations by snow-urine analysis include direct assessment of the physiological status of elk that survived winter.

Although more must be learned about how urinary characteristics relate to body composition, actual values of U:C and K:C ratios, rates of change of these values, and the temporal trend of such changes facilitated detection of subtle differences in the severity of nutritional deprivation experienced by elk on different portions of the Northern Range and on the Madison–Firehole Range as winter progressed.

The demonstrated attributes of physiological assessment by snow-urine collection and chemical analysis suggest that it harbors potential as a management tool, particularly in national parks, where minimizing animal disturbance is emphasized in park policy. Continued annual assessments of this kind during winters of varying severity, and parallel evaluations of demographic events and of elk use of different portions of their ranges, should provide park management with an improved understanding of the role of nutrition in the ecological relationship between varying environmental factors and the variation of the elk population. The more complete the understanding of this relationship, the more predictable will be the effects of habitat changes on the elk population, thus enabling managers to make more informed decisions concerning habitat and elk management.

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An Index of Winter Severity for Elk

Phillip E. Farnes

Snowcap Hydrology
P.O. Box 691
Bozeman, Montana 59771

Abstract. A simple procedure for indexing the severity of winters for wildlife would help wildlife managers and the public assess the relative severity of any given winter and its effect on wildlife. The index of winter severity has a scale from −4 for the most severe winter to +4 for the mildest winter; 0 represents an average winter. The index incorporates the minimum daily temperatures below a threshold level (wherein basal metabolic rate increases with colder air temperatures), the snow water equivalent (the amount of water contained in the snow pack) that impedes animal movement and increases the effort required to obtain forage), and the precipitation during the previous summer that determines forage production. Long-term weather station and snow course data on the winter range were used to represent conditions on the lower northern winter range. Statistical procedures were used to determine probability levels for the different variables. The values from the 1 to 99% probabilities were converted to the −4 to +4 scale. The index of winter severity for elk (*Cervus elaphus*) for the lower northern winter range in and north of Yellowstone National Park was calculated for 1949 through 1993. Index of winter severity and the northern elk herd recruitment rate is compared for 1974 through 1992. There is some relation between index of winter severity and hunter harvest outside the park and between index of winter severity and recent elk population.

Key words: *Cervus elaphus*, elk, temperature, winter severity, Yellowstone National Park.

Various methods and procedures have been used to represent winter severity (Lamb 1963; Verme 1968). These include some measure of temperature, wind, snow, or other meteorological data. Generally these methods use means or departure from means to quantify variability.

The index of winter severity (IWS) uses temperatures below a specified threshold of −18° C (Farnes 1991). When temperatures are below the levels that create additional metabolism, the elk must intake additional forage or supply metabolism needs from fat reserves. Air temperatures warmer than this threshold temperature has little effect on the basal metabolic rate (Irving 1964). To approximate the effects of winter air temperatures on elk (*Cervus elaphus*), the accumulated sum of minimum daily temperatures below −18° C was used to represent the temperature component of the winter severity. This threshold value was based on data of effective critical temperature by Nelson and Leege (1982). Also, because weather records are tabulated in Fahrenheit, the degrees below −18° C (0°F) could be easily accumulated. Winter temperature of data was obtained from National Weather Service Climatological Station records for the Yellowstone National Park station located at Mammoth (National Oceanic and Atmospheric Administration, Asheville, North Carolina, Climatological data from Montana and Wyoming).

Snow influences the energy expended for travel and the amount of energy required to move the snow to obtain forage. Snow depth is a poor indicator of the resistance to travel or the volume of snow covering forage. New fallen snow may settle in depth to half or one-third of the original depth without losing any of its water content.

The Soil Conservation Service (SCS) has coordinated the cooperative snow survey program since the mid-1930's. Monthly measurements of snow depth and snow water equivalent (SWE) at specific locations named snow courses are compiled by the SCS. The 1 April SWE, which is generally the maximum amount for the winter, for Crevice Mountain and Lupine Creek snow courses on the lower northern winter range were used to represent the seasonal snow variable in the index (Soil Conservation Service, Portland, Oregon, Centralized Forecast System computerized data base for survey data from Montana and Wyoming).

The majority of forage utilized by elk on the winter range is produced annually and is related to available spring moisture. Early growing season moisture on the northern range comes from snow melt and rainfall and is adequate for initiating plant growth.

Rainfall later in the growing season, however, is more variable and more significant to total forage production. Moisture falling after July is not as significant in producing forage, particularly if there is deficient moisture earlier in the season. The amount of forage produced in a given year on the winter range was indexed by the June–July precipitation for the summer preceding the winter being indexed. Precipitation data were obtained from the Yellowstone National Park Climatological Station at Mammoth (National Oceanic and Atmospheric Administration, Asheville, North Carolina, Climatological data from Montana and Wyoming). The temperature, snow, and forage variables were combined into one index representing the winter severity.

Study Area

The lower northern winter range encompasses the lower elevations of the Yellowstone River drainage including Crevice Creek, Lava Creek, and Blacktail Deer Creek in the vicinity of Mammoth Hot Springs in Yellowstone National Park and extends north of the park into Montana in the vicinity of Gardiner and Corwin Springs. Elevations are about 1,500–2,600 m. In mild winters, the majority of the northern elk herd winters within the park, but over one-third of the herd may leave the park in severe winters.

Data from several locations were used to develop the IWS for the lower northern range. Temperature and precipitation data came from the Yellowstone National Park (Mammoth) Climatological Station (1,890 m). Snow water equivalent data came from Lupine Creek (2,249 m) and Crevice Mountain (2,560 m) snow courses.

Methods

The procedure used to evaluate water supplies from various sources came from Shafer and Dezman (1982). It was adapted to compare the range of temperature, snow pack, and precipitation using a common scale and to calculate the IWS.

The probability of nonexceedence (PN—the chance of an event not being exceeded) was obtained from a normal probability analysis of each variable for the period of record (1949–93). Using probability of each variable provides a means to compare the variability among variables. To compress the range of probability of nonexceedence (1–99%) to a range of from −4 to +4, subtract 50 and divide by 12.25. The equation for calculation of each variable is

$$\text{variable index} = \frac{PN - 50}{12.25}$$

For example, the index for a probability of nonexceedence of 1% is

$$\frac{1-50}{12.25} = \frac{-49}{12.25} = -4$$

The index for a probability of nonexceedence of 50% is

$$\frac{50-50}{12.25} = 0$$

and the index for a probability of nonexceedence of 99% is

$$\frac{99-50}{12.25} = \frac{49}{12.25} = +4$$

For the lower northern winter range in and near Yellowstone National Park, the IWS for the winter season was calculated by weighting the snow variable as 40%, the temperatures variable as 40%, and the forage variable (June and July precipitation) as 20% (Table). These weightings come from discussions with various researchers and wildlife managers that suggest the effects of snow and temperatures may be about equal with somewhat less effect related to the total forage production (G. Bowser, M. Meagher, H. Picron, N. Romme, L. Wallace, and C. Youmans, personal communication).

Results and Discussion

The severity of the winter is one of the factors that influence winter mortality, reproduction success, and movement of elk out of the park. Using data from Houston (1974) and Yellowstone National Park (1992) for 1949–92, the average hunter harvest was more than 2,000 elk outside the park in years of from severe to very severe winters (−2 to −4; Fig. 1). On milder years (−2 to +4) the average hunter harvest was 700 elk. From 1949 to 1979, the average of 29% of the elk counted for the 3 winters with a severity index from −4 to −2 were outside the park. An average of 4% the elk were outside of the park in the six winters with a severity index milder than 0 (0 to +4).

The recruitment ratio (number of elk in fall divided by number of elk in previous fall minus human-caused deaths)

$$\frac{\text{Number of elk}}{(\text{Number of elk in previous fall} - \text{human-caused deaths})}$$

Table. Variables and indices for determine the index of winter severity for lower northern winter range in and north of Yellowstone National Park.

Year	Temp.[a]	Temp. prob.	Temp. index	Snow[b]	Snow prob.	Snow index	Forage[c]	Forage prob.	Forage index	IWS[d]
1948–49	445	1	−4.0	28.1	9	−3.3	2.34	23	−2.2	−3.4
1949–50	237	37	−1.1	21.4	46	−0.3	2.58	29	−1.7	−0.9
1950–51	210	40	−0.8	21.3	46	−0.3	4.91	90	+3.3	+0.2
1951–52	175	53	+0.2	32.3	2	−3.9	3.35	53	+0.2	−1.4
1952–53	94	80	+2.4	19.3	61	+0.9	4.44	82	+2.6	+1.8
1953–54	69	85	+2.9	2.38	30	−1.6	1.81	13	−3.0	−0.1
1954–55	201	42	−0.7	19.5	60	+0.8	4.52	84	+2.8	+0.6
1955–56	320	9	−3.3	26.8	14	−2.9	3.69	63	+1.1	−2.3
1956–57	295	13	−3.0	20.0	55	+0.4	2.72	32	−1.5	−1.4
1957–58	10	94	+3.6	13.7	90	+3.3	2.83	36	−1.1	+2.5
1958–59	154	61	+0.9	18.7	65	+1.2	4.87	90	+3.3	+1.5
1959–60	305	11	−3.2	11.1	95	+3.7	3.40	54	+0.3	+0.3
1960–61	54	88	+3.1	15.1	84	+2.8	1.55	9	−3.3	+1.7
1961–62	365	4	−3.8	25.7	19	−2.5	1.66	10	−3.3	−3.2
1962–63	291	14	−2.9	13.4	91	+3.3	3.92	69	+1.6	+0.5
1963–64	97	79	+2.4	20.2	53	+0.2	3.40	54	+0.3	+1.1
1964–65	249	26	−2.0	26.2	17	−2.7	4.45	82	+2.6	−1.4
1965–66	110	76	+2.1	14.6	87	+3.0	4.64	86	+2.9	+2.6
1966–67	84	82	+2.6	30.1	5	−3.7	2.21	20	−2.4	−0.9
1967–68	113	75	+2.0	24.6	25	−2.0	4.43	82	+2.6	+0.5
1968–69	124	72	+1.8	22.8	37	−1.1	4.45	82	+2.6	+0.8
1969–70	145	65	+1.2	23.1	34	−1.3	3.98	70	+1.6	+0.3
1970–71	137	68	+1.5	27.6	11	−3.2	3.43	55	+0.4	−0.6
1971–72	160	59	+0.7	26.8	18	−2.6	2.25	21	−2.4	−1.2
1972–73	289	15	−2.9	15.0	85	+2.9	4.11	75	+2.0	+0.4
1973–74	182	50	0.0	31.0	3	−3.8	2.70	32	−1.5	−1.8
1974–75	163	58	+0.7	24.1	26	−2.0	1.74	12	−3.1	−1.1
1975–76	112	75	+2.0	28.6	8	−3.4	3.19	47	−0.2	−0.6
1976–77	52	88	+3.1	13.4	91	+3.3	5.66	97	+3.8	+3.3
1977–78	147	64	+1.1	25.5	20	−2.4	3.40	54	+0.3	−0.4
1978–79	470	1	−4.0	23.8	30	−1.6	2.21	20	−2.4	−2.7
1979–80	197	45	−0.4	18.4	67	+1.4	2.44	26	−2.0	0.0
1980–81	58	87	+3.0	10.0	97	+3.8	3.15	46	−0.3	+2.7
1981–82	191	46	−0.3	24.2	27	−1.9	3.77	65	+1.2	−0.6
1982–83	52	88	+3.1	19.1	62	+1.0	3.59	60	+0.8	+1.8
1983–84	293	14	−2.9	16.9	76	+2.1	4.88	90	+3.3	+0.3
1984–85	274	18	−2.6	20.2	54	+0.3	5.12	93	+3.5	−0.1
1985–86	155	61	+0.9	18.3	67	+1.4	2.98	40	−0.8	+0.8
1986–87	81	83	+2.7	11.7	95	+3.7	4.09	73	+1.9	+2.9
1987–88	138	68	+1.5	14.3	88	+3.1	5.10	93	+3.5	+2.5
1988–89	312	10	−3.3	24.1	27	−1.9	1.42	8	−3.4	−2.8
1989–90	134	68	+1.5	21.8	43	−0.6	3.32	51	+0.1	+0.4
1990–91	329	8	−3.4	18.2	68	+1.5	2.11	18	−2.6	−1.3
1991–92	67	86	+2.9	16.5	78	+2.3	1.31	6	−3.6	+1.4
1992–93	175	53	+0.2	18.8	49	−0.1	5.98	99	+4.0	+1.3

[a] Accumulated daily minimum temperature in ° F below 0° F at Yellowstone National Park (Mammoth) October through March.

[b] 1 April snow water equivalent, inches, Crevice Mountain plus Lupine Creek snow courses.

[c] June plus July precipitation, inches, at Yellowstone National Park (Mammoth) for previous summer.

[d] Index of winter severity (IWS) = 0.4 (temperature index) + 0.4 (snow index) + 0.2 (forage index).

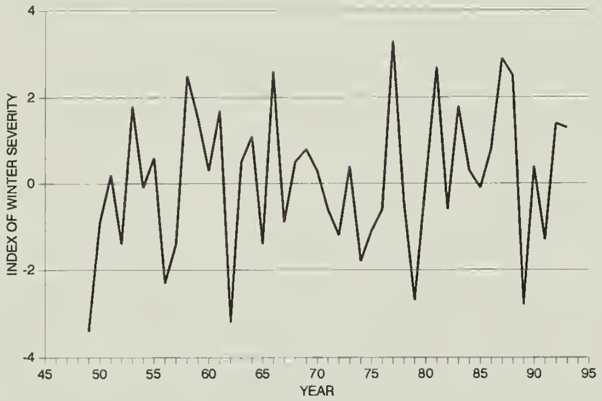

Fig. 1. Index of winter severity—lower northern range, 1949–1993.

from 1973 to 1992 (Yellowstone National Park, Wolves for Yellowstone?, unpublished report to the Congress) indicates mild winters generally correspond with higher recruitment ratios (Fig. 2). If complete data were available for calf mortality in the spring, the combination of winter severity and calf mortality could be used to estimate population trends. The index of winter severity provides a numerical scale to represent the severity of each winter. Extremely mild or severe winters are usually obvious to the public and wildlife managers. Other winters, however, have subtle differences that are not obvious but may relate to elk movement, mortality, or reproduction. Using daily temperatures below that which influences the basal metabolic rate more accurately represents the effects of temperature on the elk than using mean monthly temperature. Using snow water content more accurately represents the true bulk of the snow that impedes travel or must be moved to obtain forage. Production of forage is significant when winter range is limited or herd size is large enough to remove most of the annual growth each winter. The combination of these three components into one index can rank a given winter severity according to the combined effects of different elements on a specific winter range (Table).

Management Implications

The index of winter severity provides wildlife managers and the public with a simple measure of the relative severity of any given winter and what effects it has on elk wintering in a specific area. As accuracy of annual elk counts improves, correlations between winter severity and recruitment ratio should improve.

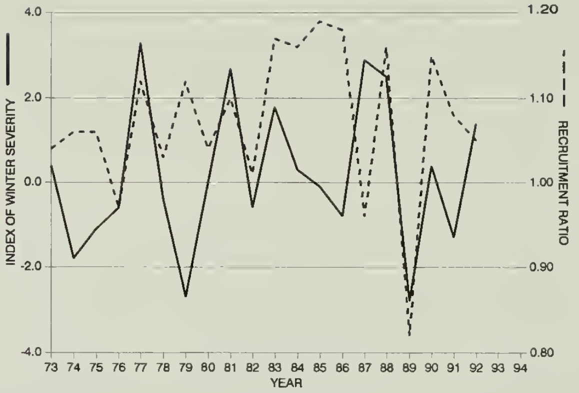

Fig. 2. Index of winter severity and northern elk herd recruitment ratio, 1973–1992.

The index of winter severity can then be used to estimate reproduction and size of the fall herd. Low index winters (more severe) generally indicate increased mortality, reduced reproduction, and expanded migration. High index winters (more mild) generally indicate good survivability and reproduction with animals well distributed across the winter range. A series of mild winters (1981–88) resulted in an increase of 5,000–6,000 elk whereas the severe winter of 1989 resulted in a decrease of 3,000–4,000 elk. (Yellowstone National Park, Table 19, p. 4–35, unpublished report to the Congress).

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Range Expansion by Bison of Yellowstone National Park

Mary Meagher

National Park Service
Resource Management Division
P.O. Box 168
Yellowstone National Park, Wyoming 82190

The bison (*Bison bison*) of Yellowstone National Park have existed as an isolated population since the park was established in 1872 (Meagher, 1973a). The bison that inhabited the Yellowstone River valley immediately north of the park were exterminated during the 1860s; those on the park's northern range were gone by the early 1890s. Bison from ranched herds introduced in 1902 interbred with the remnant original bison. The resulting population was influenced variously by ranching activities and regulation of population numbers by removals (reductions) through 1966. Except for a few males, bison seldom moved beyond park boundaries; they occupied traditional winter ranges with seasonal migrations to summer ranges (Meagher, 1973a).

During the past dozen years the population on the northern winter range expanded from the traditional core along the lower Lamar River, occupied new foraging areas within the park, and moved outside. Further expansion was disrupted because of conflicts with human interests (Meagher, 1973b, 1974, 1989). The factors which apparently contributed to the changes are presented here.

The study area (Fig. 1) encompassed all but the higher elevations at the fringes of the 100,000-ha northern winter range (Houston, 1982). Elevations ranged from about 2,030 m at the upper limits to 1,550 m at the lower. Bison foraged on discontinuous sites on open bottomlands and lower adjacent slopes, but their travel routes sometimes traversed forest areas and steep slopes. Long cold winters and short cool summers characterize the climate, but there is great variation in conditions across the winter range and between years (Houston, 1982). Much of the annual precipitation occurs as snow. During recent winters the ground was nearly snow-free much of the time near Gardiner at the north boundary.

Population counts, distribution, and group size were obtained by air, using a Piper Supercub. Ground observations provided supplemental detail. Movements were assessed by changes in group locations, visible travel trails in snow, and from unusual numbers of droppings along the road. Snow-course water-content records, supplemented by narrative field notes, provided information on winter severity.

The winter of 1975–1976 was exceptionally severe. As a result of two arctic storms in November followed by thaws the winter range was covered at the ground surface by a hard layer estimated at 150 mm in the Lamar area. Subsequently, more snow accumulated and consolidated. The snow courses recorded approximately 190% of the 20-year average water content for December 1975. During the entire winter, water content was well above 100%. The next winter was mild followed by 2 winters somewhat above average. All winters 1980–1987 were below average in severity.

Bison counted on the northern range in mid-winter increased approximately three-fold 1976–1987 (Table 1). The high count in 1985 of 661 bison included a temporary shift (Meagher, 1973a) of about 100 animals from Pelican Valley about 40 km south of the study area. During winter 1984–85, the State of Montana removed 88 bison outside the park. The removal and the temporary nature of the shift from the south probably accounted for the drop to a count of 539 in 1986.

Beginning winter 1975–1976, mixed herds (females and juveniles with one to several older males) moved west of the traditional winter range. Initially, the major movement followed the Yellowstone River, with smaller movements most winters thereafter (Table 1.). Attempts to block these movements (Meagher, 1989) precluded a detailed assessment of undisturbed movement patterns. These bison returned eastward in spring.

In early January 1976, bison were first seen traveling the plowed road westward from the Tower area. A group of 15 moved about 10 km west the 3rd week of January; by 13 February a group of 13 was observed near Blacktail Deer Creek. A maximum of 59 bison was recorded in the Blacktail area the 3rd week of March 1976 (Table 1). Travel has occurred annually since December 1980; the bison generally have moved earlier and in greater numbers since then. Beginning winter 1982–1983, mixed groups continued beyond Blacktail to Mammoth and Gardiner. Later some groups apparently bypassed the Blacktail area and other foraging sites en route to travel directly to lower elevations. Return to the traditional winter range occurred in spring.

The bison used two major travel routes (Fig. 1). The natural topographic route along the Yellowstone River from Tower to Gardiner was the primary route initially (Table 1). In 1982–1983, the plowed road became the primary route. Bison sometimes traveled the 32 km from Tower to Mammoth in 1 day. Numbers of animals on the road route were much greater than those on the river route. When human interference precluded use of the primary routes, the bison detoured across steep terrain, or traveled along tributary drainages.

In the 1960s the area between the bridge at Tower and the Lamar Canyon about 10 km to the east formed the core winter range (Fig. 1). Although mixed herds occasionally were found from Soda Butte west to the Hellroaring area (Meagher, 1973a), most groups concentrated on the Slough Creek bottoms, and sedge flats and swales across the valley of the lower Lamar River. A mixed herd of 12–20 first used the meadows west of the Yellowstone River at Tower in March 1975 for about a month; use was annual thereafter.

Use by mixed herds in the Blacktail area during the winter of 1975–1976 was confined to foraging sites north of the road, especially near the ponds. Annual use began in 1980–1981, and expanded to creek bottoms south of the road in 1985–1986. During the mild winter of 1986–1987, use was widespread north and south of the road including upland sites where groups were not seen before.

Six males and one female visited Mammoth in April 1976. Annual use by a few males began the next winter. In late February 1980, three females and nine males appeared in Mammoth. Mixed herds with a larger proportion of females and calves began to use the Mammoth area in winter 1982–1983, and moved toward Gardiner. In 1983–1984 the bison began to cross the park boundary on Reese Creek.

In winter 1984–1985 some of the first groups bypassed the Blacktail area enroute to Mammoth and beyond. On 22 November 1984 a mixed herd of 14 appeared near Gardiner; by 26 November they crossed Reese Creek. On 20 November 1986, 68 were seen in the Blacktail area; on the 21st this herd increased to 100 and moved west. They encountered a newly installed cattleguard and fence, but by 25 November 1986, moved to lower elevations using the Rescue Creek drainage.

The bison foraged on suitable sedge bottoms and swale areas throughout the Mammoth–Gardener area. Similar sites were used between Gardiner and the boundary at Reese Creek, but use patterns were complicated by occasional human disturbance. Beyond the boundary the bison were disturbed intentionally by attempts to force them back into the park (Meagher, 1989).

Nearly two-thirds (385) of the northern range bison were west of the traditional winter range on 22 January 1987. Attempts by mixed herds north of the Yellowstone River to expand beyond the park boundary occurred most winters after 1975–1976. Similar attempted expansion south of the river has occurred since 1983–1984.

The unusually severe winter of 1975–1976 apparently provided the initial impetus that led to the westward movements or stress dispersal of bison on the northern range. However, winter conditions subsequent to 1975–1976 did not appear to be sufficiently severe to contribute to the continued movements and increase in numbers. Movements on the river route occurred during winters of 1977–1978 and 1978–1979 which were above average in severity, but snowfall (and severity) every winter since has been below average. The largest movements recorded to date, spanning the entire winter, occurred during exceptionally mild conditions of 1986–1987. Intensive management at the Buffalo Ranch at Lamar Ranger Station apparently precluded similar movements by bison after a comparable stress dispersal in 1943 when approximately 130 of about 750 bison moved down the river trail. The next winter, 405 of 757 bison were removed (Meagher, 1973a). This removal probably

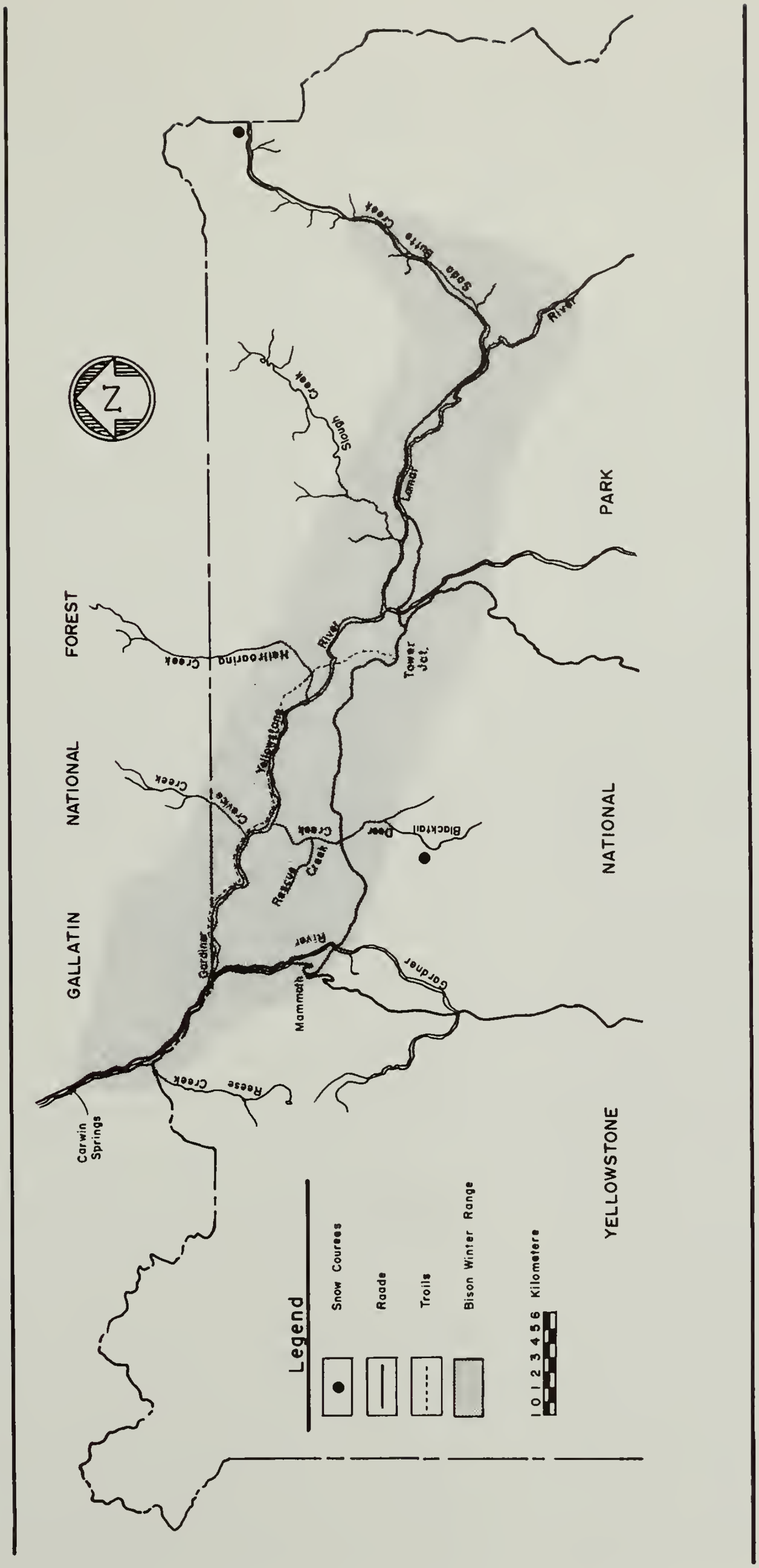

Fig. 1. The northern winter range of bison in Yellowstone National Park.

Table 1.—Period of bison use and maximum numbers west of the traditional northern winter range, Yellowstone National Park, 1976–1987.[a]

	Blacktail area			Mammoth–Gardiner–Reese			River Trail			
Winter	First date	Last date	Maximum numbers	First date	Last date	Maximum numbers	First date	Last date	Maximum numbers	Winter count
1975–1976	5 Feb.	21 Mar.	59	29 Mar.	12 Apr.	7[b]	5 Feb.	31 Mar.	84	200
1976–1977		no activity			no activity			a few males		209
1977–1978		a few males			a few males		24 Feb.	28 Mar.	78	219
1978–1979		a few males			a few males		14 Mar.	19 Mar.	80	262
1979–1980		moved through		24 Feb.	8 Apr.	12[b]	2 Mar.	8 Apr.	29	233
1980–1981	1 Dec.	18 Dec.	34		a few males			no activity		255
1981–1982	17 Feb.	18 Feb.	15	8 Apr.	29 Apr.	9[b]	12 Feb.	18 Feb.	11	329
1982–1983	15 Jan.	mid Feb.	75	21 Feb.	21 Mar.	51		no activity		434
1983–1984	30 Nov.	19 May	28	26 Feb.	19 Apr.	64	5 Mar.	10 Mar.	14	416
1984–1985	16 Jan.	3 Mar.	60	16 Nov.	26 Apr.	79	27 Feb.	14 Mar.	67	661
1985–1986	20 Nov.	6 Apr.	151	7 Dec.	5 Apr.	241		Mar	48	539
1986–1987	20 Nov.	30 Apr.	297	25 Nov.	1 Apr.	229	1 Dec.	20 Feb.	44	594

[a] Movements during fall are not included. Maximum numbers are not additive.

[b] Mammoth area only, group composed mainly of males.

included many of the older experienced females, commonly the leaders (McHugh, 1958), and may have been a more significant factor than other ranch activities such as winter feeding of hay. After daily road plowing between Tower and Mammoth began in the late 1940s (B. Hape, pers. comm.), a few males sometimes travelled this route, but mixed herds did not until 1975–1976.

The movements of 1976–1987 were not significantly correlated (r – 0.39, $P > 0.05$) with population increases on the northern range. Brief fall movements of groups, first seen September 1984, might be termed excursions or explorations, and were suggestive of a population at ecological carrying capacity (Caughley, 1979). However, availability of adequate forage for increased numbers of bison did not appear to be a factor in the movements during recent mild winters. In 1986–1987 available forage for the increased population appeared more than ample, as a result of a wet summer in 1986 and lack of snow in winter. The northern range was pock-marked throughout the winter with the feeding craters of elk (*Cervus elaphus*) and bison, indicating that both species could travel and forage essentially at will. Yet the first movement of about 100 bison occurred when the snow cover west of Tower was 60–80 mm, with little more to the east. These animals initially bypassed the extensive, easily accessible Blacktail foraging areas. Also, park records indicated that ≥200 bison usually wintered in the Lamar area from about 1952 through 1964 regardless of the severity of the winter. During the mild winter of 1986–1987 <200 bison were counted there on 11 aerial surveys.

Use of the plowed road for relatively easy and energy-efficient travel probably facilitated learning and a rapid increase in numbers. The road traverses suitable foraging sites, and that would have further encouraged use. This route appears to be the least likely under undisturbed conditions. The Yellowstone River gradient (Fig. 1) forms a natural topographical route for several species of wildlife, where the trail maintained by the National Park Service probably has facilitated travel in a few rough areas. Movement might have been confined to the river trail in the absence of the plowed road, but it seems probable that without human efforts to block the river trail, major movements there also would have increased.

Prior experience with particular routes and new foraging areas may have been a major factor in the rapid increase in large movements. Leadership may shift among several older females (McHugh, 1958). This, with intermingling and shifting of group members (Lott and Minta, 1983; Rutberg, 1984; Van Vuren, 1983), would facilitate learning. Repetitive air observations indicated that knowledge of various travel routes and new foraging areas was widespread.

The acquired knowledge of areas having less snow appears to have added impetus to the bison movements. Apparently bison have inhabited deep snow areas in Yellowstone for centuries (Meagher, 1973a). Mixed groups were observed to forage regularly in snows 600 mm deep (Houston, 1982):

however, Telfer and Kelsall (1984) rated bison as poorly adapted for snow. They may do best where deep snows do not persist.

Historically, bison were extremely gregarious (Roe, 1970). Group size appears related to habitat interspersion, with larger groups in more open habitat (Van Vuren, 1983), and on flatter ground (Rutberg, 1984). Bison appear to be generalist foragers, requiring large quantities of forage (Houston, 1982). The habitat in Yellowstone National Park is mostly forested except for the valleys which are the ungulate winter ranges. Houston (1982) noted that a combination of wet meadows, swales, and mesic grasslands accounted for 70–90% of bison observed feeding, but there are relatively few such sites that are both extensive and accessible for the aggregation of large groups in winter. Eleven aerial surveys in winter 1986–1987 suggested that larger aggregations occurred more often in the new areas, but the correlation was not significant (r Blacktail = 0.42, r Mammoth–Gardiner–Reese = 038; $P > 0.05$). The ultimate cause of large groups of bison is not clear. Homogeneity and density of forage, facilitation of sight and communication among individuals, less snow, or some combination of these factors may be involved.

Bison distribution on the northern winter range appeared to be unstable geographically by 1987. In contrast, the northern Yellowstone elk appear to have undergone a gradual expansion of habitat use and reestablishment of migratory patterns. Elk movements involved only a portion of the population, with a variably sized migratory segment which correlated with severity of winter weather (Houston, 1982). In bison, essentially all the population was moving except for some scattered males, regardless of winter conditions. McCullough (1985) characterized bison as showing truly nomadic long-range movements with migratory patterns demonstrable in some locations. The present northern Yellowstone situation may represent an intermediate stage between a migratory and a nomadic pattern of land use.

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Summer Range and Elk Population Dynamics in Yellowstone National Park

Evelyn H. Merrill and Mark S. Boyce

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The limitation of food resources in winter is often pointed out as the mechanism that creates density-dependent effects in ungulate populations. Nutrition during winter and spring particularly influences female reproductive performance and juvenile survival. Poor nutrition of females during gestation increases weight loss, depressing calf birth weight and delaying birth date (Sadlier 1969; Thome, Dean, and Hepworth 1976; Robinson 1977; Hamilton and Blaxter 1980). In turn, low birth weight and late birth decrease neonatal survival (Sadlier 1969; Guinness, Clutton-Brock, and Albon 1978; Clutton-Brock, Major, Albon, and Guinness 1987). As a population increases, winter survival decreases among light-born calves and the number of late-born calves increases (Clutton-Brock et al. 1987; Clutton-Brock, Albon, and Guinness 1988).

Winter weather can modify density-dependent effects or act independently. In red deer (*Cervus elaphus*), birth weight is closely related to temperatures during the latter stages of gestation but is not correlated with population density (Albon, Guinness, and Clutton-Brock 1983). Picton (1984), however, found in Montana that weather can have significant effects on calf recruitment in elk, but only when populations are high. Survival of elk calves in northwestern Wyoming depends on both climate and population size, whereas cow survival is mediated by climate (Sauer and Boyce 1979, 1983; Boyce 1989). In Yellowstone National Park, population size and winter weather affect calf recruitment in elk (Houston 1982).

Little research has focused on the consequences of summer forage dynamics to ungulate population dynamics, primarily because high-quality forage is usually abundant and the extensive summer ranges of most ungulates are not easily surveyed. Klein (1970) argued, however, that even though winter population size and weather may regulate population numbers, summer-forage quality is responsible for decreases in body size of deer at high population levels. Indeed, experimental evidence indicates that mule deer fawns on marginal or low nutritional diets after weaning are lighter in body weight and smaller in most skeletal parameters by mid-December (Verme and Ozoga 1980b). Because survival and age of maturity are related to body weight (Hamilton and Blaxter 1980; Saether and Haagenrud 1983; Lindstedt and Boyce 1985; Albon et al. 1986), limited growth during summer due to poor nutrition may reduce recruitment and reproductive performance.

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We have suggested elsewhere that annual variation in summer-forage quality in Yellowstone National Park is primarily related to phenological development (Merrill et al. 1988). During winters of heavy snow accumulation, plant phenology on summer ranges is delayed, providing high quality forage through late summer, whereas in low-snowfall years greenup occurs early, providing high-quality forage early in the season. We showed that annual variation in plant phenology can be detected on summer ranges in Yellowstone National Park using remote sensing.

In this chapter we test the hypothesis that food resources on summer ranges explain a significant portion of the variation in population growth and calf recruitment of elk in Yellowstone National Park beyond that attributable to population size and winter weather. We predict increased calf recruitment and population growth in years when high-quality forage is available early in the spring and late into the fall.

STUDY AREA

We studied data from elk populations that winter on the northern range of Yellowstone National Park. The geology of this region has been described by Keefer (1972), and general descriptions of soils and vegetation in the park are given by Despain (1973), Meagher (1973), and Barmore (1985). Elevations range from approximately 1,500 to 3,300 m. The climate of the park is characterized by long, cold winters and short, dry summers. Climatic patterns vary considerably within the park (see Houston 1982). Mean annual precipitation is 41.5 cm and 67.0 cm at Mammoth, Wyoming, and Cooke City, Montana, respectively. Mean daily temperature at Mammoth is –7.3° C in January and 18.3 ° C in July; at Cooke City temperatures are –10. 3° C and 13.9° C for January and July, respectively.

Winter range used by the northern elk herd is generally a stappe or shrub steppe with interspersions of conifers. High-elevation summer ranges include more continuous coniferous forests, sagebrush–grasslands, wet meadows, herb lands, and alpine tundra.

We focused our study on the portion of elk summer range along the northeastern boundary of the park from Mount Norris to the north, southeast to Miller Creek, and southwest to the Mirror Plateau. Some elk that summer in this area also winter in the Sunlight and Crandall drainages east of the park (Rudd 1982), but most winter along 80 km of the Lamar, Yellowstone, and Gardner River drainages (Houston 1982).

METHODS

Population Characteristics

Population numbers, sex and age classification, and harvest information for elk were obtained from Houston (1982), Meagher (unpubl. data), Singer (1988b), and the Montana Department of Fish, Wildlife, and Parks (1987). Because annual population surveys were made from December to late January, we assumed that survey numbers did not include the majority of mortality that occurred that winter.

Hunting eliminates elk from the northern herd when animals move out of the park into Montana. Harvest from Unit 316 north of the park in Montana, which occurs in September and October, includes a relatively small number of animals (80–146 elk) that would winter within the park. Elk harvest from the late Gardiner hunt (Unit 313) generally occurs in January and February. Harvest levels have been variable in this unit, peaking at 1,462 animals killed in 1984. Early harvests from Unit 313 probably include both resident and park elk (K. Alt and F. Singer, personal communication).

Climatic Data

Our selection of climate variables was based on observations offered by Houston (1982), who indicated that Cooke City has a cooler, wetter climate than Mammoth and best represents conditions on elk summer range (Houston 1982), whereas Mammoth best represents winter range. Mean temperature and total precipitation were obtained from weather stations at Cooke City, Montana, and Mammoth, Wyoming, for the months November through August (U.S. Department of Commerce and National Oceanic and Atmospheric Administration 1970–1988). When possible, missing weather data for these stations were obtained from regressions from either Yellowstone Lake, Tower, or Mammoth weather stations.

A winter-severity index was calculated from December through March precipitation and temperature measurements from Mammoth. This index provides a single numerical estimate of relative severity of winter by summing inverse signs (+ or –) of deviations from average monthly precipitation and temperature. Our index was similar, but negative to the index as described by Houston (1982). Signs for precipitation were reversed, because snow impedes feeding and increases locomotive costs, that is, below-average temperature contributes to a positive winter-severity index and above-average precipitation contributes to negative winter severity. Consistent with

Houston (1982), we used winter weather data from Mammoth, Wyoming.

Summer Range Phytomass

Vegetation was sampled in 1,300 plots at twenty-five sites scattered across the study area (figure 17.1). Vegetation data and spectral values taken from Landsat Multi-Spectral Scanners for the same field sites on August 6, 1987, were used to derive an algorithm which predicted green herbaceous phytomass from spectral values. This algorithm was used in conjunction with Landsat imagery from previous years to calculate annual green herbaceous phytomass (kg/ha) in summer for eleven years between 1972 and 1987 on a 330-km portion of the summer range. Only nonforested areas were included in our calculations. Based on the among-site variation for 1987 we then estimated green herbaceous phytomass for Landsat images from 1972 to 1987. Details of these methods are given by Merrill et al. (1988).

Estimates of green herbaceous phytomass exhibited a strong pattern dependent on the date of the satellite pass, which we suspect is largely attributable to annual variations in phenology. To correct for this effect, we calculated the average seasonal decline in green phytomass during 1972–1987 using a maxima function. Throughout this chapter, summer phytomass will refer to the difference between the average green herbaceous phytomass for a particular date and our estimate of green herbaceous phytomass.

Use of these estimates as forage available to elk on summer ranges assumes (1) that our estimates of herbaceous green biomass paralleled growth patterns of plants actually used by elk, and (2) that nonforested communities contributed most to nutrient acquisition by elk, because these are the only communities for which herbaceous phytomass estimates can be made using remote sensing.

Since a strong quadratic correlation was found between yearly estimates of summer pytomass and winter precipitation ($r = .81, p < .01, n = 11$:Merrill et al. 1988), we used this relationship to estimate summer phytomass for three years for which we had elk population data (1971, 1977, and 1985).

Data Analysis

The relations among ungulate population characteristics, winter severity, and summer phytomass, X_is, were evaluated using multiple regression (Kleinbaum and Kupper 1978) of the general form

$$y(t) = b_0 + b_1 N(t) + b_2 X_2 + \ldots \quad \text{(Eq. 1)}$$

where b_i is the regression coefficient for each independent variable and $N(t)$is the total winter count at t. Here, per capita population growth rates are defined

$$r(t) = \ln\{[N(t+1) + H(t+1)]/[N(t) - LGH(t)]\} \quad \text{(Eq. 2)}$$

where $N(t)$ is the winter population count minus adult males in year t (see Houston 1982), $LGH(t)$ is kill of

Figure 17.1 Capacitance meter used for sampling green herbaceous phytomass on Mount Norris, northeastern Yellowstone National Park.

elk during the late Gardiner hunt (Unit 313) in year *t*, and H(*t* + 1) is the harvest from Unit 316 in year *t* + 1. Proportion of cow elk with calves (approximately eight months) or yearlings (approximately twenty months) "at heel" was transformed using an arcsine–square root transformation (Zar 1974) prior to data analysis.

Multiple-regression models of per capita growth rates were rewritten as difference equations. These equations were used for predicting the dynamics of elk populations based on population size, summer phytomass, in the form

$$N(t+1) = N(t)\exp[b_0 = b_1 N(t) + b_i X_i(t) + \ldots] \quad (Eq.\ 3)$$

with b_i defined to be the regression coefficient and X_is to be the independent variables, as in table 17.1. By using mean values of climate and summer phytomass (X_i), this model collapses to a different equation approximation of the logistic model, with *N* ultimately converging on carrying capacity, *K*, that is, where $r(t) = 0$. We also used this model to calculate predicted values of $N(t)$ for each year where $X_i(t)$ was assigned observed values for year *t*.

Table 17.1 Multiple-regression models for elk population parameters as a function of environmental variables during 1971–1988, Yellowstone National Park.

Dependent variable	Coefficients b_i	Variables X_i	r	p	n
$r(t)$	0.43		.936	<.03	8
	–0.0003	$N(t)$			
	–0.0230	Winter(t)			
	–0.00036	Phyto(t)			
$C(t+1)$	0.8		.890	<.01	9
	–0.000022	$N(t)$			
	–0.00018	Phyot(t)			
$YR(t+1)$	0.514		.880	<.05	9
	–0.000019	$N(t)$			
	–0.005	Winter(t)			
	–0.0002	Phyto(t)			

Notes: *N* = winter count of elk conducted by the National Park Service.

Winter = Winter-severity index based on Mammoth weather data for December–March.

Phyto = average herbaceous green phytomass (kg/ha) on summer range estimated for over 330 km and corrected for date.

C = arcsine–square root of the proportion of cow elk with calves at heel.

YR = arcsine–square root of the proportion of cow elk with yearlings at heel.

$r(t)$ = per capita growth rate for elk defined at equation 2.

RESULTS

Summer phytomass and winter weather had significant effects on per capita growth rate of elk and bison after accounting for the effects of population size (table 17.1). Summer phytomass explained 77 percent of the variation in elk population growth rates after accounting for population size and weather effects (figure 17.2). The proportion of cow elk with calves at heel was significantly correlated with summer phytomass ($r^2 = .61, p = .05, n = 9$) as was the proportion of cow elk with yearlings at heel ($r = .74, p < .05, n = 9$) after the effects of population size were removed. Winter severity contributed significantly to variation in yearling recruitment ($p < .05$), but not calf recruitment ($p > .10$).

Using equation 2 and coefficients from table 17.1, and solving for *N* where $r = 0$, we predict a *K* of approximately 14,522 elk, assuming long-term average winters and summer phytomass. The logistic curve associated with this carrying capacity is illustrated by the solid line plotted in figure 17.3. If average winter weather and summer phytomass are similar to those during 1985–1988, however, a *K* of 17,819 elk would prevail. This value compares favorably with a mean count of 17,445 for 1985–1988. Furthermore, using equation 3 with coefficients from the first model in table 17.1, the mild winters in recent years predict almost precisely the large count of 19,043 elk observed in 1988 (figure 17.3).

Our results indicate that summer phytomass has a significant effect on the population dynamics of elk in Yellowstone Park, although its expression is complicated by density and weather effects. Density-dependence effects on pregnancy rates, number of cows with calves at heel, and calf survival during a period when park removals kept population levels below

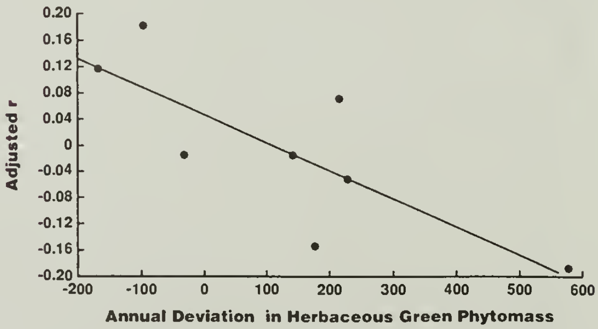

Figure 17.2 Per capita growth rate for elk (eq. 1) corrected for winter severity and population size, as a function of herbaceous green phytomass on summer range corrected for date.

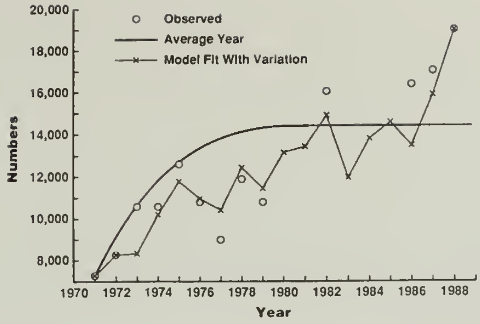

Figure 17.3 Observed winter census of elk in Yellowstone National Park plotted with a logistic fit to the data (solid line). The line with Xs indicates the counts predicted from equation 3 using observed values of winter severity and summer phytomass.

carrying capacity have already been reported (Fowler and Barmore 1979; Houston 1982). Population numbers are currently at or above carrying capacity where we would expect density-dependent effects to be fully expressed (Fowler 1987).

Winter weather explained a significant amount of variation in two of the three population parameters for which we had data. Because winter weather effects on elk calf survival to the first winter (autumn cow:calf ratios) have been well documented (Fowler and Barmore 1979; Houston 1982; Clutton-Brock et al. 1987), especially at high population levels (Picton 1984), we suspect that with a larger data set we would have detected such an effect. Data used in estimating number of cows with calves at heel was highly variable, representing both ground and helicopter surveys from various observers. Also, different investigators sampled in different areas, potentially creating bias and inflating the among-year variance in population parameters. For example, more calves are usually seen near roads, where counts concentrated in early years (Singer 1988b). Singer (1988a) reviews variation in distribution that may influence sampling, but we are not aware of any systematic biases that would affect our results.

After the effects of population size were removed, summer phytomass explained a significant amount of variation in all the population parameters we examined. Elsewhere we have described that less green phytomass is available in middle to late summer in years when green-up (1) occurs early in spring on ungulate summer ranges and a large proportion of the available ungulate forage is cured by early summer, or (2) is delayed so that green biomass does not reach average levels by midsummer (Merrill et al. 1988). This conclusion was based on a quadratic correlation between green summer phytomass in midsummer and December–March precipitation ($r = .81, p < .01, n = 11$) and suggests that snow accumulation and melt exert an important influence on summer plant phenology.

We suggest that early spring green-up results in high nutrition during the latter stages of gestation, which increases birth weight and juvenile survival (Thorne, Dean, and Hepworth 1976; Clutton-Brock et al. 1987) and is reflected in high male yearling:cow ratios. High nutritional levels at these stages also decrease maternal weight loss, allow cows both to obtain a threshold body weight necessary for conception and to enter the winter with large fat reserves.

In years of high snow accumulation, delayed phenology may provide a higher quality diet for a longer period in late summer and fall than in years of early or average phenological development. Clutton-Brock and Albon (1989) found that when September was dry or rainfall was high, a smaller proportion of red deer milk hinds conceived and overwinter survival of calves and yearlings was lower than in average years. They concluded that drought and heavy rainfall was associated with early decline in food availability and high rains with increased heat loss.

We have focused our attention on summer ranges used by the northern elk herd. Without further investigation, we cannot rule out the possibility that production on summer range is correlated with influences on winter range. For example, delayed phenology may retard the timing of the growth cycle in plants on the winter range so that nutrients normally translocated to roots are fixed in the aerial portions during summer senescence and therefore available (Anderson and Scherzinger 1975).

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ELK POPULATION PROCESSES IN YELLOWSTONE NATIONAL PARK UNDER THE POLICY OF NATURAL REGULATION[1]

Michael B. Coughenour
Francis J. Singer

Natural Resource Ecology Laboratory
Colorado State University
Ft. Collins, Colorado 80523 USA

Abstract The interrelations of weather, plant production and abundance, and elk population dynamics on Yellowstone's northern winter range were examined for a 23-year period when there was minimal human offtake from the herd. Significant correlations between precipitation and plant production, between elk population responses and precipitation, and between elk population responses and elk population density strongly suggested that forage limited elk population growth. Although population responses to density have been documented previously in Yellowstone, responses to precipitation have not. Correlations between elk population responses and annual precipitation were presumably consequences of plant growth responses to precipitation and subsequent effects on elk nutritional status. Population regulation was most consistently achieved through the responses of juveniles rather than adults. Winter mortality of juveniles was primarily correlated with elk numbers, whereas recruitment was primarily correlated with precipitation. Adult mortality rates were not significantly correlated with elk numbers, but were correlated with precipitation. Per capita rate of increase was negatively correlated with elk number but 55% of the variance was density-independent. There was evidence that winter weather affected the elk, but season-long weather indices had poor predictive power. A stage-structured population model using regression equations of mortality and recruitment rate responses to precipitation and elk numbers predicted that the population could vary within a range of approximately 16,400 ± 2,500 sighted elk (mean ± 1 SD).

Key words: Cervus elaphus; *elk; natural regulation; population; Yellowstone National Park.*

Introduction

The effectiveness of ecological controls on ungulate populations, even in the largest wildlife reserves, is still debated. Ungulate populations may be regulated without human interference through food limitation (Caughley 1976, Sinclair 1977, Sinclair et al. 1985, Novellie 1986, Fryxell 1987, Dublin et al. 1990, Owen-Smith 1990), predation (Bergerud et al. 1983, Messier and Crete 1985, Borner et al. 1987, Fryxell et al. 1988), disease (e.g., Sinclair et al. 1985), and weather (e.g., Picton 1979, 1984, Mech et al. 1987, Merrill and Boyce 1991). Although food-limited ungulate populations should tend towards dynamic equilibria with forage (Caughley 1976), a population may be unable to track the dynamic equilibrium when interannual forage variability is high (Caughley 1987, DeAngelis and Waterhouse 1987, Ellis and Swift 1988). There is a broad continuum of human disruption of these natural mechanisms. Unnaturally large ungulate concentrations and attendant range damage may occur where wildlife reserves are small compared to the ungulate's natural range, particularly where reserve boundaries do not circumscribe an ecologi-

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cally complete habitat, or where migratory or dispersal movements have been impaired (Jewell and Holt 1981, Owen-Smith 1983, Coughenour 1992). Impaired dispersal is not a problem in very large African and Alaskan unfenced wildlife reserves, however (e.g., Murie 1944, Sinclair and Norton-Griffiths 1979, Fryxell and Sinclair 1988). Somewhere along this spectrum lies the northern Yellowstone elk *(Cervus elaphus)* population of Yellowstone National Park (hereafter YNP). YNP is a moderately large (889,571 ha), unfenced reserve, partially surrounded by human land use and hunting corridors that act as partial barriers to ungulate movements and, until 1995, lacked the most significant predator of ungulates, the wolf *(Canis lupis).*

If one management objective is to conserve natural processes within the reserve, then human controls on ungulate populations are justifiable if, and only if, there is scientific evidence that ecological limitations on population growth have broken down and the habitat is not ecologically complete (Cole 1971). Otherwise, human interventions could interfere with the natural processes of population regulation. Conversely, nonintervention should be justified with evidence that natural population processes are intact. The 1916 U.S. National Park Service (NPS) Organic Act directed that the fundamental purpose of the parks is to "conserve the scenery and the natural and historic objects and the wild life therein." Conditions within parks should "be maintained as nearly as possible in the conditions that prevailed when the area was first visited by white man. A national park should represent a vignette of primitive America" and the NPS should make an effort to restore "an illusion of primitive America" (Leopold et al. 1963). The preservation of pristine ecosystems, and thus natural processes, has been a part of NPS management philosophy throughout the agency's existence (Houston 1971, Baur 1987).

Human interventions and noninterventions with the northern Yellowstone elk herd have been controversial. For 70 or more years, there have been divergent viewpoints on the nature and effectiveness of ecological limitations on that population (see Houston 1982 and Coughenour and Singer 1991 for reviews). The herd was intensively culled from 1935–1968. On average, 2,040 elk were removed each year in an attempt to alleviate or prevent presumed range damage. By 1935, early park managers believed elk were too abundant because they were protected from hunting inside the park, wolves were eliminated by the 1930s, native American hunters were absent, and migrations out of the park were impaired by human occupation and unrestricted hunting (Graves and Nelson 1919, Skinner 1928, Grimm 1939, Cahalane 1943, Pengelly 1963). The carrying capacity of the winter range has been calculated at 5,000–7,000 elk based upon numerous questionable assumptions about available foraging area, forage production, forage requirements, and proper levels of use to maintain good range condition (Grimm 1939, Cooper 1963). Artificial regulation was partly based on the assumption that elk populations with low rates of increase and high mortalities were unnatural (Cole 1971). Thus, "economic carrying capacity," i.e., the number of animals that maximizes animal production and minimizes "wastage," was apparently confused with the nonconsumptive "ecological carrying capacity," i.e., the number of animals that results from food limitation (Houston 1971, Caughley 1976, and see Coughenour and Singer 1991).

From 1962–68 negative public sentiments about large elk culls increased to national proportions (Olsen 1962, 1968, Kay 1990). Private hunters, in particular, objected to the government culls. In 1967, U.S. Senator McGee (Wyoming) chaired a subcommittee which led to a hearing, and a directive from the U.S. Department of the Interior and the NPS to stop the culling (Kay 1990).

From 1962–69, the policy of artificial regulation was questioned on scientific grounds, in view of the paucity of data about how populations of ungulates were regulated in pristine ecosystems, questionable assumptions about the role of predation, theoretical and empirical evidence that herbivores should come into a natural balance with their forage, and the clear mandate that natural processes be preserved in national parks (Cole 1971). Furthermore, elk appeared to have an ecologically complete habitat, including ample winter as well as summer range within the protected area (Cole 1971). Thus, there appeared to be a strong possibility that artificial regulation was inconsistent with the objectives and management policies of natural areas (Cole 1971).

Since 1968, the northern Yellowstone elk herd has been managed under a philosophy of natural regulation, on the premise that most of the elk herd existed in an ecologically complete habitat, and that "...over a series of years, naturally regulated ungulate populations were self-regulating units. They regulated their own mortality and compensatory natality in relation to available winter food and their population size" (Cole 1971, Houston 1976). Food limitation is the central mechanism of the natural

Table 1. Northern Yellowstone elk counted during winter censuses, sightability-corrected estimates, and offtake from the regular hunt (approximately 19 October–30 November) including Montana units 313 and 316, and the late hunt (usually 15 December–15 Febuary).

Year	Actual winter count	Sightability-corrected winter count	Regular hunt offtake	Late hunt offtake
1968/69	4305		46	
1969/70	5593		50	
1970/71	7281		82	
1971/72	8215		149	
1972/73	9981		265	
1973/74	10529		316	
1974/75	12607		252	
1975/76	12014		327	1207
1976/77	8980*		219	
1977/78	12680		239	803
1978/79	10838		311	70
1979/80	10108		189	487
1981/82	16019		344	1015
1985/86	16286		456	1059
1986/87	17007	23350	893	843
1987/88	18913	22779	379	215
1988/89	10991*	22048	487	2352
1989/90	14829	20964	833	423
1990/91	9451*	16036	301	684

* The actual count was considered to be poor. See *Methods: Elk Population Analyses* for method of correction.

regulation hypothesis. Predation was proposed to assist, but not be essential to the natural regulation process. Recent analyses have suggested that wolf reintroduction might reduce northern Yellowstone elk herd size 5–30% (Boyce 1993, Mack and Singer 1993). There are divergent views about the effect of hunting by native Americans (Houston 1982, Kay 1990).

Under the natural regulation policy the herd grew from <4,000 in 1967 to approximately 12,000 by 1975 (Table 1). Hunting offtake outside the park was increased from 165 per year from 1968–75 to 1,246 elk per year from 1975–91, but the herd nevertheless grew to nearly 19,000 sighted elk by 1988. Vegetation on windswept and often snow-free areas, a small fraction (<5%) of the winter range, was fully utilized by the elk even at the end of the period of artificial reductions (Cole 1971, Houston 1976, Cayot et al. 1979). Herbaceous vegetation on the winter range has not degraded (Houston 1982, Coughenour 1991, Frank and McNaughton 1992, 1993, Coughenour et al. 1995, F.J. Singer, K.K. Symonds, and A. Harding, *unpublished manuscript*), but riparian woody plants, particularly willows (*Salix* spp.) and aspen *(Populus tremuloides),* have declined. Most of the willow declines occurred during the 1920s–1940s (Kay 1990, Singer et al. 1994) when 10,000–15,000 elk were believed present. Aspen cover declined since the park was established, and there has been very little recruitment of large-stemmed aspen stands since 1870–1890, which was a unique period ecologically (Warren 1926, Romme et al. 1995).

Our objective here is to investigate whether the northern Yellowstone elk herd has been limited by food and winter weather under the natural regulation policy from 1969–91. The potential effects of elk on vegetation and soils, and the appropriateness of the plant-herbivore system are treated elsewhere and are beyond the scope of this study. Previous research has provided evidence that the northern Yellowstone elk herd is regulated by density-dependent competition, presumably for food (Houston 1982, Merrill and Boyce 1991). There has been little documentation showing that ecological carrying capacity varies in response to interannual forage production. Elk die-

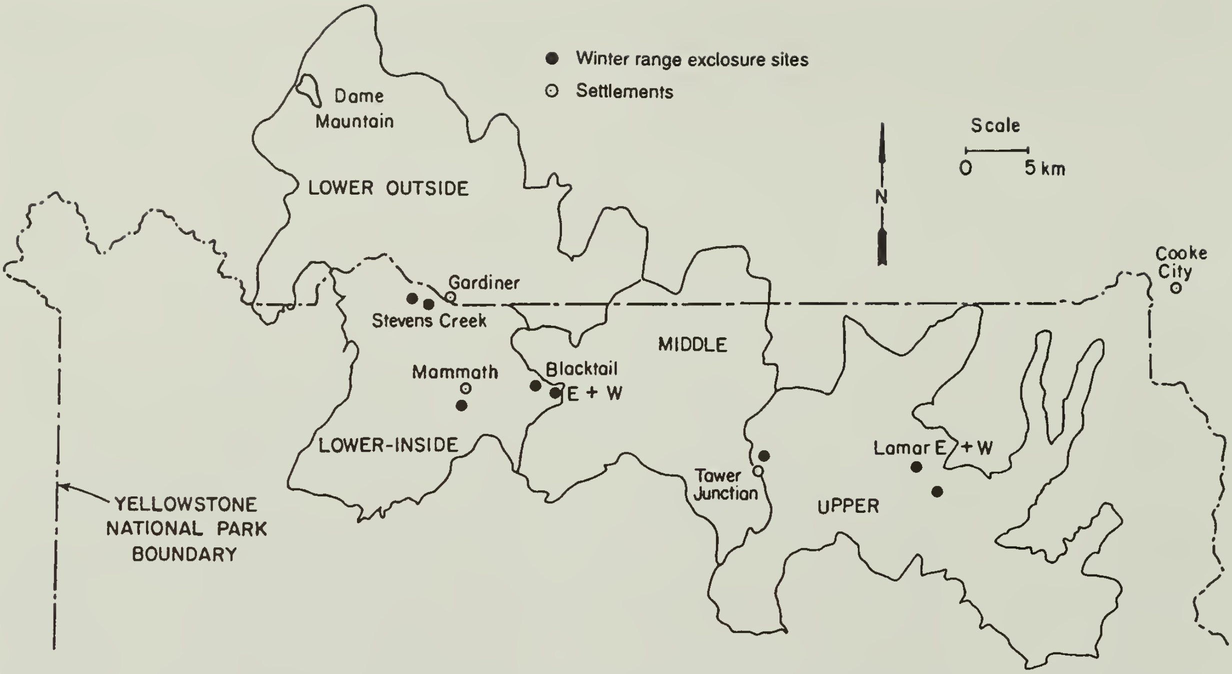

Figure 1. The northern Yellowstone elk winter range showing outside, lower, middle, and upper elk count sectors.

offs and poor recruitment have long been associated with severe winter weather (Skinner 1928, Pengelly 1963, Houston 1982, Merrill and Boyce 1991). We examine elk population and distribution data collected on Yellowstone's northern winter range from 1969–90, forage production and precipitation data from 1935–88, and 1969–90 weather data, to determine whether forage supply, precipitation, and winter weather have limited the size and growth rate of the elk population. If forage limits elk population growth, we expect to observe the following relations:

(1) Intraspecific competition for a limited supply of available forage will result in significant positive correlations between population size and mortality, and negative correlations between population size and recruitment. As population size increases, the proportion of newborns and subadults in the population will decline.

(2) Forage production will be positively affected by precipitation.

(3) Population parameters will be correlated with annual precipitation. Recruitment rates should be higher and mortality rates lower during or immediately following wet years. If plant growth is limited by water and elk are limited by plant production, then significant positive correlations should be observed between population growth and precipitation or between recruitment and precipitation (e.g., Owen-Smith 1990).

(4) Population responses will be time-lagged behind precipitation. Winter calf mortality should be negatively correlated, and summer calf recruitment should be positively correlated with plant growth in the previous summer. Higher winter calf proportions will be positively correlated with precipitation two summers prior, since winter calf proportion reflects previous winter and summer mortality.

Methods

Study Area

The current northern Yellowstone elk winter range encompasses lands inside and outside the northern portion of the park, mainly at low elevations in the Lamar and Yellowstone River valleys (Fig. 1). Houston (1982) delimited an area of 100,000 ha which included 17,000 ha of land outside the park that was available to elk by 1982. The elk range has expanded, however. A current range size of 140,000 ha was defined by connecting outermost animal locations observed during aerial surveys 1986–90.

About 100,000 ha of the 140,000 ha lie within Yellowstone National Park while 40,000 ha lie north of the park boundary on Gallatin National Forest and private lands. The boundary shown in Fig. 1 corresponds to the outermost perimeter of elk count units covering 141,921 ha, of which 97,238 ha lie within the park. Two new count units at the northernmost end of the range were added in 1986, bringing the total area counted to 148,893 ha.

Elevations of the northern winter range vary from 1,500–2,400 m. Mean annual precipitation ranges from 24 cm at Gardiner, Montana (1,731 m elevation), to 39 cm at Mammoth (2,032 m), 41 cm at Tower (2,056 m), 35 cm at the Lamar Ranger Station (2,112 m), and 65 cm at Cooke City (2,445 m). Most of the northern winter range is steppe or shrubsteppe (55%), dominated especially by Idaho fescue *(Festuca idahoensis),* bluebunch wheatgrass *(Pseudoroegnaria spicatum),* and big sagebrush *(Artemisia tridentata).* Conifer forests *(Pseudotsuga menziesii, Pinus contorta)* cover 41% of the range, along with small amounts of aspen *(Populus tremuloides,* 2.0 %), and willow *(Salix* spp., 0.4%).

Weather Data

Daily precipitation, snowfall, and minimum and maximum temperatures in the study area were recorded from 1929–91 at Mammoth Hot Springs, 1931–91 at Tower Falls, 1929–76 at Lamar Valley, 1936–91 at Gardiner, and 1967–91 at Cooke City. Precipitation data were summarized by site and season (fall, September–October; winter, November–March; spring, April–May; summer, June–August). Precipitation from September of the preceding year through August of a given year was summed to yield "water-year precipitation," which is meaningful because fall and winter precipitation may be stored in the snowpack or soil, and because plant growth measurements were always made prior to mid-September. Gardiner, Montana precipitation data were used in correlations with plant growth measurements for the "lower" winter range (Fig. 1). The average of precipitation data at Mammoth, Tower, and Lamar was used in correlations of plant growth measurements on the "upper" winter range. Water-year precipitation for the winter range as a whole was obtained by averaging Gardiner, Mammoth, Lamar, and Tower data.

Winter severity indices were calculated using probit analyses of April snow depths and minimum winter temperatures (Farnes 1995). The percent probability of nonexceedence (PN) of the mean was subtracted by 50% and divided by 12.25 to compress the range of 1% through 99% (PN) to -4 through +4. Farnes's index ranged from -4 = most severe, to 0 = normal, to +4 = most mild. Separate indices were calculated for snow and temperature. A combined snow and temperature severity index was calculated as the average of the snow and temperature severity indices.

Forage Biomass

Herbaceous biomass production data collected in Yellowstone were utilized in our analyses of production-precipitation relationships. Measurements of herbaceous (grass, forb, half-shrub) standing crops on the Yellowstone winter range were made by park personnel using "volume plots" in 1935–41, 1947 (n = 14–16 plots per year), 1949, and 1950 (n = 4 plots per year) (Grimm, 1935–38, Gammill, 1939–41, Kittams 1948–50). All herbage was clipped from a 32.7 m x 32.7 m area in mid- to late summer, air-dried and weighed. Herbaceous plant growth was studied in more detail in 1986–88 (Coughenour 1991, Singer 1995). In mid- to late summer, peak standing crops were sampled inside and outside 2-ha exclosures constructed from 1958–62. In 1986, biomass was measured in 10 1-m^2 quadrats; in 1987, 15 0.25-m^2 quadrats were randomly located within each of 10 m x 10 m paired plots at each exclosure (Singer 1995). Plots were paired inside vs. outside with respect to slope, aspect, and soil. There were two plot pairs at Mammoth, two at Blacktail, one at Junction Butte, two at Lamar, and two at Stevens Creek. In 1987 and 1988, biomass was sampled in four 0.25-m^2 circular quadrats randomly located within each of four 5 m x 5 m plot pairs at each of four exclosures (Coughenour 1991). Biomass on all quadrats was clipped to ground level, sorted, oven-dried and weighed. Green standing biomass of grass and forbs plus dead forb biomass was taken as a best estimate of current season production, since nearly all standing dead grass appeared to be carried over from prior seasons. In 1987, when biomass was sampled on two dates, the maximal of the two values was taken as being the "peak" biomass for the season. Data taken outside the Mammoth exclosure in 1986 were not used because a local group of elk had not migrated off the winter range and had been grazing there prior to sampling.

Forage measurements taken from lower winter range sites at 1,500–2,000-m elevation were distinguished from those taken from higher winter range sites. The lower winter range included areas below

Mammoth and near the park boundary at Gardiner, Montana (Fig. 1). Lower winter range growing conditions are relatively xeric, and the much lower snowfall, faster melting and wind removal of snow from the slopes result in easy access to forage and high use by wintering elk. Correlations and regressions were calculated separately for the corresponding upper and lower range precipitation data.

Elk Population Analyses

Elk total numbers and ratios of calves, yearling males (spikes), and bulls to cows from 1969–90 were estimated by YNP biologists (Barmore 1980, Houston 1982, Singer 1991). Elk were counted from fixed-wing aircraft during a 1–3-day period in early winter (December–January) 1952–79 (Houston 1982). Two aircraft were used to count elk in the winter of 1981/82 but no more counts were made until 1985/86. From 1985/86 to 1990/91 elk counts were completed in a single day using four aircraft simultaneously. The winter range was divided into 68 count units based on topographic features. All units were fully surveyed in complete counts, whereas partial counts were conducted by fully surveying only a portion of the total 68 count units.

Aerial censuses were affected by factors that influence the "sightability" of the animals such as tree cover, snow cover, group size, and observer. Sightability-corrected estimates can be made by developing an empirical model of how sightability is affected by these factors in each census. Sightability models were derived from the numbers of radio-collared animals observed from fixed-wing aircraft in each census 1986/87 to 1990/91 (Singer and Garton 1994). Unseen animals were radio-located from a second fixed-wing aircraft. Eleven counts during winters of 1986/87 to 1990/91 were corrected for sightability (Singer and Garton 1994); however, only five were complete counts conducted during early winter. Six were partial counts or late-winter counts, and thus were not used in our analyses. Three of the five complete counts were "good," with sightability proportions of 0.70–0.91, and two were "poor," with sightabilities of 0.49–0.65 (Table 1).

Since sightability estimates were made in five out of 19 data-years (Table 1), we performed analyses using all 19 years of uncorrected count data rather than omitting 14 years of uncorrected data. However, certain of the counts provided exceptionally low estimates because of poor counting conditions. Those counts were obviously inconsistent with counts in the prior and subsequent years. The count in winter 1976/77 was poor (Houston 1982), so a calibrated sex and age class population projection model (Mack and Singer 1993) was used to estimate the ratio of population size in 1976/77 to that in 1975/76, which was 0.82:1. This yielded a sightability-uncorrected estimate, which was used in statistical tests and plots. Counts in winters of 1988/89 and 1990/91 were also exceptionally poor. Sightability estimates were available for counts in these two years, however. Sightability-uncorrected estimates for those two years were derived by reducing the sightability-corrected estimates by the mean fraction sighted in the other "good" counts (sightability proportion of 0.75).

Classifications were conducted from helicopters or on the ground. Winter range elk classification samples were separated into four elevation sectors: (1) upper sector, including the Lamar Valley, where winter snow depths are deepest and tend to average 0.6–0.7 m; (2) middle sector where snow depths are only slightly less, approximately 0.5 m, (3) lower-inside park sector where the ground is bare or snow depths are <0.3 m, and (4) lower-outside park sector, at lowest elevations with similarly shallow snow depths, and where the 3-month-long hunting seasons affect the migratory elk (Fig. 1).

In classification counts, "calves" were those animals less than one year old. "Spikes" were <1-year-old animals. "Spikes" were male (bull) elk that would be approximately 1.5–1.75 years old in December–January (yearlings). "Cows" were female elk >2 years old. "Bulls" were male elk > 2 years old. Calf:cow, spike:cow, and bull:cow ratios were compared between sectors of the early- and late-winter range, using the Friedman two-way analysis by ranks test with count units as replicates. Bull ratios are not reported prior to 1988 for early winter or 1985 for late winter, since classifications were done from the ground along the park roads and trails, and tended to underrepresent higher elevation winter range sites favored by bull elk.

Two annual hunts affect the elk herd as they move outside the park into Montana. A regular hunt occurs during 19 October to 30 November, and a late hunt occurs 15 December to 15 February. Data on hunter harvests obtained from the Montana Department of Fish and Game were used to estimate pre-hunt elk population sizes. Hunting removals averaged <9% of the herd in these sectors each year (Table 1).

Winter calf mortality rate was calculated as

$$\mathrm{wclfm}_t = \frac{(\mathrm{aclf}_t - \mathrm{ayrl}_{t+1})}{\mathrm{aclf}_t},$$

where aclf_t is number of calves estimated to have been present in autumn of elk-year *t* (Fig. 2), and ayrl_{t+1} is number of yearlings estimated to be present in autumn of the subsequent elk-year *t+1*. The number of animals in autumn is estimated as the number counted in the winter count, plus the number taken off during the regular hunting season. The number of fall yearlings is

$$\mathrm{ayrl}_{t+1} = \mathrm{aspk}_{t+1}(1+\mathrm{fmr}),$$

where aspk_{t+1} is the number of yearling males in autumn of year *t+1* and fmr is a typical ratio of female to male yearlings (0.66:0.44, Houston 1982). The equation for winter calf mortality thus assumes negligible mortality of yearlings during the summer.

Summer calf mortality rate can be estimated as

$$\mathrm{sclfm}_{t\text{-}1} = \frac{(\mathrm{adcow}_t \times \mathrm{brth}_t) - \mathrm{aclf}_t}{(\mathrm{adcow}_t \times \mathrm{brth}_t)},$$

where brth_t is births per adult cow in year *t*, and adcow_t is number of adult cows in year *t*. Adult cow number in autumn (adcow) is the total number of pre-hunt (autumn) cows (acow), minus the number of pre-hunt yearling females. The birth (calving) rate is based on observed pregnancy rates, which appear to vary in response to elk density. When the elk population was small in 1967/68 (4,272 elk), a pregnancy rate of 0.87 was observed (Houston 1982). A pregnancy rate of 0.82 was observed in 1952 when the population was >13,500 (Houston 1982), and in 1990/91 a pregnancy of 0.82 was noted when the population was 12,024 (T. Lemke, *personal communication*). However, when the population was 17,773 in 1986/87, a pregnancy rate of 0.61 was observed (T. Lemke, *personal communication*). Thus, we assumed that pregnancy rate varies in proportion to elk population size within these ranges.

An estimate of calf recruitment rate into the population over the prior summer is

$$\mathrm{clfr}_{t\text{-}1} = \frac{\mathrm{aclf}_t}{\mathrm{adcow}_t},$$

expressed as calves per adult cow. This estimator for calf recruitment rate is not influenced by uncertainties in values for pregnancy rates, whereas the summer calf mortality estimator is. Actual recruitment, however, is influenced both by pregnancy and by summer calf mortality. Only if pregnancy rate were a constant would recruitment rate be solely influenced by summer mortality.

Cow mortality was calculated as the difference in cow numbers from one fall to the next and corrected for known hunting removals. Furthermore, we accounted for the addition of new cows (yearling females) to the autumn population of the second year. Yearling females were estimated from spike (yearling male) numbers and a yearling female:male ratio of 0.66:0.44 (Houston 1982). Bull mortality was estimated following Houston (1982), as the difference between bull numbers in year *t* + 1 minus bull numbers in year *t* and was corrected for hunting offtake. Cow and bull mortalities were converted to mortality rates (number dying per number alive) by dividing the total mortality by the population size at the beginning of the period.

Winter of 1988/89 mortalities were estimated differently. The direct count in early winter of 1988/89 was poor (10,908 elk seen). A sightability-corrected estimate was 22,048 elk. Sightability-corrected estimates of two counts made in April 1989 were 12,590 and 13,367 elk, mean 12,978 elk. In total, 2,352 elk were removed during the late hunt. Thus, we estimate that 6,718 elk died. Lemke and Singer (1989) counted and classified carcasses on and north of the park boundary. They estimated a proportional carcass composition of 0.46 calves, 0.21 bulls, and 0.33 cows. Thus, 3,090 calves, 1,410 bulls, and 2,217 cows died. Based on early-winter herd composition, the winter mortality rates were then estimated as 0.83 of the calves, 0.60 of the bulls, and 0.14 of the cows. The calf mortality rate is in agreement with the value of 0.84 determined by studies of radio-collared calves marked as newborns (F.J. Singer, K.K. Symonds, and A. Harding, *unpublished manuscript*).

The actual per capita rate of increase (r_a) was defined by

$$\frac{dN}{dt} = r_a N$$

and

$$N_{t+1} = N_t e^{r_a \Delta t},$$

where Δt equals one year, and N_t is population size in year *t*. Thus, r_a was calculated as

$$r_a = \ln\left(\frac{N_t+1}{N_t}\right),$$

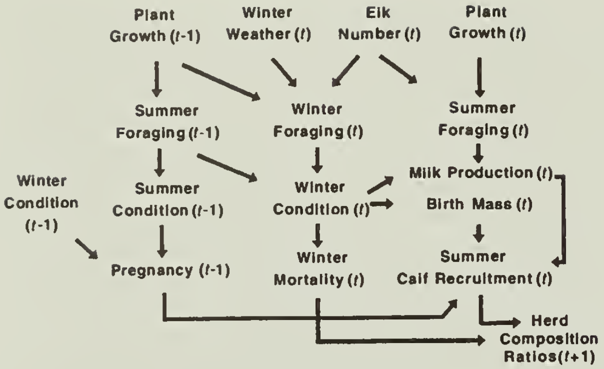

Figure 2. Causal pathways and time lags between plant growth and elk population responses in elk-years $t - 1$, t, and $t + 1$. An elk-year begins on 1 November.

where N_t is the post-hunt population size in year t (pre-hunt size minus hunting removal), and where N_{t+1} is the pre-hunt population size in year $t + 1$.

An "elk-year" begins just prior to the beginning of the regular hunting season. Changes in herd composition as reflected in calf:cow, spike:cow, and bull:cow ratios were potentially affected by vegetation abundance during the previous two elk-years (Fig. 2). Elk sex and age ratios in elk-year *t + 1* (corrected to pre-hunt) might reflect (1) the effects of plant growth during the summer of elk-year $t - 1$ on summer foraging and calf survivorship in that year *(t - 1)*; (2) the effects of plant growth in summer of elk-year $t - 1$ on winter foraging, elk condition, and either winter mortality or summer calf recruitment in year t; (3) the effects of winter weather conditions on elk foraging or thermal stress in elk-year t; or (4) the effects of elk population size in elk-year t on intraspecific competition for forage in winter and summer of year t.

Winter mortality rates in elk-year t could be affected by plant growth in elk-year $t - 1$. Plant growth in year $t - 1$ may affect foraging during winter of year t or it may affect foraging during the summer of year $t - 1$ and elk nutritional status going into winter of year t (Fig. 2). Winter mortality rate in elk-year t would respond to winter weather in the current year through effects on foraging. Winter elk number in year t would affect mortality rate through competition. Summer calf recruitment in year t could respond to plant growth and total elk population size in year t, but it is more probably affected by the condition of the pregnant female and by calf birth weight, which are affected by foraging in the summer of year $t - 1$ and the winter of year t.

A stage-structured model was constructed with calf, cow, and bull elk classes. Recruitment and mortality rates of each class were modeled using the best equation determined from forward stepwise multiple regression analyses, with precipitation amounts and elk number as the independent variables. The exact equations are given in the *Results.* The model was initialized with elk numbers in 1968/69. The model was tested against observed elk sightings from 1969–90. The model was then run for 30 simulations, 28 years each, randomly choosing each year of weather from the 1931–90 data set. Normally distributed stochastic variation with a standard deviation of 25% of observed mean recruitment or mortality rate was added to simulate variance not explained by the regression models.

Results

Aboveground Plant Biomass

Total live plus dead biomass measured on the early volume plots from 1935–50 varied from 17–120 g/m^2 on higher winter range sites and from 14–115 g/m^2 on the lower winter range sites. Mean total standing crop was 52.8 ± 25.0 g/m^2 (mean ± 1 SD) on lower winter range sites, compared with 66.6 ± 30.5 g/m^2 on higher winter range sites. Total biomass was significantly correlated with water-year precipitation (Tables 2 and 3). The slope of the regression line indicated an increase of approximately 1.8 g/m^2 of biomass for each cm of precipitation. More of the variation in total biomass was explained by seasonal (58–59%) than by water-year (34%) precipitation models (Table 3). Total biomass appeared to respond most strongly to spring precipitation, but summer and fall precipitation also contributed significantly to explaining the variance. Winter precipitation explained little of the variance in total biomass, and so was eliminated in the backwards regression procedure.

Green plant biomass 1986–88 was most strongly correlated with winter precipitation inside exclosures and with spring precipitation outside exclosures (Table 2). Green biomass was not correlated with summer or fall precipitation, either inside or outside exclosures. Winter precipitation alone explained 51% of the variance in green biomass inside exclosures, while spring, fall, and summer precipitation amounts were eliminated in the backwards regression analysis (Table 3). Green biomass

Table 2. Correlation coefficients *(r)* of the 1986-88 estimates of green herbaceous biomass (g/m^2) inside or outside exclosures, or total (live plus dead) herbaceous biomass outside exclosures 1935-41, 1947, 1949-50, 1987-88, with seasonal or water-year precipitation or elk number. For green biomass inside, $n = 18$ (3 years x 6 sites); for green biomass outside, $n = 16$ (sites x years) (Mammoth sites were excluded due to summer grazing). For total biomass outside, $n = 24$ (sites x years).

	Green biomass		Total biomass
Factor	Outside	Inside	Outside
Precipitation			
Fall	-0.01	0.08	0.25
Winter	0.27	0.72†	0.17
Spring	0.49*	0.14	0.42*
Summer	0.29	0.35	0.49*
Water-year	0.38	0.53*	0.55†
Elk Number			0.26

* $0.01 < P < 0.05$

† $P < 0.01$

inside exclosures was more strongly correlated with winter precipitation than total water-year precipitation.

Elk Distributions

The proportion of the elk herd counted north of YNP, including known hunting offtake (Table 4), was not correlated with winter temperature ($r = -0.20$) or snow ($r = -0.41$) severity indices ($n = 16$ years). The proportion of elk that were counted plus harvested north of the park was not significantly correlated with years since cessation of artificial control in 1968 ($r = 0.21$, $P = 0.43$). However, the total number of elk counted north of the park each winter was weakly correlated with years since cessation of artificial control ($r = 0.47$, $P = 0.06$), suggesting that migration increased. A significant portion of the variance in total elk north of park was related to time and winter severity in a multiple regression analysis ($r^2 = 0.42$, $P = .026$). The numbers of elk counted on Dome Mountain at the northernmost extremity of the winter range increased markedly after 1988 as a result of the large migration in winter 1988/89.

Calf:cow ratios varied among sectors of the winter range in early winter (Table 5) during seven of nine years for which classification data were available (Friedman test, $P < 0.01$). The Jonkhere ordered-alternative test suggested calf:cow ratios were ordered from highest to lowest in the sectors as follows: lower-outside = lower-inside > middle > upper ($S = 36$, $P < 0.04$). Spike:cow ratios were lower in the middle and upper sectors during four of eight winters of early winter classifications (Table 5, $P < 0.05$). These results suggested a greater tendency of cow-calf groups and yearlings to migrate to lower elevations in winter.

Calf:cow ratios differed among various sectors of the winter range during five of six late-winter periods (Friedman test, $X^2_r = 69$, $P < 0.01$). The Jonkhere ordered alternative test indicated calf ratios were ordered from highest to lowest in the sectors as follows: outside = lower > middle > upper ($S = 41$, $P < 0.03$). Spike:cow ratios varied among sectors during only one of five late winters ($P < 0.05$) and the pattern was the opposite of that observed during early winters; harvests of spikes outside the park and migrations may have obscured patterns of yearling survivorship. Bull:cow ratios were higher in the middle and upper sectors of winter range than in the lower sectors during three winters, 1985–88 ($P < 0.05$). The response was reversed in the winter of 1988/89, when more bulls were observed outside the park ($P < 0.05$) in late winter. However, this could have resulted from the unusually high hunting offtake of cows (1,864) relative to bulls (48) in the winter hunt in 1988/89.

Calf:cow ratios declined in some or all sectors between early and late winter during four of five winters in which data were available (Table 5), suggesting significant differential over-winter mortality rate of calves compared to cows. Low relative mortality of calves in winter 1989/90 could have been the result of a moderate winter and reduced population size. Spike:cow ratios declined over all winters. Bull:cow ratios declined during two winters and increased in two winters.

Elk Population Responses

Negative correlations were observed between winter spike:cow ratio and elk number in the previous elk-year ($r = -0.84$, $P < 0.001$), and between bull:cow ratio and elk number in the previous elk-year ($r = -0.78$, $P < 0.001$). Calf:cow ratio was not significantly correlated with population size ($r =$

Table 3. Backwards elimination regression analysis of green biomass (1986-88) inside ($n = 16$) or outside ($n = 18$) exclosures, or total live-plus-dead biomass outside ($n = 20$) exclosures (1935-41, 1947, 1949-50) with fall (FALL), winter (WINT), spring (SPRN), and summer (SUMR) precipitation amounts (cm) and significant regressions on total water-year (WTYR) precipitation (cm). Value in parenthesis is probability of exceeding F, based on Type II sum of squares, followed in the last model by the partial correlation coefficient of the variable. Partial r^2 of eliminated variables can be computed by difference in r^2 between successive models. All terms not significant at $P < 0.1$ level were eliminated to yield the final model.

Dependent variable	Independent Variables	r^2	P
Total biomass outside	= -25.79 + 2.30 FALL (0.070) - 0.55 WINT (0.618) + 9.45 SPRN (0.008) + 2.37 SUMR (0.043)	0.59	0.007
	= -27.99 + 2.20 FALL (0.071, 0.10) + 8.92 SPRN (0.007, 0.29) + 2.38 SUMR (0.038, 0.19)	0.58	0.002
	= - 0.33 + 1.83 WTYR (0.340)	0.34	0.007
Green biomass inside	= 10.61 + 2.73 FALL (0.533) + 3.97 WINT (0.002) + 2.03 SPRN (0.620) - 0.79 SUMR (0.345)	0.59	0.021
	= 32.97 + 0.72 FALL (0.648) + 4.01 WINT (0.001) - 0.41 SUMR (0.197)	0.58	0.008
	= 35.70 + 3.98 WINT (0.007) - 0.31 SUMR (0.147)	0.58	0.002
	= 32.60 + 3.74 WINT (0.001, 0.51)	0.51	0.001
	= 34.04 + 0.87 WTYR (0.024)	0.28	0.024
Green biomass outside	= -57.57 + 8.24 FALL (0.030) + 0.37 WINT (0.639) + 9.47 SPRN (0.004) - 1.32 SUMR (0.188)	0.65	0.014
	= -52.56 + 7.65 FALL (0.024) + 9.22 SPRN (0.003) - 1.081 SUMR (0.185)	0.64	0.005
	= - 21.87 + 3.79 FALL (0.006, 0.34) + 6.37 SPRN (0.001, 0.24)	0.58	0.003

-0.43). Calf:cow and bull:cow ratios were positively correlated with precipitation in year $t - 2$ (Fig. 3). Spike:cow ratio was also correlated with precipitation, but the relationship was weaker ($y = -3.9 + 0.34x$, $r^2 = 0.27$). Calf:cow ratio was positively correlated with winter ($r = 0.47$, $P < 0.05$) and summer ($r = 0.48$, $P < 0.05$) precipitation in year $t - 2$. Spike:cow ratio was significantly correlated with winter precipitation in year $t - 2$ only ($r = 0.44$, $P < 0.05$). Bull:cow ratio was not significantly correlated with precipitation in any single season.

Herd composition was not significantly correlated with any measure of winter weather severity including winter temperature, winter

Table 4. Winter severity indices and numbers of elk north of Yellowstone National Park, 1970-91.

Year	Winter temperature severity index*	Winter snow severity index*	No. elk counted north of park†	Proportion of herd north of park‡	No. elk counted on Dome Mountain north of park
1970/71	1.5	-3.2	600	0.082	
1971/72	0.7	-2.6	1300	0.158	
1972/73	2.9	2.9	800	0.080	
1973/74	0.0	-3.8	800	0.076	
1974/75	0.7	-2.0	2786	0.221	
1975/76	2.0	-3.4	1700	0.189	60
1976/77	3.1	3.3	500	0.039	80
1977/78	1.1	-2.4	2200	0.203	258
1978/79	-4.0	-1.6	1500	0.138	389
1979/80	-0.4	1.4			
1980/81	3.0	3.8			
1981/82	-0.3	-1.9	1097	0.068	
1982/83	3.1	1.0			
1983/84	-2.9	2.1			
1984/85	-2.6	0.3			477
1985/86	0.9	1.4	2998	0.184	135
1986/87	2.7	3.7	1723	0.101	298
1987/88	1.5	3.1	483	0.026	105
1988/89	-3.3	-1.9	5290	0.338	1938
1989/90	1.5	-0.6	3400	0.229	2139
1990/91	-3.4	1.5	1400	0.097	722

* The ranking indes varies from -4.0, most severe, to +4.0, mildest (Farnes (1994).

† Data from Houston (1982) and F.J. Singer (*unpublished data*).

‡ Includes elk taken in the regular hunt prior to the count.

snowfall, winter temperature severity index, winter snow severity index, winter snow and temperature index, or snow water contents in year t - 1. Correlations between spring precipitation in year t - 1 and calf:cow (r = -0.40), spike:cow (r = -0.40), and bull:cow (r = -0.30) ratios were nearly, but were not, statistically significant (P > 0.05).

Forward stepwise multiple regression analyses of herd composition parameters showed the sensitivity of calf:cow ratio to precipitation (Table 6). Winter and summer precipitation, or water-year precipitation, were included in the best models for calf:cow ratio. Elk numbers did not enter into calf:cow ratio models. Elk numbers entered first into models for spike:cow and bull:cow ratios. Water-year precipitation explained less of the variance in spike:cow and bull:cow ratios than did elk numbers. Fall and spring precipitation amounts both helped explain variations in bull:cow ratios. No seasonal precipitation amount entered significantly into the spike:cow ratio model.

Calf mortality rates were generally higher than cow and bull mortality rates. Summer calf mortality rate was 0.52 ± 0.16 (mean ± 1 SD), n = 16 years. Mean winter calf mortality rate was 0.32 ± 0.29, n = 15 years. Mean cow mortality rate was 0.08 ± 0.09, n = 15. Mean bull mortality rate was 0.18 ± 0.18, n = 15. Summer calf mortality rate was significantly higher than winter calf mortality rate (P = 0.05, t = 2.0). Summer calf mortality rate was negatively correlated with precipitation (Fig. 4A), but it was not correlated with elk population size (r = 0.33) or any winter severity index, including winter and spring precipitation, or temperature or snow severity indices in year t. Summer calf recruitment rate was positively correlated with winter (r = 0.52, P < 0.05), summer (r = 0.54, P < 0.05) and water-year precipitation (Fig.

Table 5. Elk herd composition on lower, middle, and upper sectors of the northern winter range and outside the park boundary in early and late winter. "Lower-in" and "Lower-out" refer to lower sectors inside and outside the park, respectively.

	No. calves per 100 Cows		No. spikes per 100 Cows		No. bulls per100 Cows		Sample Size	
	Early	Late	Early	Late	Early	Late	Early	Late
1982/83								
Lower-In	46		6				780	
Upper	27*		7				250	
Total	41		6				1030	
1983/84								
Lower-In	47		18				581	
Upper	25*		5*				364	
Total	38		12				945	
1984/85								
Lower-In	48		12				433	
Upper	24*		3*				461	
Total	34		7				894	
1985/86								
Lower-Out	56	35		3		1	3039	779
Lower-In	66	57*		4		18	583	414
Middle	52	25		3		32	305	1565
Upper	32*	20*†		5		28*	2446	454
Total	48	30†	4	3	26	21	5363	3212
1986/87								
Lower-Out	42	32*		4		6	1930	1759
Lower-In	46	22		6		16	1253	2276
Middle	36	18		6		18	895	4836
Upper	21*	19*†		13*		50*	1496	522
Total	33	22†	7	6	16	16	5574	9393
1987/88								
Lower-Out	44	21*		5		2	1560	724
Lower-In	48	27†		4		8	485	1497
Middle	40	21†		4		27	985	2672
Upper	32*	17		5		168*	1667	356
Total	40	25†	5	4	19	26	4967	7470
1988/89								
Lower-Out	30	19				27		1615
Lower-In	18	8†	7	3	19	14	956	817
Middle	25*	6†	2	3	31	20	962	794
Upper	24	4*†	2	1	28*	10*	695	1011
Total		9†	3	2	26	19†	2613	4237
1989/90								
Lower-Out		37*		4		32		413
Lower-In	21	41	3	3	19	19	737	1109
Middle	19	15	4	3	22	18	3255	1131
Upper	18	19†	6*	3	17*	13†	1487	287
Total	19	20	5	3†	20	14†	5479	2940
1990/91								
Lower-Out	28	21					319	357
Lower-In	42	27	10		12		2207	624
Middle	23	30	8		15		1281	288
Upper	21*	27	5		13		2210	1627
Total	27	26	6		13		6017	2896

* Significant difference among winter range areas ($P < .05$).
† Significant different between early and late season ($P < .05$).

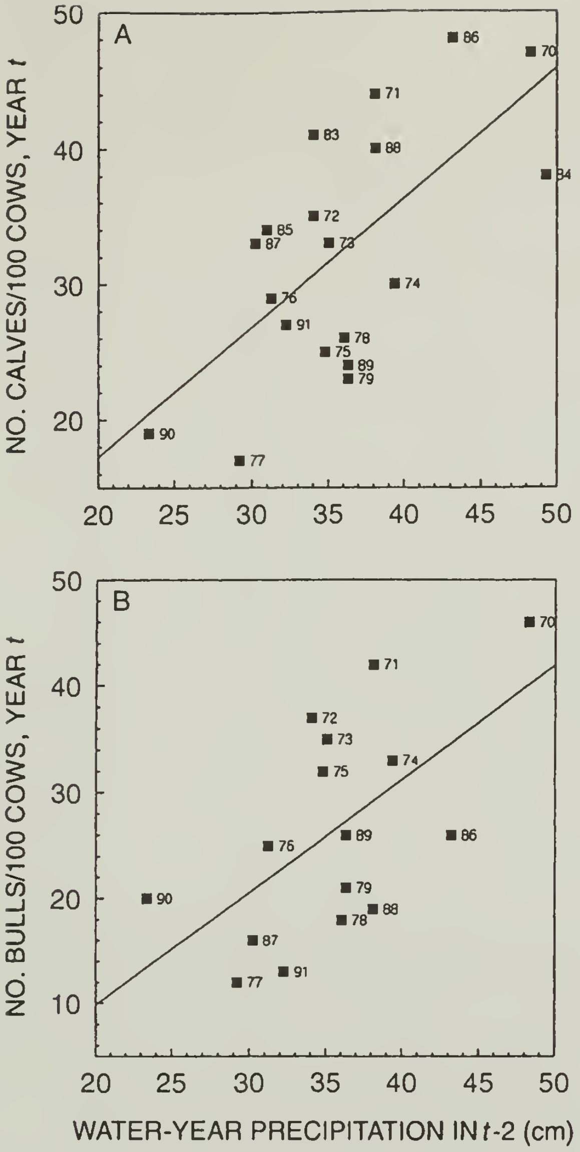

Figure 3. Relations between ratios in early winter 1970-90 (year t) to water-year precipitation of two seasons prior (year t - 2): (A) calf:cow, $y = -1.9 + 0.95x$, $r^2 = 0.43$, and (B) bull:cow, $y = -11.6 + 1.07x$, $r^2 = 0.36$. Points are labeled by year, where year 68 is winter 1967/68, for example.

4B), and negatively correlated with elk number (Fig. 5A). Winter calf mortality rate was negatively correlated with fall ($r = -0.54$) and water-year precipitation (Fig. 4C) in year t - 1. Winter mortality rate was strongly correlated with elk number (Fig. 5B). There were no correlations between winter calf mortality rate and any measure of winter weather severity, although winter mortality rate was correlated with spring precipitation in year t ($r = 0.61$, $P < 0.05$).

Cow mortality rate was not correlated with water-year precipitation ($r = -0.02$) or elk number ($r = 0.28$). Although cow mortality was not correlated with any measure of winter weather severity in year t, it was positively correlated with precipitation in the previous spring ($r = 0.54$, $P < 0.05$). Bull mortality rate was negatively correlated with water-year precipitation (Fig. 4D), and with fall ($r = -0.75$, $P < 0.01$) and summer ($r = -0.78$, $P < 0.01$) precipitation in the previous year. Like cow mortality, bull mortality was positively correlated with spring precipitation in the previous year ($r = 0.54$, $P < 0.01$), and was not correlated with any measure of winter weather severity in the current year. Bull mortality rate was not significantly correlated with elk number ($r = 0.39$).

Per capita rate of increase was not significantly correlated with water-year precipitation ($r = 0.46$, $P = 0.06$), but a trend was present. Per capita rate of increase was positively correlated with fall precipitation ($r = 0.58$, $P < 0.05$) and negatively correlated with spring precipitation ($r = -0.49$, $P < 0.05$) in year t - 1. The per capita rate of increase was negatively correlated with total elk numbers (Fig. 6, Table 7). By definition of carrying capacity, K, in the logistic equation, the actual per capita rate of increase (r_a) is equal to zero when population size (N) equals K:

$$\frac{dN}{dt} = rN\left(\frac{K - N}{N}\right), \qquad \textit{and}$$

$$r_a = r\left(\frac{K - N}{N}\right),$$

where r is the intrinsic rate of increase. In Fig. 6, along the lowest line of r_a vs. N, r_a = zero at approximately 10,000 sighted elk. Conversely, the uppermost line of r_a vs. N in Fig.6 defines a maximal K of approximately 18,000 sighted elk.

Forward stepwise regression analyses indicated that summer calf recruitment was most closely tied to precipitation rather than elk number (Table 7). Summer and winter precipitation were both retained in the best model. Elk number entered the model first, followed by winter and then summer precipitation. Then elk number was removed in the forward stepwise regression procedure, to leave only winter and summer precipitation in the final model. The final model based upon precipitation had a higher r^2 and was more significant than the model based upon

Table 6. Forward stepwise regression analyses of arcsine of calf, spike, and bull ratios during elk-year t against precipitation in the winter (WINT), fall (FALL), summer (SUMR), spring (SPRN) of elk-year t - 1, and winter elk numbers (ELK) in elk-year t; or against water-year precipitation (WTYR) and ELK. Value in parenthesis is probability of exceeding F. Partial r^2 of eliminated variables can be computed by difference in r^2 between models. All terms in the last model are significant at the $P = 0.15$ level. Variables not entered in the last model did not meet the $P = 0.15$ significance level. Number of years is given in n.

Dependent Variable	Independent Variables	r^2	P	n
Arcsine (Calf:Cow$_t$)	$= 0.156 + 0.016\ \mathrm{WINT}_{t-2}$	0.23	0.036	19
	$= 0.056 + 0.014\ \mathrm{WINT}_{t-2}$ (0.047) $+ 0.009\ \mathrm{SUMR}_{t-2}$ (0.051)	0.40	0.017	19
	$= -0.032 + 0.010\ \mathrm{WTYR}_{t-2}$	0.41	0.003	19
Arcsine (Spike:Cow$_t$)	$= 0.018 - 8.03 \times 10^{-6}\ \mathrm{ELK}_{t-2}$	0.71	0.001	16
	$= 0.085 + 0.0022\ \mathrm{WTYR}_{t-2}$ (0.117) $- 6.5 \times 10^{-6}\ \mathrm{ELK}_{t-1}$ (0.002)	0.77	0.001	16
Arcsine (Bull:Cow$_t$)	$= 0.502 - 1.97 \times 10^{-5}\ \mathrm{ELK}_{t-2}$	0.60	0.007	15
	$= 0.401 + 0.011\ \mathrm{FALL}_{t-2}$ (0.149) $-1.69 \times 10^{-5}\ \mathrm{ELK}_{t-2}$ (0.003)	0.67	0.001	15
	$= 0.214 + 0.229\ \mathrm{FALL}_{t-2}$ (0.030) $+ 0.220\ \mathrm{SPRN}_{t-2}$ (0.091) $- 1.86 \times 10^{-5}\ \mathrm{ELK}_{t-2}$ (0.001)	0.75	0.001	15
	$= 0.229 + 0.0063\ \mathrm{WTYR}_{t-2}$ (0.141) $- 1.52 \times 10^{-5}\ \mathrm{ELK}_{t-1}$ (0.011)	0.67	0.001	15

elk number alone (Table 7). The most significant models for summer calf mortality included summer and winter, or water-year, precipitation.

In contrast, elk number was the first variable to enter the model for winter calf mortality rate (Table 7). Fall precipitation contributed less to the regression. When the number of elk counted was excluded from the analysis, fall and winter precipitation both entered as significant negative terms in a model for winter calf mortality rate. The only significant regression model for cow mortality rate included a positive effect of spring precipitation the prior year. Bull mortality rate was best modeled as decreasing in response to summer and fall precipitation, although water-year precipitation was also a moderately good predictor. The number of elk counted was not a significant correlate with bull mortality rate. The best model for per capita rate of increase included elk numbers and fall precipitation. Although spring precipitation was a significant correlate with per capita rate of increase ($r = -0.49$, $P < 0.05$), it did not significantly enter the model (Table 7). No model of per capita rate of increase based upon water-year precipitation was significant.

The empirical elk population model was based upon equations developed in Table 7. The best equation for calf recruitment rate included summer and winter precipitation. The best winter calf mortality equation included fall precipitation and elk numbers. Cow mortality was best predicted from spring precipitation, and bull mortality was best predicted from fall and summer precipitation. The empirical population model predicted observed numbers of sighted elk from 1969–90 well, using annual hunt rates of 2% of calves and cows and 5% of bulls (Fig. 7). Over the 30 stochastic simulations using the same hunting rates, elk numbers increased, then fluctuated about 16,400 ± 2,500 sighted elk (mean ± 1 SD), varying from lows of approximately 10,000 to highs of approximately 23,000 elk (Fig. 8).

Discussion

Plant Biomass Responses to Precipitation

The positive correlation of aboveground plant biomass with water-year precipitation is in agreement with many studies that have shown that grassland

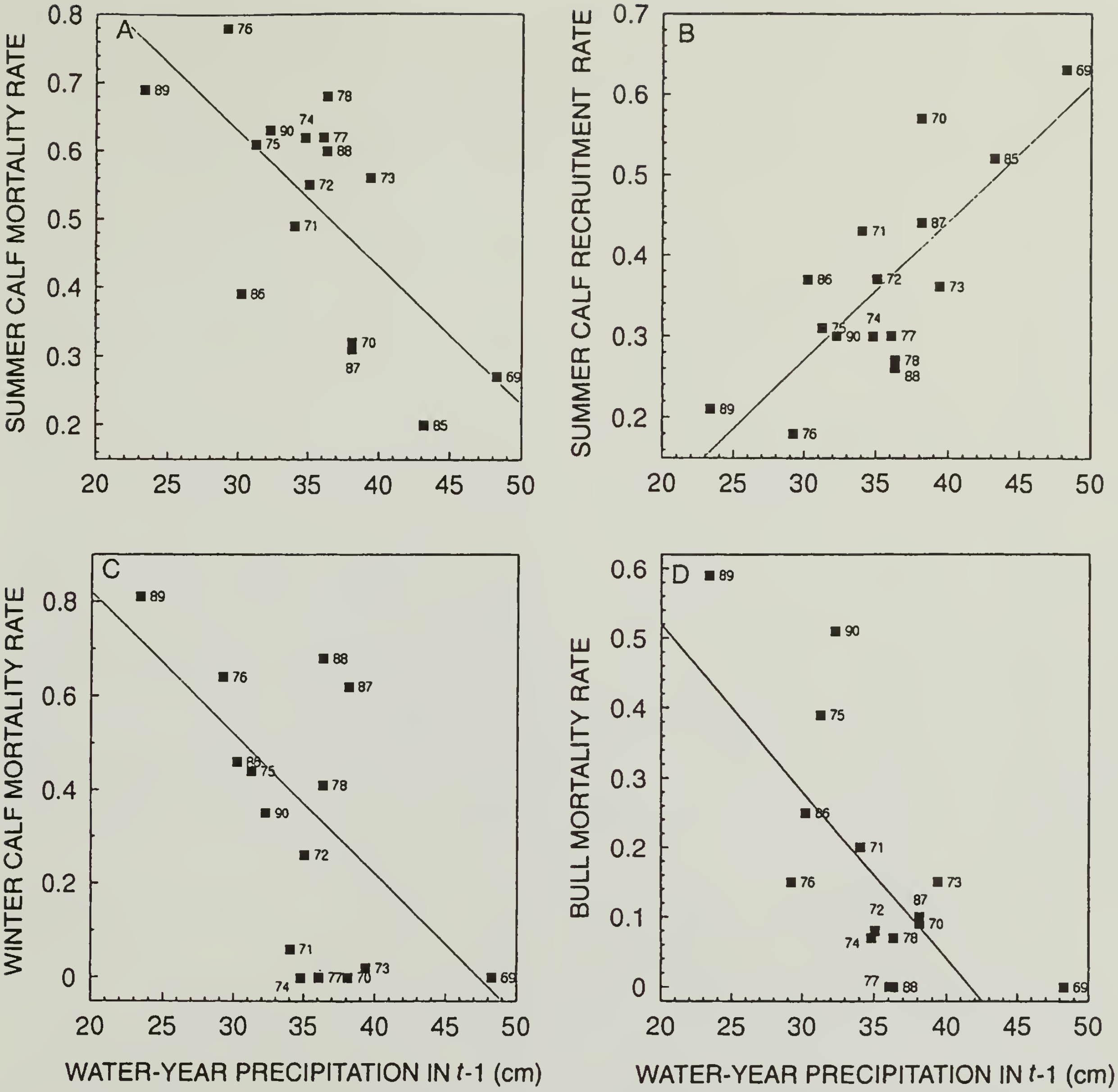

Figure 4. Year *t* responses to prior water-year precipitation (year *t* - 1) of (A) summer calf mortality; (B) summer calf recruitment; (C) winter calf mortality, $y = 1.42 - 0.03x$, $r^2 = 0.37$, $P = 0.01$; and (D) bull mortality (see Table 7 for other regression equations and significance). Points are labeled by year, where 68 is summer of 1968 or winter of 1967/68, for example.

primary productivity is influenced by precipitation (Sims and Singh 1978, Webb et al. 1978, Sala et al. 1988). Most grasslands are water-limited, and are commonly replaced by forests in more mesic climates (e.g., Borchert 1950). The variance in plant biomass data from Yellowstone was not fully explained by precipitation, however. The unexplained variance could have been caused by differences in plants, soils, and landscape positions among plots and sampling sites, and by differences in sampling methodologies. More extensive sampling, integrating over a broader area, could provide a tighter correlation, as more of the among-plot and among-site variance is averaged out (e.g., Sala et al. 1988). Ideally, long-term plant growth data should be collected from the same sites every year, so as not to

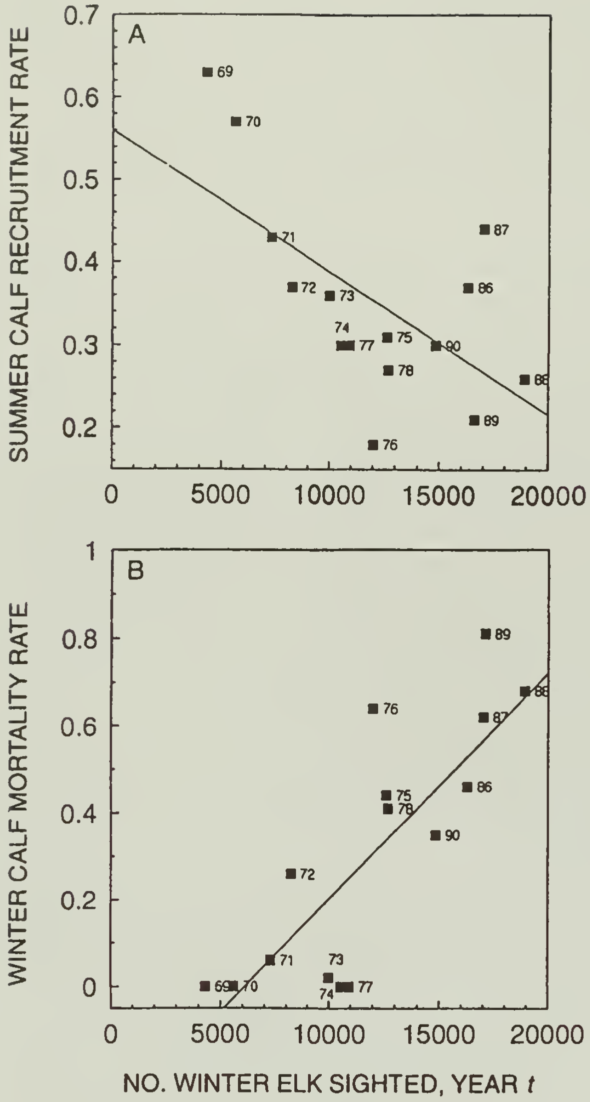

Figure 5. (A) Summer calf recruitment, and (B) winter calf mortality responses in year *t* to winter elk number in year *t* (see Table 7 for regression equations). Points are labeled as in Fig. 4.

confound site and climate effects. Although the ideal long-term data set was not available, we believe the evidence shows that forage biomass is positively affected by precipitation on the northern Yellowstone elk winter range. Data from many other grassland studies support this conclusion.

Plant biomass production was influenced by the distribution of annual precipitation among seasons. Plant biomass was predicted more accurately from equations based upon seasonal precipitation amounts than upon total water-year precipitation. The fact that green and total biomass amounts outside of exclosures were correlated with spring, summer, and fall precipitation, while green biomass inside exclosures was correlated mainly with winter precipitation, suggests that grazing alters the importance of precipitation in different seasons. Possibly, the accumulation of standing dead shoots inside exclosures reduced evaporative losses of winter precipitation from bare soil, and increased interception of spring precipitation by dead leaves and litter, with consequent evaporative loss from these surfaces. By summer, however, soil moisture was not significantly different inside vs. outside of exclosures (Coughenour 1991, Singer and Harter 1995). Total biomass outside exclosures in 1988 was comparable to that in 1987 (Singer et al. 1989, Coughenour 1991) despite the drought in the summer of 1988. Regression results indicated that spring precipitation contributed more grams total biomass per centimeter of water than did precipitation in other seasons. The correlations between spring precipitation and green and total biomass outside exclosures suggests that above-average spring precipitation in 1988 could have supported ample plant growth, but the dry summer of 1988 caused earlier senescence.

The increase in elk numbers from 1969–88 has apparently had little effect on peak herbaceous standing crop on the winter range. Forage biomass

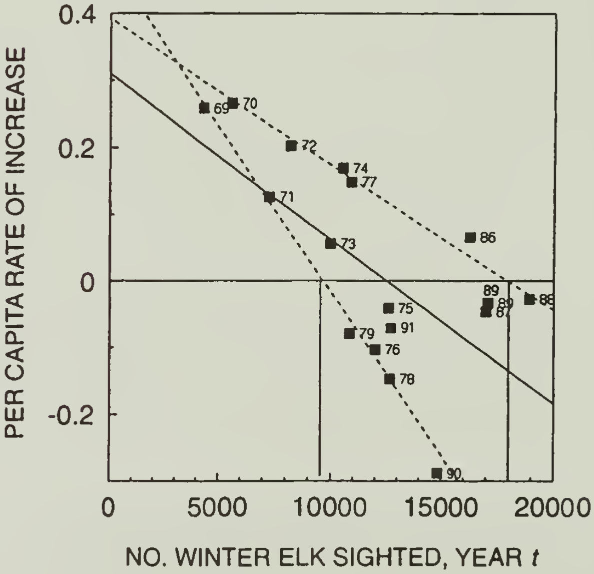

Figure 6. Elk population per capita rate of increase in year *t* vs. winter elk number (see Table 7 for regression). Minimum and maximum lines (dashed) are related to corresponding ecological carrying capacity *(K)* values, where rate of increase (r_a) equals zero.

Table 7. Forward stepwise regression analyses of elk recruitment and mortality rates during elk-year *t* and per capita rate of increase (r_a) against precipitation in the winter (WINT), fall (FALL), summer (SUMR), and spring (SPRN) of elk-year *t* - 1, and winter elk numbers (ELK) in elk-year *t*; or against water-year precipitation (WTYR) and ELK. Value in parentheses is probability of exceeding *F*. Partial r^2 of added or eliminated variables can be computed by the difference in r^2 between models. All terms in the last model are significant at the *P* = 0.15 level. Variables not entered in last model did not meet the *P* = 0.15 significance level. Number of years is given as *n*.

Dependent Variable	Independent Variables	r^2	*P*	*n*
Summer calf recruitment rate	$= 0.570 - 1.8 \times 10^{-5} ELK_{t-1}$	0.42	0.009	15
	$= 0.320 - 1.3 \times 10^{-5} ELK_{t-1}$ (0.050) $+ 0.018\ WINT_{t-1}$ (0.090)	0.55	0.008	15
	$= 0.116 - 0.843 \times 10^{-5} ELK_{t-1}$ (0.196) $+ 0.020\ WINT_{t-1}$ (0.043) $+ 0.010\ SUMR_{t-1}$ (0.010)	0.66	0.007	15
	$= -0.083 + 0.024\ WINT_{t-1}$ (0.013) $+ 0.016\ SUMR_{t-1}$ (0.011)	0.57	0.004	16
Summer calf mortality rate	$= 0.754 - 0.0186\ SUMR_{t-1}$	0.23	0.063	16
	$= 1.01 - 0.025\ WINT_{t-1}$ (0.093) $- 0.0184\ SUMR_{t-1}$ (0.051)	0.38	0.044	16
	$= 1.23 - 0.020\ WTYR_{t-1}$	0.47	0.003	16
Winter calf mortality rate	$= -0.330 + 5.44 \times 10^{-5} ELK_{t-1}$	0.68	0.001	15
	$= -0.090 - 0.027\ FALL_{t-1}$ (0.140) $+ 4.79 \times 10^{-5} ELK_t$ (0.0007)	0.73	0.003	15
Cow mortality rate	$= -0.063 + 0.022\ SPRN_{t-1}$	0.30	0.036	15
Bull mortality rate	$= 0.581 - 0.033\ SUMR_{t-1}$ (0.001)	0.60	0.001	15
	$= 0.646 - 0.033\ FALL_{t-1}$ (0.001) $- 0.022\ SUMR_{t-1}$ (0.011)	0.77	0.001	15
	$= 1.00 - 0.024\ WTYR_{t-1}$	0.51	0.003	15
Per capita rate of increase	$= 0.321 - 2.47 \times 10^{-5} ELK_t$ (0.003)	0.45	0.003	17
	$= 0.119 + 0.023\ FALL_{t-1}$ (0.057) $- 1.93 \times 10^{-5} ELK_t$ (0.015)	0.57	0.002	17

measured from 1986–88, when 16,000–19,000 elk were counted, was similar to forage biomass from 1935–50, when 10,000–13,000 elk were counted. This is consistent with comparisons of current live standing crop and total cover inside and outside exclosures (Coughenour 1991, Coughenour et al. 1995, Singer 1995) and aboveground primary production (Frank and McNaughton 1992, 1993), which have failed to show conclusive negative effects of elk herbivory on herbaceous vegetation.

Elk Population Responses

The hypothesis that the northern Yellowstone elk herd is nutritionally limited was supported by two relationships. First, the elk appeared to respond to precipitation. Elk population responses to precipitation were most likely caused by variations in forage productivity, given that we have shown forage abundance is correlated with precipitation. Second, the elk population grew less rapidly when elk were more abundant. This strongly suggests that the elk were competing for a limiting resource. Because elk are not limited by water, and they are nonterritorial during winter (Boyd 1978), the limiting resource was most probably food.

Population recruitment appeared to be strongly influenced by precipitation. Early winter calf:cow ratio was highly correlated with precipitation, but was not significantly correlated with population size. Precipitation strongly affected summer calf recruitment and mortality. In contrast, elk numbers had little or no effect on calf:cow ratio, summer mortality, or recruitment. The correlation between precipi-

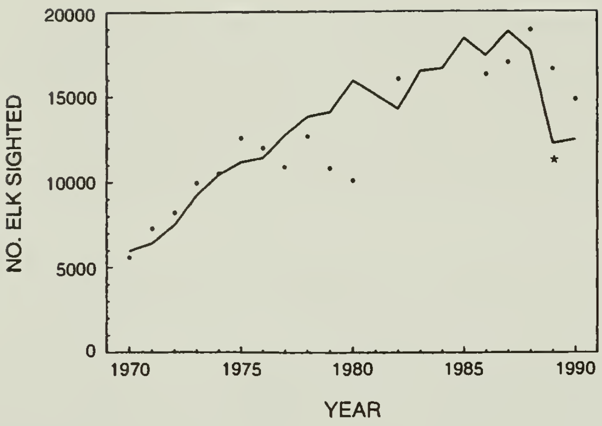

Figure 7. Comparison of observed (points) and simulated (line) numbers of elk. The aseterisk shows the number of elk actually sighted in winter 1988/89.

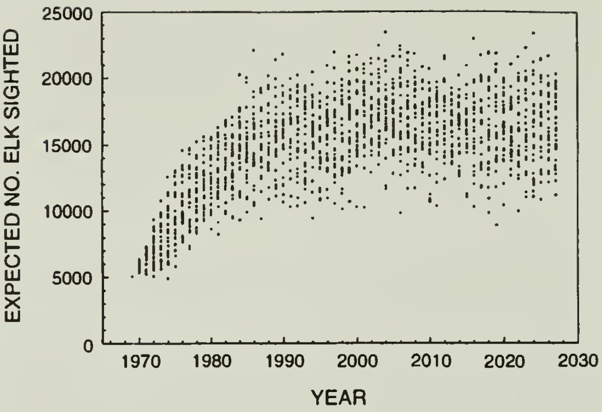

Figure 8. Numbers of elk over time in 30 stochastic simulations.

tation and recruitment rate was stronger than that between precipitation and summer mortality, suggesting that natality rate could also have been influenced by precipitation. The weak response to population size is consistent with red deer *(Cervus elaphus)* summer calf survival, which also did not vary in relation to population size (Guinness et al. 1978, Clutton-Brock et al. 1982). Survival rates of juvenile kudu *(Tragelaphus strepceris)* were also more strongly influenced by rainfall than by population density (Owen-Smith 1990). Survival rates of African buffalo *(Syncerus cafer)* calves were not significantly correlated with population density, although a trend was evident and the sample size was small (Sinclair 1977). Juvenile buffalo mortality may have been more influenced by precipitation. The buffalo population was mainly regulated through the adults, because adult mortality was tightly coupled with population size but juvenile mortality was not.

Calf survival during winter was probably influenced by different factors than was survival during summer. Seasonal foraging environments are different, as are the processes leading up to winter vs. summer stresses (Fig. 2). The apparent effect of elk density on winter calf mortality rate was stronger than the apparent effect of precipitation. In studies by Lowe (1969), Guinness et al. (1978), Staines (1978), and Clutton-Brock et al. (1987), winter survival of elk and red deer *(Cervus elaphus)* calves similarly declined with increasing population size. During the winter, foraging area is restricted by deeper snows at higher elevations. This probably amplifies calf mortality responses to elk density. Nevertheless, fluctuations in forage density within the available foraging area influenced winter mortality, as suggested by a significant correlation between winter calf mortality and precipitation in the previous year.

Winter weather and foraging conditions are likely to be more stressful during winter than summer. Decreasing potassium:creatinine ratios and increasing urea:creatinine ratios through the winter indicated increasing nutritional deprivation and catabolism of lean body, respectively (DelGiudice et al. 1991). Much of the effect of winter stress upon cows carrying calves may not be exhibited until summer, however, when the cumulative over-winter stress affects mortality and recruitment of spring-born calves. The fact that summer calf mortality rate (mean 0.52) exceeded that in winter (mean 0.33) (t = 2.5, $0.01 < P < 0.05$) is consistent with the hypothesis that winter stress has less of an effect on the 6-8 month-old overwintering calves than on the smaller newborns in spring-summer. Similarly, winter mortality in red deer was determined by birth date, population density, and home range, but summer calf mortality was determined by calf birth weight and age of the cow (Guinness et al. 1978). Differences in juvenile mortality in donkeys were related to the nutrition of lactating females (Choquenot 1991). Mech et al. (1987) found that snow accumulation in the winter prior to birth strongly affected survivorship juvenile deer and moose. Owen-Smith (1990) also found that juvenile kudu survivorship was correlated with rainfall in the preceding year, through effects on the nutritional status of adult females.

A large fraction of the variance in bull mortality rate was explained by precipitation, yet elk population size did not affect bull mortality rate. In other studies, survival rates of adult males declined with increasing population size (Anderson 1958, Flook 1970, Clutton-Brock et al. 1982). Bulls may be more sensitive to plant production because they are more likely to deplete their energy reserves during the rut in fall, and they tend to use habitats where foraging is more difficult because of deeper snow, less abundant forage or steeper topography (e.g., Watson and Staines 1978, Clutton-Brock et al. 1982, F. Singer *unpublished data*). In Yellowstone, there were higher bull:cow ratios at higher elevations in three of five late winters. The poorer habitats that bulls use may be relatively abundant and there may be little competition for them, thus explaining the lack of effect of elk population size. Competition among bulls would be limited to these distinct habitats, where competition between bulls and calf–cow groups would be small or nonexistent. Therefore, either bull mortality rate is regulated in a density-independent manner or density effects arise from competition with other bulls, rather than all of the elk in the herd. Bull mortality rate was not correlated with bull density ($r^2 = 0.01$), so the former explanation is more plausible. The susceptibility of bulls to density-independent factors was illustrated when severe snow patterns, coupled with reduced winter forage caused by the 1988 fires and a dry summer, were accompanied by a large bull mortality in winter 1988/89 (Lemke and Singer 1989, Singer et al. 1989: Fig. 8a). A lower fraction of the older bulls than of cows or spikes migrated from traditional ranges that winter, including winter ranges that had burned (Singer et al. 1989).

Population dynamics were determined primarily by calf, spike, and bull survivorships, whereas cows appeared more resistant to changes in forage and elk number: no cow responses to density or to precipitation effects on forage were observed. Juveniles and males are probably especially vulnerable to changes in forage supply. Calves are competitively subordinate to mature animals in winter foraging (Houston 1982) and may begin winter with smaller energy reserves. Cows that carry calves and then nurse are more prone to experience energy deficits, with the dependent calves suffering disproportionately. Bulls not only experience large energy demands during the rut in fall, but they also may use more marginal habitats than cows. Analogous results were observed in African kudu (Owen-Smith 1990) where precipitation-related calf survival was the key factor in population fluctuations. Cow elk survival was unaffected by precipitation. As with kudu, cow elk conferred population resilience against fluctuations in resource abundance.

Correlations between mortalities in year t and plant growth in year $t - 1$ could have reflected elk responses to forage limitations in the summer or winter (Fig. 2). However, the primary forage limitations probably occurred during winter. Nonforested transitional and summer ranges are more productive than winter ranges because of their higher elevation and precipitation (e.g., Frank and McNaughton 1992, 1993, Merrill et al. 1993). Forested summer range is much less productive, but is quite expansive. Nutritionally-based estimates of carrying capacity that accounted for habitat productivities and areas indicated that summer range K values are at least twofold greater than winter range K values (Coughenour and Singer 1996). Negative correlations between summer range plant production and population rate of increase could be a consequence of higher snowfall limiting elk foraging while providing increased moisture to support plant growth (Merrill and Boyce 1991).

The number of elk that can be supported varies considerably among years, as indicated by the high unexplained variance (55%) in the correlation between per capita rate of increase and elk number (Fig. 6). This variance translates into a large uncertainty in ecological carrying capacity (K). Although the median K would be 14,000 counted elk, the range of possible K values is quite broad (10,000–18,000 elk). The median K value agrees very closely with the prediction of a population model based upon a regression equation for r_a (Merrill and Boyce 1991).

The empirical state-structured population model provided realistic simulations of elk population dynamics (Fig. 7). The major deviation from observed values occurred in 1979–80, fewer elk than predicted were seen. Variability in counting conditions introduces errors into the data, however. The large increase from 1980–82 suggested by the data may not actually have occurred. The ability of the model to simulate the data lends support to its predictions that population size continued to increase throughout the 1980s, but that further increases over the long term should not be expected. Numbers of sighted elk should fluctuate about a mean of approximately 16,400, which is approximately 2,500 more elk than the median K estimated by the r_a vs. N analysis (Fig. 6), and approximately 1,400 more elk than the K of 15,000 estimated by Houston (1982). The apparent decline between 1975 and 1980 (Fig. 7) gave the impression that the population had reached *K,* and probably biased mathematical estimates of *K* downwards.

Winter Weather Effects

We could not document any significant effects of season-long winter severity on elk population dynamics based on winter severity indices. Merrill and Boyce (1991) found that a modified Lamb's winter severity index was correlated with population rate of increase and spike:cow ratio (an index of yearling recruitment), but there was no correlation with calf:cow ratio. Picton (1984) observed that the intensity of winter effects on Montana elk population growth rates depended upon the size of the elk population relative to carrying capacity *(K);* climatic effects were significant only when elk populations were at carrying capacity. The northern Yellowstone elk population has varied near or above *K* (defined as in Fig. 6) since 1974/75, so mortality and population growth rates should have been correlated with winter severity indices, based upon Picton's observation.

Indices of winter-long severity reflect winter-long average or cumulative conditions and, consequently, are insensitive to short periods of extremely severe weather. For example, a large portion of the die-off in the winter of 1988/89 occurred in a 2-week period in late February (T. Lemke, *personal communication*), although that winter was not severe according to the winter-long snow-severity index (Table 4). Snow crusting is promoted by short intervals of warm weather, yet no winter severity index accounts for crusting. Winter severity may be more detrimental late in the season than early. In late winter, animals have depleted their energy reserves more completely and forage is more grazed down or weathered. Winter severity could be more detrimental when forage supply is low. The dry summer of 1988/89 likely produced less forage, and the forage probably cured earlier.

Other evidence did suggest that the elk are affected by severe winter weather. Severe winter weather clearly contributed to die-offs in 1974/75 (Cole 1983), as well as 1919/20 (Houston 1982), and 1988/89 (Singer et al. 1991, Coughenour and Singer 1996, Farnes 1996). Physiological evidence of nutritional stress is associated with declines in calf:cow ratios from early to late winter (DelGiudice et al. 1991). Bull and cow mortality rates were positively correlated with spring (April–May) precipitation in the prior year, per capita rate of increase was negatively correlated with spring precipitation in the prior year, and winter calf mortality was positively correlated with spring precipitation in the current year. Spring precipitation could be more stressful because rain-on-snow or alternating periods of warm and freezing temperatures would produce a crust; because elk would more probably have exhausted their energy reserves by then; and because the insulating capacity of elk coats may be decreased by wet spring snow or rain during cold temperatures. Early spring precipitation effectively lengthens the winter by restricting access to the summer range. Adult elk would have less time on the summer range, culminating in lower energy reserves the following winter and possibly explaining the 1-year time lag between spring precipitation and adult mortality.

Elk distributions and foraging appeared to be spatially constrained by deep snows. The winter range itself is obviously delimited by deeper snow at higher elevations, and there are probably also important limitations on available foraging area within the outermost perimeter of the winter range. This constraint was noted by Grimm (1939), who estimated approximately 41,000 ha were available during an average February. Houston (1982) estimated about 45,000 ha were available during periods of maximum compression. Interannual variations in snow depth and available foraging area contributed to interannual variations in *K* in a spatial-dynamic ecosystem model (Coughenour and Singer 1996). The density-independent effects of snow cover on elk foraging probably contributed significantly to elk population dynamics. Models of nutritionally based elk carrying capacity and linked energy balance and population processes are sensitive to the effects of snow depth on forage intake rate and habitat selection (Coughenour and Singer 1996). When the population is near carrying capacity, and where forage supply is not as moisture-limited as in grasslands, fluctuating snow depths could be paramount. Thus, Mech et al. (1987) concluded that snow accumulation, with subsequent nutritional limitation, was the main determinant of changes in Minnesota deer and Isle Royale moose populations, despite significant amounts of predation.

Differences in calf:cow and yearling male:cow ratios among elevations suggest that cows with calves and yearlings had a greater tendency to migrate to lower elevations than did cows without calves (Table 5). These movements are especially significant because winter calf mortality greatly affects population growth rate. If cow-calf groups are restricted to a smaller area during winter than the herd as a whole, then available forage is effectively reduced and competition is effectively elevated.

Increased migrations have probably mitigated the effects of winter severity and drought on elk populations through increases in forage. Data from early counts, 1916–62, indicated that 15–30% of the herd migrated outside the park in most years, with up to 60% migrating during very severe winters and less than 10% during mild winters (Houston 1982). The fraction migrating remained mostly well below 15% from 1964–74. The numbers of elk migrating north of YNP then increased in response to severe weather during the winter of 1974/75, with subsequent migrating proportions exceeding 15% in half of the years counted. Reduced disturbances from livestock grazing, largely due to recent land acquisitions (Olsen and Black 1990), probably reinforced the increased migrations. Higher numbers of animals migrating outside the park could have reflected increased total herd size because the proportion of the herd migrating did not increase (Table 4), but the herd may have increased, in part, because more elk migrated out of the park. According to a nutritional model of carrying capacity (Coughenour and Singer 1996) areas outside the park provide 36% of the total elk winter range forage base.

Implications for Elk Management Policy

Management of elk in YNP has been controversial (Pengelly 1963, Cole 1971, Beetle 1974, Cayot, et al. 1979, Chase 1986, Baur 1987, Kay 1990, Boyce 1991*a*, Coughenour and Singer 1991), largely because there have been many different conceptual models for elk population regulation. Several resource managers and authors have felt that the elk herd cannot regulate itself at a level that prevents range damage because predators are absent and humans have preempted winter range habitat outside the park (Rush 1932, Cahalane 1943, Chase 1986, Kay 1990). Others have hypothesized that there is an ecologically complete habitat for elk in and just outside northern YNP, and food, rather than predation, controls elk population sizes in nature (Cole 1971, 1983, Houston 1982, Boyce 1991*b*). There are multiple definitions of carrying capacity, each one appropriate to a unique set of management objectives (Caughley 1976, McNab 1985, Coughenour and Singer 1991). Some authors have interpreted ecological carrying capacity as a stable equilibrium between elk and forage, while others allow that carrying capacity may be dynamic, so the elk population can never reach a steady state.

This analysis of the Yellowstone elk population data indicates that forage supply does limit the population. Although there is density-dependent competition for food, density-independent fluctuations in forage supply and forage availability prevent the population from ever attaining a static equilibrium. Density-independent factors include fluctuating precipitation and forage production, and variations in snow depth, areal extent, and hardness. Variability of spring precipitation is another source of density independence: cow and bull mortality rates are higher and intrinsic rate of increase tend to be lower following a year with a wet spring. Although cow mortality varies independently from density, density-dependent calf and bull mortality is sufficient to regulate the population. Insensitivity of cow mortality to precipitation or forage production is stabilizing and provides population "inertia." Together, these response patterns indicate that population regulation is "density-vague," and numbers should vary rather than attain a static equilibrium. The demographic properties of the population will ensure its persistence despite this variability, however.

Ecological carrying capacity (ECC) estimates based upon these data should be carefully interpreted. The median ECC based on an assumed intrinsic rate of increase of zero at equilibrium is 14,000 elk whereas the empirical population model suggests 16,400 elk. The fraction of elk actually sighted during elk counts is much lower (approximately 75% in good counts). Thus, actual mean ECC is approximately 22,000 elk. A nutritionally based estimate of actual mean ECC is 21,000 elk (Coughenour and Singer 1995). These estimates may be higher than earlier 14,000–15,000 sighted elk at ECC estimated by Houston (1982) and Merrill and Boyce (1991), because elk use of lands outside the park has increased since their estimates. These estimates are much higher than earlier estimates of carrying capacity (Grimm 1939, Cooper 1963) for many reasons. Both of the earlier estimates were based on assumptions that no winter range existed outside the park. Mean areas available for foraging during the winter (due to snow) were of 42,000 ha (Grimm 1939) or 18,300–27,800 ha (Cooper 1963), which precluded use of any of the forage on the remaining one-half to two-thirds of the area at any point during the winter. Cooper assumed that no forage in woodlands or forests should be utilized, and provided no forage production data for the winter range. The "forage acre factor" method used by Grimm (1939) was abandoned long ago because it is inaccurate and based on questionable assumptions (Houston 1982).

Food limitation of the elk population is but one of several phenomena suggested to be valid criteria for continued application of the natural regulation policy. It was also suggested that herbivory should not cause vegetation to retrogress to early successional states (Cole 1971, 1983). Data from short- and long-term elk exclosures indicate that herbaceous vegetation did not retrogress from 1968–90 (Houston 1982, Frank 1990, Coughenour 1991, Frank and McNaughton 1992, 1993, Coughenour et al. 1995, Singer and Harter 1995). Elk browsing suppressed the heights and diameters of aspen and riparian willow, however, long prior to termination of human controls on elk in 1968 (Kay 1990, Chadde and Kay 1991, Singer et al. 1994). Decline in beaver, drier climate, fire suppression, altered hydrology, and market hunting for elk prior to 1870 may also have affected these plant species, in combination with herbivory (Singer et al. 1994, Romme et al. 1995). Importantly, aspen and willow are small components (1–5%) of the elk diet (Singer and Norland 1994) and they have not been shown to limit elk population size. Thus, elk abundance is regulated by herbaceous plants, and is and probably always has been largely decoupled from woody browse. Finally, models suggest that recently reintroduced wolves may lower elk numbers by 5–30% (Boyce 1993, Mack and Singer 1993), but it is unlikely that 5–30% fewer elk would result in increased aspen and willow, since leader use of those species did not decline during the period of reductions to <4,500 elk (Barmore 1980, Singer et al. 1994).

Observed and empirically simulated population responses supported the hypothesis that the northern Yellowstone elk herd is regulated through food limitation, through both density-independent fluctuations in total available forage and density-dependent fluctuations in the forage available to each elk. These findings are consistent with other analyses of Yellowstone elk (Barmore 1980, Houston 1982), red deer (Guinness et al. 1978), and many other large herbivores (e.g., Sinclair 1977, Sinclair et al. 1985, Novellie 1986, Mech et al. 1987, Sheperd and Caughley 1987, Messier et al. 1988, Dublin et al. 1990, Owen-Smith 1990, Choquenot 1991). Whether past, current, or future numbers of elk are "acceptable" or "natural," or whether *a* self-regulated elk–plant system with minimal human intervention is more or less desirable than other alternatives, or *other* elk–plant systems, are different questions requiring different methods of assessment.

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Niche relationships within a guild of ungulate species in Yellowstone National Park, Wyoming, following release from artificial controls

Francis J. Singer[1] and Jack E. Norland

Division of Research
P.O. Box 168
Yellowstone National Park, Wyoming 82190

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Abstract. Niche relationships and diet overlaps were compared among elk (*Cervus elaphus*), bison (*Bison bison*), bighorn sheep (*Ovis canadensis*), mule deer (*Odocoileus hemionus*), and pronghorn antelope (*Antilocapra americana*) between 1967–70 and 1986–88, a period when total ungulate numbers nearly tripled on Yellowstone's northern range. Ungulate species ratios on Yellowstone's northern winter range during the latter period were 100 elk:10 mule deer :3 bison :2 pronghorns :1 bighorn. Elk numbers were positively correlated to bison, mule deer, and pronghorn numbers ($r^2 = 0.76, 0.97, 0.48$, respectively, $P < 0.01$). Few other changes in habitat use or habitat overlap occurred and diets for only 2 of the 10 species pairs, elk–bighorn (Spearman's rank order coefficient (RHO = 0.55, $P < 0.05$) and mule deer–pronghorn (RHO = 0.64, $P < 0.05$), were significantly associated with each other. Bison consumed more grass and fewer sedges, mule deer more fringed sage (*Artemisia frigida*) and more rabbit-brush (*Chrysothamnus* spp.), and bighorn sheep more grasses and fewer sedges, while pronghorns ate less saltsage (*Atriplex nuttalli*) but more big sagebrush (*Artemisia tridentata*) during 1986–88 than during 1967–70. Bison expanded their range and bison and bighorn sheep used a wider variety of habitats. We found little evidence of change in competitive interactions between ungulate species. A few diet and habitat overlaps increased, the opposite of the prediction from the competitive exclusion principle amongst species, suggesting that intraspecific competition was more important. Several explanations are proposed for the lack of changes in niche relationships during a period of near tripling in density of the ungulate guild.

Introduction

Park managers in Yellowstone National Park embarked upon a program of natural regulation of all of Yellowstone's ungulates, beginning in 1968 (Cole 1971; Houston 1976, 1982). Prior to 1968, and especially from 1942 to 1968, elk, bison, and pronghorn antelope were artificially reduced through trapping and shooting on the park's northern winter range (Houston 1982). After 1968, native ungulates were allowed to increase with little influence by human controls within the park (Cole 1971; Houston 1976, 1982). Concerns were expressed that natural regulation of the park's ungulates could not occur, owing to the incompleteness of the winter range within

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[1] Present address: National Park Service and Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, CO 80523, U.S.A.

the park (at least 25% of the historic northern range occurs north of the park), because of concentration of wintering ungulates within the park and the removal of a significant predator, the gray wolf (*Canis lupus*) (Skinner 1928; Pengelly 1963; Chase 1986). Between 1968 and 1988, elk counts increased from about 5000 to an average of 17 000 and bison from about 100 to about 700, mule deer probably increased from an unknown lower number to 2300, and pronghorns from about 150 to about 500 (Houston 1982; Meagher 1973, 1989; Singer 1991). Based upon theoretical considerations and population growth rates, Houston (1982) concluded that elk were probably not competing with the less abundant ungulates through 1979. It has been predicted that the larger numbers of elk result in range deterioration and greater interspecific competition between elk and the other ungulates (Chase 1986; Kay 1987). The presence or absence of increased ungulate competition is viewed as one test of the natural regulation experiment (Coughenour and Singer 1991).

An unparalleled opportunity to observe niche relationships in a guild of ungulates was presented following release of populations of elk, bison and pronghorns from artificial controls in Yellowstone National Park. Alternatively, strong intraspecific competition within the rapidly increasing elk population might override the effects of interspecific competition resulting in increased niche overlaps between elk and the other species (Fretwell and Lucas 1969). In addition, diffuse competition, operating over a relatively brief period of 20 years, could also have resulted in increased diet and niche overlaps as species use habitats and forages more opportunistically (Jaksic and Delibes 1987). The competitive exclusion principle (Gause 1934; Hardin 1960; Jaeger 1972) states, "when two species jointly utilize a vital resource that is in short supply, either in abundance or availability to the species, one of the species will eventually eliminate the other from the habitat where their distributions overlap." When two species are in competition for resources, natural selection will favor the separation of their requirements (Sale 1974).

Interspecific competition occurs when one species diminishes another's population growth (Miller 1967; Hallet and Pimm 1979). Elk are often reported to dominate in competitive interactions with other native North American ungulate species (Mackie 1970, 1981; Hudson et al. 1976; Collins and Urness 1983; Oldemeyer et al. 1971). The following explanations have been proposed for this reported domination:

1. Elk are habitat and diet generalists. They tend to use a broader array of habitat resources (Hudson et al. 1976) and dietary resources (Hudson et al. 1976, Jenkins and Wright 1988) than the other guild ungulates.
2. Elk are good dispersers and rapidly exploit newly created habitats (Geist 1982).
3. Elk have a greater digestive capacity (larger rumen to body size ratio) than the smaller North American ungulates, such as mule deer and bighorn sheep, suggesting elk may compete more successfully in situations of poor range conditions (Collins and Urness 1983).

We report niche relationships between elk and four other native ungulates, mule deer, bison, pronghorn, and bighorn sheep, on the northern winter range of Yellowstone National Park during a period of release of elk from artificial controls. Our investigation was conducted during winter from 1986 to 1988 (period 2), a period of high ungulate density. We compared our data with similar observations gathered by Barmore (1980) for the winters of 1968–70 (period 1), a period of low ungulate density.

If large increases in numbers of elk and other ungulates had increased competition, we hypothesized that the following would provide evidence of intraor interspecific competition:

1. An inverse correlation between density and productivity of one (intraspecific) or more (interspecific) ungulate species (Houston 1982, p. 180).
2. Range extension or increased dietary or habitat use breadth by individual species (Fretwell and Lucas 1969).
3. Increased use of less palatable forages.
4. Increased dietary or habitat overlap between ungulate species as population densities increase (scramble competition sensu MacArthur and Pianka 1966; Schluter 1981). Ungulate species pairs with similar food habits might decrease their habitat overlap as populations increase (Lamprey 1963; Hudson 1976; McCullough 1980).

Study Area

The studies were conducted on the northern winter range of Yellowstone National Park as described by Barmore (1982) and Houston (1982). The northern winter range is approximately 100 000 a in size and about 83% of the area is within the boundaries of Yellowstone National Park (Houston 1982). The northern winter range contains the Yellowstone and Lamar river valleys. The northern winter range lies between 1500 m and 2400 m elevation. Soils are derived from glacial debris of andesitic and sedimentary origin (Houston 1982). Both studies concentrated on that part of the northern winter range in the park between Tower Junction and the northern boundary along the Yellowstone River (Figs. 1, 2).

The climate of the study area is characterized by long, cold winters with substantial amounts of snow, and short, cool summers. Mean temperatures during the winters of period 1 (-3.5° C, –5.8° C, –5.3° C during 1967, 1968, 1969, respectively) were close to the 20-year average ($\bar{x} = -4.9°$ C) while precipitation (4.01 cm, 3.63 cm, 2.43 cm) was mostly above the long-term average ($\bar{x} = 2.46$ cm). Mean temperatures during the winters in period 2 (1.7 and –5.5° C during 1987 and 1988, respectively) were above and below the long-term average. Precipitation (1.09 and 1.01 cm) was far below the 20-year average.

The vegetation of the northern range is a mix of steppe, shrub-steppe, and forest, with small areas of riparian habitats. Further descriptions are found in Houston (1982), Barmore (1980), Mueggler and Stewart (1980), and Steele et al. (1983). The vegetation classification used in this paper was developed by Barmore (1982):

1. *Xeric grasslands* occur on poorly developed, droughty soils on a variety of exposures and slopes below 1829 m and on moderate to steep south slopes at elevations up to 2438 m. Plant biomass is low. Vegetation is dominated by graminoids, primarily bluebunch wheatgrass (*Agropyron spicatum*), Sandberg bluegrass (*Poa secunda*), junegrass (*Koeleria macrantha*), and needle-and-thread (*Stipa comata*) at low to intermediate elevations. Idaho fescue (*Festuca idahoensis*) is more abundant at higher elevations.
2. *Mesic grasslands* occur on north slopes at low elevations (>1829 m) and on level to steep slopes at intermediate elevations with a north or east aspect. Soils are fine-grained with high moisture-holding capacity. Plant production is high with large amounts of cover and litter covering the soil surface (Frank 1990). Vegetation is dominated by Idaho fescue, junegrass, bluegrasses (*Poa* spp.), needlegrasses (*Stipa* spp.), and basin wild rye (*Elymus cinereus*).
3. *Sagebrush grasslands* occur at low to intermediate elevations. The overstory is dominated by big sagebrush (*Artemisia tridentata*). The understory is dominated by bluebunch wheatgrass, junegrass, Idaho fescue, needlegrasses, bluegrasses, and basin wild rye.
4. *Sedge-grass meadows* occur in areas where the water table is close to the surface. Plant cover and standing biomass levels are high. Grasses and sedges dominate, along with small patches of shrubby cinquefoil (*Potentilla fruticosa*).
5. *Aspen* (*Populus tremuloides*) stands have a high amount of standing biomass and production, with a variety of grasses, forbs, and shrubs in the understory.
6. *Coniferous forest* is dominated by Douglas-fir (*Pseudotsuga menziesii*), with varying amounts of lodgepole pine (*Pinus contorta*), subalpine fir (*Abies lasiocarpa*), and Engelmann spruce (*Picea engelmannii*) in the overstory. Most stands have a closed canopy but Douglas fir may form a savanna with grassland as the understory.
7. *Old fields* were cultivated or irrigated prior to park acquisition in 1932 and they occur on the lowest elevations in the study area.
8. *Willow communities*, found along the watercourses or other areas of high soil moisture, are dominated by willows (*Salix* spp.). The willow type is found in long linear patches.

Methods

Population Trends

Elk and bison were counted from small fixed-wing aircraft (Super Cub) during early winter, typically December or January, of periods 1 and 2 (Meagher 1973, 1989; Houston 1982; Singer 1991). Pronghorns and bighorn sheep were counted during spring green-up each year, typically March or April, using Super Cubs (Barmore 1980; Houston 1982; Keating 1982; Meagher 1973; 1989; Meagher et al. 1992; Singer 1990). Mule deer were counted during spring green-up each year, using a helicopter after 1979 and by ground counts and fixed-wing counts prior to 1979 (Barmore 1980; Houston 1982; Singer 1990). In late winter (March-April), elk and mule deer were classified from a helicopter, bison from a Super Cub, and pronghorns and bighorn sheep from the

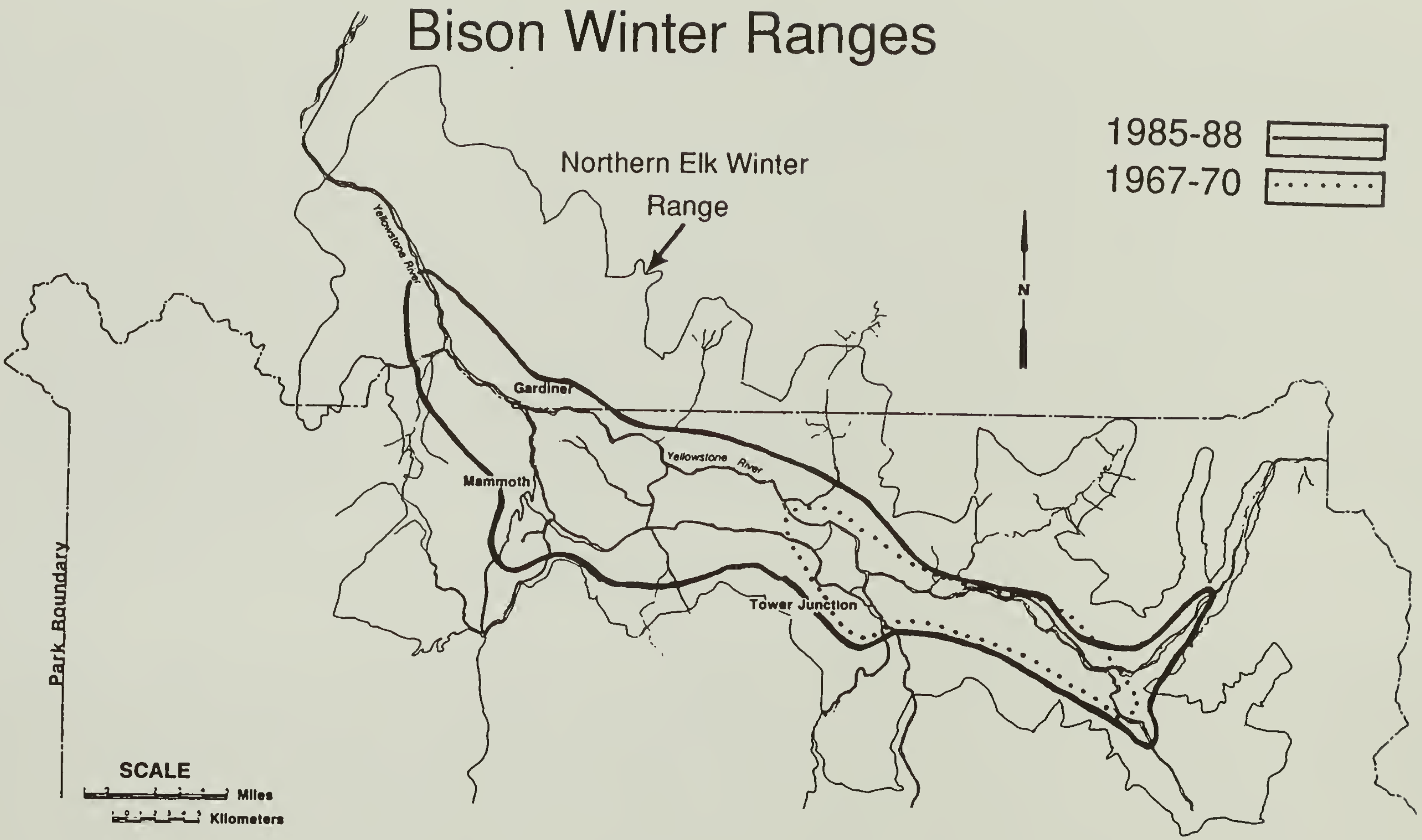

Fig. 1. Expansion of the bison winter range between periods 1 and 2 in the northern winter range of Yellowstone National Park.

ground using 20-45× spotting scopes (Houston 1982; Singer 1991; Yellowstone National Park files). Ratios of near-year-old juveniles : adult males : 100 adult females were reported. Elk numbers were correlated with numbers of the other ungulates to test the hypothesis that increased populations of elk suppressed populations of less abundant species. We compared the slopes of the regression lines on population growth for all five species of ungulates between 1968 and 1988 to determine if each species increased at the same rate.

Habitat Selection

Animals were observed from the same 50 km of park roads during both study periods, as well as along 25 km of foot or ski trails during period 2. The number of animals, slope, aspect, snow depth, and vegetation type were recorded for each ungulate group. Slope and aspect variables of the habitat were combined into the following categories for animal observations: (1) level with no aspect, (2) moderate slope (10–20%), north- and east-facing, (3) moderate slope, south- and west-facing, (4) steep slope (21%+), north- and east-facing, (5) steep slope, south- and west-facing, and (6) ridgetop. Both studies emphasized open areas where animals are easily observed.

Ungulates were observed once every 1.5–3 weeks from early December to mid-March during both study periods. Winter ranges of elk, bison, mule deer, bighorn sheep, and pronghorns were delineated for each period (Table 1) following Barmore (1980), Houston (1982), Meagher (1989), and Singer (1991). Availabilities of vegetation categories and slope/aspect categories were determined from interpretation of aerial photos (Table 1) within the winter ranges delineated for each species each study period.

Vegetation and habitat availabilities were determined for period 1 by mapping and calculating actual areas and for period 2 by using a nonmapping method (Marcum and Loftsgaarden 1980).

Habitat use was evaluated relative to habitat availability by means of the preference index of Ivlev (1961):

$$E = p_i - q_i / p_i + q_i \qquad [1]$$

where p_i is the proportion of use of resource category i, and q_i is proportion of the availability of that resource category. The index ranges from −1 (least preferred) to +1 (most preferred). Bootstrap methods were used to generate expected confidence intervals for habitat use; observed use outside of these ranges implies habitat preference or avoidance. For each overlap and breadth index a bootstrap sample of 1000 was derived. Confidence intervals (CI) were constructed from the bootstrap distribution around the empirical determination of the overlap and breadth measure, and were computed by the biased corrected (BC) percentile method of Efron (1982). Only the CIs are reported because exact tests of significance have yet to be established (Hinkley 1988). The CIs derived by the BC method are not supported in all cases (Hall 1988), but they are an improvement upon standard intervals (Efron 1988). Those comparisons where there was no overlap between two CIs were considered statistically significant. In certain instances the BC method produced CIs that did not include the empirical measure

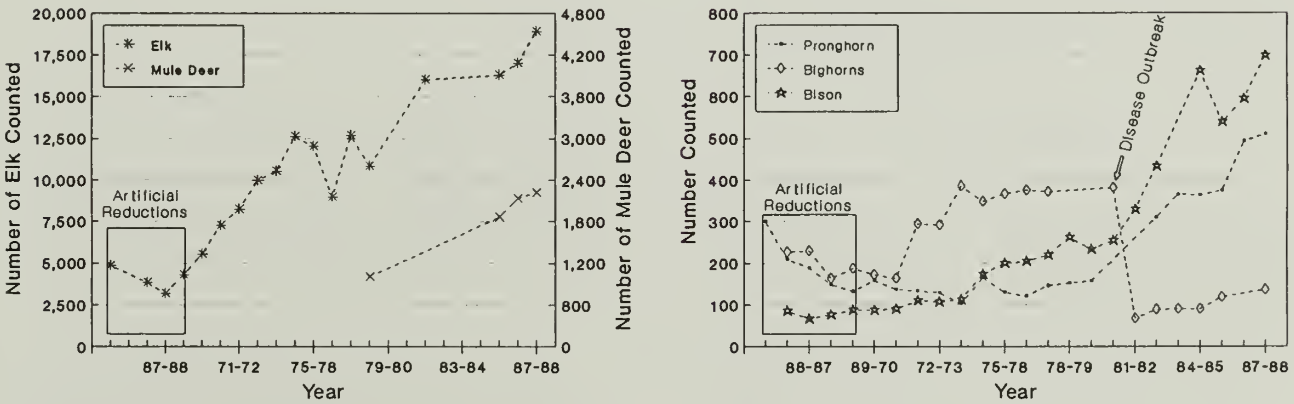

Fig. 2. Trends in the populations of five ungulate species on the northern winter range of Yellowstone National Park following cessation of artificial controls in 1968.

Table 1. Habitat preferences and corresponding bootstrap confidence intervals (Ivlev's index, given in parentheses; $\alpha = 0.05$) of elk, mule deer, pronghorns, bighorn sheep, and bison for the slope/aspect habitat dimension in Yellowstone National Park during periods 1 and 2.

	Level terrain	Mod N + E	Mod S + W	Steep N + E	Steep S + W	Ridgetop
Elk						
Period 1	–0.26	–0.0027	0.10	0.18	0.16	0.38
	(–0.45,–0.15)	(–0.16,0.14)	(–0.075,0.26)	(–0.1,0.36)	(–0.014,0.31)	(0.083,0.55)
Period 2	0.10[a]	–0.05	0.24	–0.76[a]	–0.64[a]	0.48
	(–0.09,0.23)	(00.26,0.085)	(0.067,0.4)	(–0.93,–0.67)	(–0.92,–0.55)	(0.33,0.61)
Mule deer						
Period 1	0.21	0.0028	–0.026	–0.40	–0.52	0.35
	(0.11,0.31)	(–0.22,0.16)	(–0.26,0.15)	(–0.54,–0.28)	(–0.83,–0.26)	(–0.12,0.56)
Period 2	0.11	0.016	–0.043	–0.53	–0.54	0.42
	(–0.14,0.3)	(–0.24,0.18)	(–0.76,0.28)	(–0.1,–0.28)	(–1,–0.41)	(–0.134,0.59)
Pronghorns						
Period 1	0.34	–0.5	0.31	–0.92	–0.68	0.38
	(0.25,0.44)	(–0.83,–0.29)	(–0.14,0.51)	(–1,–0.87)	(–1,–0.17)	(–0.041,0.56)
Period 2	0.34	–0.36	–0.16	–0.76	–0.73	0.28
	(0.27,0.4)	(–0.59,–0.15)	(–0.49,0.05)	(–0.97,–0.71)	(–1,–0.61)	(0.097,0.41)
Bighorn sheep						
Period 1	–0.52	–0.18	–0.03	–0.26	0.05	0.67
	(–0.75,–0.33)	(–0.54,0.008)	(–0.51,0.2)	(–0.5,–0.09)	(–0.15,0.21)	(0.60,0.76)
Period 2	0.20*	–0.44[b]	0.27	–0.91	–0.71	0.67
	(–0.11,0.26)	(–0.83,0.29)	(–0.25,0.51)	(–1,–0.83)	(–1,–0.63)	(0.54,0.75)
Bison						
Period 1	–0.22	0.54	–0.18	–0.78	–0.68	0.18
Period 2	0.43	–0.65	–0.15	–1	–1	–0.07
	(0.41,0.48)	(–0.93,0.44)	(–0.66,0.18)			(–0.45,0.23)

Note: Observations included 12 surveys of the study area during period 1 and 14 surveys during period 2. No CIs were developed for bison in period 1 because, since the population was small and restricted, too few groups were observed to allow CIs to be calculated.

[a] Denotes comparison between 1967–1970 and 1986–1988, with CIs that do not overlap.

[b] The percentile method was used to derive CIs rather than the BC method.

found for that index. In these cases, the percentile method was used to construct the CIs (Hall 1988). This method is preferred when habitat availability varies or when distributions are altered by migrations or preconditioning (Mueller and Altenberg 1985; Koslow and Stewart 1988; Llewellyn and Jenkins 1987).

Dietary Selection

Food habits for period 1 were based on sampling during 1965–1968, except for those of elk, which were collected from 1962–1967. Rumens from 256 elk, 24 pronghorn, 20 mule deer, and 11 bison shot on the northern winter range were subjected to volumetric analysis (Greer et al. 1970; Barmore 1980; Houston 1982). Bighorn sheep food habitats were determined on the basis of feeding sites (Oldemeyer et al. 1971).

Food habits for period 2 were determined from microhistological analysis of fecal samples collected during three winters, 1985–1988. Each sample was a composite of 5 g of fresh fecal material from 6–12 pellet groups. Botanical composition of the diet was expressed as a percent relative cover of identifiable plant fragments in 200 random microscope fields (Washington State Univ., Wildlife Habitat Lab, Pullman). Bighorn diets were also determined using microhistological techniques during the winter of 1980–1981 (Keating et al. 1985). Annual winter means were compared between periods 1 and 2 using *t* tests. Comparisons were restricted to principal forage species, those comprising 2% or more of a species' diet.

Niche Breadth and Overlap

Schoener's (1968) index was chosen to represent overlap between habitat niche and dietary niche:

$$D_{jk} = 1 - 0.5 - \Sigma p_{ij} - p_{ik} \qquad [2]$$

where the p_{ij} and p_{ik} are the utilization of the *i*th resource by the *j*th and *k*th species. The Schoener index was shown by Linton et al. (1981) and Abrams (1980) to be least biased when true overlap was between 7 and 85%, as in our study. The Schoener index is not restricted by assumptions of competition, and the measure is not overly sensitive to little-used resource variables.

Niche and dietary breadths were indexed by the measure of Smith (1982):

$$[3] \qquad \mathrm{FT} = \Sigma(p_i q_i)0.5$$

where p_i is the proportion of resource *i* used, q_i is the proportion of resource *i* available. Smith's measure ranges from 0 to 1.

Ungulate use of snow depths habitat categories was portrayed by Levins' (1968) index:

$$[4] \qquad B = 1/\Sigma\, p_i 2$$

where p_i is the proportion of resource *i* used. Levins' index ranges from 1 to the number of resource categories considered.

Changes in niche overlap and breadth from period 1 to period 2 were compared through the use of a bootstrap sampling method described above in "Habitat Selection" (Mueller and Altenberg 1985). The analyses were conducted on individual animals rather than on groups. The bootstrap distribution is a more appropriate test when the data may come from contaminated distributions and are influenced by nonindependence of animals in a group (Mueller and Altenberg 1985; Koslow and Stewart 1988; Llewellyn and Jenkins 1987). Similarities between ungulate diets are expressed using Schoener's index of overlap (Schoener 1968) and Spearman's rank order correlation coefficient (RHO).

Results

Population Trends

The elk population increased rapidly from 1967 to 1988, following the cessation of population control measures in the park (finite rate of increase, λ = 1.09; Fig. 2). Aerial counts of elk during period 1 averaged 4829, but counts during period 2 averaged 17 402, an increase of about 260%.

Mule deer numbers increased by about 122% from 1979 to 1988 during a period of consistent helicopter counts (λ = 1.14; Fig. 3). No helicopter counts of deer were available prior to 1979. In winter, snow in most of the northern Yellowstone winter range within Yellowstone Park is too deep for mule deer and only 5% of the mule deer herd wintered in the park. Although the herd increased overall between 1979 and 1988, the numbers of deer wintering within the park boundaries declined by at least 57% between periods 1 and 2. Numbers of mule deer within the park declined from 230 ± 41 ($\bar{x} \pm$ SE) in period 1, according to fixed-wing aircraft or ground counts (less efficient) ($n = 3$ counts) to 98 ± 14 in period 2, counted from a helicopter (more efficient) ($n = 3$ counts; $P = 0.05$, Fisher exact probability test).

Bison numbered about 85 during period 1, but following release from control measures, increased to 539–850 during period 2 (Houston 1982, p. 167; Meagher 1989) (Fig. 2; λ = 1.14). The winter range occupied by bison more than tripled during this period (Fig. 1).

Pronghorn populations were reduced to less than 150 animals during period 1, as a result of artificial controls and severe winters (Fig. 2), and numbers remained low through the 1970s. The reasons for the low numbers are unknown, but it is speculated that they might include severe winters and other factors, such as predation, which limited recruitment (O'Gara 1968; Houston 1982, p. 169). Pronghorns apparently responded to the mild winters of the 1980s, however, and the population increased 185% between 1979 and 1988 (λ = 1.25).

Bighorn sheep counts averaged 200–230 during both study periods (Fig. 2), but the populations were characterized by more variable fluctuations than those of the other ungulate species. Bighorn sheep populations increased rapidly, starting about 1968, and from 1968 to the winter of 1972–1973, numbers increased to a high of about 400–500 (Oldemeyer et al. 1971; Barmore 1980; Keating 1982, 1985; λ = 1.17). Bighorn sheep numbers declined dramatically to <100 between 1981 and 1982 as a result of an outbreak of *Chlamydia* spp. disease (Meagher 1982). After the disease outbreak, numbers increased (λ = 1.12) between 1983 and 1988.

Elk outnumbered the other ungulate species combined on the northern winter range, the ratio being 100 elk:16 other ungulates, but we found no evidence for complete suppression of population growth of less abundant species by elk. The increases in elk numbers were unrelated to bighorn sheep numbers ($r^2 = 0.02$, $P = 0.64$) between 1967 and 1988, but were positively correlated with bighorn numbers from 1969 to 1980, prior to the outbreak of *Chlamydia* disease in bighorn sheep ($r^2 = 0.90$, $P < 0.01$). Between 1967 and 1988, the size of the elk population was positively correlated with the sizes of the bison ($r^2 = 0.76$, $P < 0.01$), mule deer ($r^2 = 0.97$, $P = 0.01$), and pronghorn ($r^2 = 0.48$, P

< 0.01) populations. In addition, elk numbers were not correlated with productivity rates (arc-sine transformation of young to adult ratios in year y + 1) of pronghorns, bighorn sheep, or bison ($P > 0.05$). Too few data were available for analysis of the ratios of mule deer fawns to does.

Weather, as indexed by a z statistic score for winter precipitation and temperatures, was not correlated with mule deer or bighorn sheep numbers or pronghorn, bighorn sheep, or bison productivity ($P > 0.05$). Winter severity approached a significant correlation for numbers of pronghorns ($r^2 = 0.60$, $P = 0.06$), bison ($r^2 = 0.81$, $P = 0.08$), and bighorn sheep ($r^2 = 0.93$, $P = 0.08$).

The slope of the elk growth rate regression was significantly lower (i.e., elk grew more slowly) than the slopes of bighorn sheep and bison growth rate regressions ($F = 5.06$, $P < 0.001$), Tukey-Kramer multiple comparison test). No other slopes of population growth rate regressions for ungulates differed significantly ($P > 0.05$).

Habitat Selection

Elk increased their area of occupied winter range by about 25% between periods 1 and 2. Elk used level terrain more and steep terrain (S and W slope) less during period 1 than period 2 (Table 1). Bighorn sheep also increased their use of level terrain during period 2. Bison numerically increased their use of terrain with deeper snows (level and steep N and E slopes) and decreased their use of terrain with shallow snows (exposed S and W slopes). The entire herd was less than 100 animals during period 1, and since our CIs were based on observations of animals, none could be calculated for period 1. These differences for bison were probably biologically significant, since most of the small and confined bison herd (80–90 animals) was observed during each survey in period 1; the herd's habitat use and distribution were obviously well sampled. Extensive flights by fixed-wing aircraft during period 1 verified that the bison herd was confined to the Lamar Valley in winter (Meagher 1973).

Table 2. Vegetation habitat preferences and corresponding bootstrap confidence intervals (Ivelv index, given in parentheses; $\alpha = 0.05$) of elk, mule deer, pronghorns, bighorn sheep, and bison for the vegetation habitat dimension during periods 1 and 2 in Yellowstone National Park.

	Xeric	Mesic	Sagebrush	Sedge–Meadow	Aspen	Conifers	Old Fields	Willows
Elk								
Period 1	0.12	0.16	–0.047	–0.33	0.24[a]	0.36	–0.96	–0.24
	(–0.08,0.27)	(–0.05,0.30)	(–0.17,0.032)	(–0.69,–0.098)	(–0.43,0.36)	(–0.22,0.44)	(–1,–0.93)	(–0.48,–0.1)
Period 2	–0.33	0.17	0.035	0.53	0.15[a]	–0.42[b]	0.92[a]	0.44[a]
	(–0.79,0.012)	(–0.07,0.36)	(–0.06,0.1)	(–0.83,0.69)	(–0.72,0.12)	(–0.55,–0.32)	(–1,0.54)	(–1,0.45)
Mule deer								
Period 1	–0.13	0.35	0.21	0.35	–1	–0.29	0.07	0.81
	(–0.26,–0.02)	(–0.11,0.56)	(0.04,0.29)	(F128M-1, 0.65)		(–0.87,–0.16)	(0.87,–0.16)	(0.24, 0.90)
Period 2	–0.09	–1[b]	0.02[a]	–1	–1	–0.15	–1[b]	0.99
	(–0.54,0.15)		(–0.11,0.12)			(–0.88,0.22)		(–1,0.95)
Pronghorns								
Period 1	0.13	0.19	–0.46	–1	–1	–1	–0.26	–1
	(0.084,0.19)	(–0.61,0.53)	(–0.99,–0.11)				(–1,–0.21)	
Period 2	0.36[b]	–0.6	–0.08	–1	–1	–0.95	0.38[a]	
	(0.23,0.46)	(–1,0.076)	(–0.19,0.0008)			(–1,–0.9)	(–1,0.38)	
Bighorn sheep								
Period 1	0.51a	–0.11	–0.84	–1	–1	–0.41	–1	–1
	(0.49,0.53)	(–0.49,0.085)	(–0.98,–0.77)			(–1,–0.15)		
Period 2	0.15[b]	0.81	0.03[b]	–1	–1	–1	–1	–1
	(–0.14,0.3)	(–1,0.89)	(–0.04,0.11)					
Bison								
Period 1	–0.11	0.22	–0.76	0.46	–0.31	–1	–1	–0.74
Period 2	–0.17	–0.24	–0.02	0.79	–1	–0.87	0.91[a]	–1
	(–0.12,0.37)	(–0.75,0.04)	(–0.13,0.03)	(0.61,0.83)		(–0.96,–0.76)	(–1,0.91)	

Note: No CIs were developed for bison during period 1 because too few groups were observed from the small population to allow CIs to be calculated.

[a] The percentile method was used to derive CIs rather than the BC method.

[b] Denotes comparisons between periods 1 and 2, with CIs that do not overlap.

Table 3. Niche overlap indices and corresponding bootstrap confidence intervals (Schoener's index, given in parentheses; $\alpha = 0.05$) of vegetation, slope/aspect, and snow habitat dimensions for all pair combinations of elk, mule deer, bighorn sheep, pronghorns, and bison in Yellowstone National Park during periods 1 and 2.

	Period 1			Period 2		
	Vegetation	Slope/Aspect	Snow	Vegetation	Slope/Aspect	Snow
Elk–Mule Deer	0.72[a] (0.48–0.77)	0.72 (0.53–0.78)	0.58 (0.42–0.68)	0.69 (0.66–0.85)	0.82[a] (0.65–0.87)	0.64[a] (0.53–0.82)
Elk–pronghorn	0.45 (0.26–0.56)	0.57 (0.39–0.62)	0.47 (0.33–0.65)	0.60 (0.51–0.72)	0.69 (0.45–0.75)	0.56 (0.54–0.85)
Elk–bighorn sheep	0.48 (0.27–0.53)	0.72[a] (0.57–0.77)	0.55 (0.42–0.72)	0.68[b] (0.58–0.80)	0.78 (0.63–0.94)	0.56[a] (0.38–0.75)
Elk–bison	0.43	0.45	0.59	0.75 (0.66–0.87)	0.57 (0.38–0.65)	0.89[a] (0.64–0.95)
Mule deer–pronghorn	0.65 (0.49–0.79)	0.76 (0.58–0.80)	0.87[a] (0.52–0.87)	0.69 (0.66–0.94)	0.73 (0.49–0.89)	0.82 (0.53–0.97)
Mule deer–bighorn sheep	0.56 (0.45–0.66)	0.51 (0.31–0.59)	0.92[a] (0.72–0.95)	0.82[b] (0.72–0.94)	0.74 (0.52–0.83)	0.83 (0.54–0.97)
Mule deer–bison	0.21	0.68	0.25	0.67 (0.64–0.84)	0.58 (0.34–0.75)	0.62 (0.61–0.89)
Bighorn sheep–pronghorn	0.89 (0.78–0.94)	0.40 (0.22–0.47)	0.91[a] (0.68–0.94)	0.84 (0.67–0.97)	0.79[b] (0.59–0.86)	0.99[a] (0.61–1.0)
Bison–pronghorn	0.19	0.84	0.20	0.68 (0.53–0.75)	0.83 (0.72–0.92)	0.55[a] (0.43–0.78)
Bison–bighorn sheep	0.24	0.26	0.28	0.69 (0.621–0.83)	0.70 (0.50–0.79)	0.55[a] (0.43–0.79)

Note: No CIs on overlap indices dealing with bison during period 1 were developed because of small sample sizes, owing to a small population.

[a] The percentile method used to derive CIs rather than the BC method.

[b] Denotes nonoverlapping CIs between periods 1 and 2.

Table 4. Niche breadth indices and corresponding bootstrap confidence interval, $\alpha = 0.05$ in parentheses for elk, mule deer, pronghorn antelope, bighorn sheep, and bison during period 1 and period 2 in Yellowstone National Park. No CIs for bison were developed during period 1 because of small samples, due to a small population confined to the Lamar Valley.

	Period 1			Period 2		
	Vegetation	Slope/Aspect	Snow	Vegetation	Slope/Aspect	Snow
Elk	0.98[a] (0.95–0.98)	0.98 (0.94–0.99)	4.78 (3.94–4.98)	0.98[a] (0.94–0.99)	0.95[a] (0.91–0.96)	3.04[a] (2.73–3.97)
Mule deer	0.99[a] (0.95–0.99)	0.96 (0.92–0.97)	3.10 (2.32–3.23)	0.96 (0.87–0.99)	0.98[a] (0.90–0.98)	1.82[a] (1.81–2.60)
Pronghorn antelope	0.97[a] (0.89–0.98)	0.85 (0.74–0.88)	2.48 (1.84–2.9)	0.93 (0.89–0.94)	0.91 (0.81–0.93)	1.42[a] (1.54–2.45)
Bighorn sheep	0.71 (0.66–0.73)	0.92 (0.85–0.94)	2.95 (2.32–3.22)	0.93[b] (0.91–0.93)	0.89 (0.78–0.90)	1.43[a] (1.54–2.46)
Bison	0.85	0.93	2.15	0.90[a] (0.86–0.92)	0.78 (0.71–0.81)	3.05[a] (2.86–4.17)

Note: No CIs for bison were developed during period because samples were small, owing to small population confined to the Lamar Valley.

[a] Percentile method used to derive CIs rather than the BC method.

[b] Denotes comparisons between 1967–1970 and 1986–1988 with CIs that do not overlap.

No change in use of slope/aspects by pronghorns or mule deer was detected between study periods.

Three species altered their use of vegetation types between periods 1 and 2 (Table 2). Mule deer used mesic vegetation types and Old fields less during period 2. Bighorns used sagebrush more and used xeric grassland types less during period 2. Elk used both aspen and conifer types less during period 2. Bighorn sheep increased their niche breadth of vegetation types by 22%, and bison numerically increased their use of vegetation types by 10% and their use of snow depths by 90% (Table 4). Bison numerically increased their habitat overlaps with those of four other ungulate species as their range more than tripled between periods 1 and 2. The average overlap in all habitat categories (vegetation, slope/aspect, snow) of bison with elk increased by 25%, with mule deer by 25%, with bighorn sheep by 28%, and with pronghorns by 39%.

Dietary Selection

Percent diet composition of elk forages or forage classes did not vary between the two study periods (t tests, $P > 0.05$; Tables 5 and 6). Pronghorn, mule deer, bison, and bighorn sheep diets, however, varied significantly between the two study periods (Tables 5 and 6). Pronghorns ate less saltsage (*Atriplex nuttallii*) during period 2 (10 vs. 0%) but more big sagebrush (33 vs. 49%; $t = 7.22$, df = 3, $P < 0.05$). Mule deer consumed significantly more fringed sage (*Artemisia frigida*) (7 vs. 18%; $t = 4.09$) and more rabbit-brush (*Chrysothamnus* spp.) during period 2 (1 vs. 7%; $t = 5.06$, df = 4, $P < 0.05$). Bison consumed fewer sedges (56 vs. 32%; $t = 8.42$, df = 3) and more grasses (34 vs. 53%; $t = 7.82$, $P < 0.05$) during period 2. Bighorn sheep ate more grasses (58 vs. 65%; $t = 13.8$, df = 3) and fewer sedges (3 vs. 1.2%; $t = 2.4$, $P < 0.05$) during period 2. No consistent trend in the use of conifers was observed (mule deer ate more, but elk ate fewer), grass (mule deer ate fewer, but bison and bighorns ate more), or shrubs (mule deer and bighorn sheep ate more, but elk ate fewer). Use of three plant groups, aspen, willows, and cottonwoods, declined during the study periods, (Houston 1982); elk ate less willow (3 vs. 0.1%), and mule deer ate less aspen and cottonwood (8 vs. 0.8%), but the differences were not statistically significant ($P > 0.05$).

Niche Breadth and Overlap

Mule deer and bighorn sheep increased vegetation type overlap from period 1 to period 2 (Table 3). No other habitat overlap change occurred between any other species pairs.

The diet overlap between elk and bighorn increased from period 1 to period 2 (Spearman's rank correlation; Table 7, $P < 0.05$; Shoener's index of overlap

Table 5. Mean percent diet composition of elk, bison, mule deer, pronghorns and bighorn sheep on the northern winter range of Yellowstone National Park during 1962–1970.

	Elk ($n = 256$)	Bison ($n = 11$)	Mule Deer ($n = 20$)	Pronghorn ($n = 24$)	Bighorn sheep[a]
Grasses	79	34	32	4.2	58
Sedges	2	56	0	0	3
Rushes	tr	9	0	0	0
Forbs	3	tr	17	14	17
Shrubs					
Artemisia tridentata	2	1	19	33	2
A. fridida	0	0	7	16	2
Atriplex nuttallii	0	0	tr	10	0
Chrysothamnus sp.	tr	0	1	4	8
Salix spp./*Populus* spp.	3	0	8	0	0
Ceratoides lanata	0	0	0	12	10
Total	11	1	43	82	22
Conifers					
Pseudotsuga menziesii	1	0	8	0	0
Pinus contorta	3	0	0	tr	0
Juniperus scopolarum	0	0	1	tr	0
Total	5	tr	9	tr	0

Note: Data are from Barmore (1980), Meagher (1973), and Oldemeyer et al. (1971), n is number of rumens.

[a] Feeding sites in Oldenmeyer et al. (1971).

0.62 vs. 0.72) owing to the consumption of more grasses and fewer forbs by bighorn sheep. Mule deer and pronghorn diets overlapped more during the 1980s ($P < 0.05$; Shoener's index 0.53 vs. 0.69) because mule deer consumed fewer grasses and conifers. Mule deer–bison and pronghorn–bison diets were negatively correlated during both periods 1 and 2 ($P < 0.05$). Bighorn sheep–bison diets were negatively correlated during period 1 ($P < 0.05$) but their similarity increased during period 2 as a result of greater consumption of grasses by bison (Shoener's index increased from 0.31 to 0.53). Only bighorn sheep increased their diet overlap with two other species, elk and bison.

Discussion

Population Trends

All five ungulate species in the guild increased between periods 1 and 2, apparently as both a common response to milder weather during period 2 and as a response by elk, bison and pronghorns to cessation from controls. Competition within the rapidly increasing ungulate guild was not so overwhelming that the population growth of any species was curtailed, but we cannot state that growth rates of any species (except perhaps bison) was unaffected by one or more other species within the guild. Only the bison population grew at a near maximum reported λ value between the study periods; mule deer, elk, pronghorns and bighorn sheep were well below maximum reported λ values,

Table 6. Percent composition of diet of ungulates during period 2, the winters of November 1985 to March 1988, in the northern winter range of Yellowstone National Park based on microhistological examination of feces; only principal forages (2% of a diet) are reported.

	Elk		Bison		Mule deer		Pronghorns		Bighorn sheep (n = 15)		
	(n = 25)		(n = 20)		(n = 19)		(n = 20)		1985–1988		1980–1981[a]
	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$
Grasses											
Agropyron spicatum	12.0	5.9	7.8	5.8	2.7	3.4	1.4	2.3	15.2	8.2	20
Festuca idahoensis	17.6	10.3	11.3	9.5	6.2	8.5	7.3	18.0	16.1	7.6	3
Koeleria macrantha	6.6	5.5	5.4	10.0	1.3	1.1	0.7	1.2	8.7	6.3	9
Phleum pratensis	3.0	2.6	9.1	22.3	1.0	2.4	0.4	1.2	2.1	2.9	0
Poa spp.[a]	9.6	5.6	4.8	4.8	2.8	2.2	0.0	0.0	9.3	4.9	tr
Calamagrostis spp.[b]	5.8	3.9	1.3	2.1	0.7	1.3	0.4	0.7	0.0	0.0	0
Deschampsia caespitosa	2.6	2.9	1.9	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0
Elymus spp.[c]	1.4	1.6	1.8	1.8	2.4	2.1	0.3	0.6	2.1	2.5	tr
Stipa comata	1.3	1.9	4.4	8.8	0.6	1.2	0.5	1.0	4.2	3.1	6
Total	75.0	9.8	53.4	20.7*	18.7	17.9	10.1	12.0	65.4	23.0*	59
Sedges	8.1	6.0	32.1	19.6*	0.4	0.2	0.1	0.3	1.2	1.4*	5
Rushes	2.7	3.9	11.5	7.8	0.0	0.0	0.1	0.4	0.4	0.3	0
Forbs	3.1	3.0	1.4	1.1	15.0	12.6	7.0	6.7	7.7	6.8*	7
Shrubs											
Artemisia tridentata	3.8	3.1	0.1	0.1	23.2	15.1	48.7	18.0*	5.8	8.0	6
Artemisia frigida	1.0	2.0	0.0	0.0	17.9	16.7*	18.5	13.7	10.2	14.6	tr
Salix spp./*Populus* spp.	0.1	0.5	0.1	0.1	0.8	1.5	0.0	0.0	0.0	0.0	0
Chrysothamnus spp.[d]	1.6	2.7	0.0	0.0	7.2	4.6*	5.3	3.5	2.5	2.6	4
Ceratoides lanata	0.4	1.0	0.1	0.1	0.7	1.0	5.8	6.0	5.8	5.6	20
Total	7.8	4.1	1.3	1.6	49.7	20.9	80.5	15.7	24.5	22.1	33
Conifers											
Pinus contorta	0.3	0.6	0.1	0.1	1.1	1.4	0.0	0.0	0.0	0.0	0
Pseudotsuga menziesii	1.9	3.2	0.1	0.1	4.6	8.1	0.5	0.9	0.2	0.5	1
Juniperus scopolarum	0.0	0.0	0.0	0.0	9.9	14.1	2.0	3.5	0.7	2.1	0
Total	3.0	3.3	0.3	0.1	15.6	18.9	2.5	4.4	1.0	2.2	2
Total plants	100		100		100		100		100		

Note: *n* is the number of aggregated samples from fecal piles.

[a] Data from Keating et al. (1985).

[b] Includes *Poa pratensis*, *P. sandberghii*, *P. compressa*, and *P. juncifolia*.

[c] Includes *Calamagrostis rubescens*, and *C. canadensis*.

[d] Includes *Elymus cinereus*, *E. canadensis* and *E. glauca*.

[c] Includes mostly *Chrysothamnos nauseosus*, with some *C. viscidiflora*.

*Significantly different from period 1, *t* tests, $P < 0.05$.

Table 7. Mean diet overlap indices (Schoener 1968) and Spearman's rank correlations (RHO) for winter diets of principal forage species (2% of each diet) common to five ungulates species pairs (elk, mule deer, bison, pronghorns, bighorn sheep) in Yellowstone National Park during periods 1 and 2.

	1960s		1980s	
Species pair	Schoener's index of overlap	RHO	Schoener's index of overlap	RHO
Elk–mule deer	0.58	0.25	0.40	0.08
Elk–pronghorn	0.46	−0.29	0.33	−0.39
Elk–bighorn	0.62	0.23	0.73	0.55*
Elk–bison	0.47	−0.01	0.63	0.26
Mule deer–pronghorn	0.53	0.18	0.69	0.64*
Mule deer–bighorn	0.56	−0.17	0.51	0.16
Mule deer–bison	0.41	−0.70**	0.29	−0.79**
Pronghorn–bighorn	0.39	−0.14	0.46	0.26
Pronghorn–bison	0.28	−0.69**	0.19	−0.62**
Bighorn–bison	0.31	−0.53*	0.53	−0.20

*Significant at $P < 0.05$
**Significant at $P < 0.01$

while the elk population, in particular, increased less rapidly than the other species. Although the growth rates for all five ungulates were positive, possible inhibition of growth rates of four species remains a possibility. Picton (1984) reported no correlation between elk populations and mule deer reproduction in Montana, and he suggested that little serious competition should occur between them, although Picton (1984) reported a negative correlation between elk population size and bighorn lamb survival.

Habitat Selection

Large winter range expansions by elk (25%) and bison (300%) between the study periods, and increases in habitat niche breadths for bison and bighorn sheep might be evidence of increased intra- or interspecific competition between the two study periods (Fretwell and Lucas 1969; MacArthur and Pianka 1966; Schluter 1981). Elk did not appear to be competitively dominant over the other species (Collins and Urness 1983; Hudson et al. 1976; Jenkins and Wright 1987); elk did not increase their habitat niche breadth and they did not increase their vegetation, snow depth, topographic, or diet overlaps with any of the other species. Niche changes for bison and bighorn sheep from period 1 present the greatest potential for support of the Fretwell–Lucas model: bison increased their occupied range, habitat breadth, habitat overlaps, and diet overlaps. Bighorn sheep increased habitat breadth and habitat and diet overlaps. We stress the biological significance of the increases for bison; the small bison population was adequately sampled during period 1, but they occurred in so few groups that because of an artifact of our statistical technique, no CIs could be generated for them during period 1. Ungulates more similar in size and resource use did not diverge more in other resource parameters, as Hudson (1976) and McCullough (1980) predicted.

Food Selection

No consistent evidence was obtained of any increased use of less palatable plant forages was obtained; there were no consistent changes in the use of major plant groups or forage species among the ungulates. Use of cottonwood, aspen, and willows declined between the study periods, but these are so rare and constitute so little of the diets (<1%) of any ungulate that any declines in use were statistically insignificant. Long-term vegetation measures do not indicate declines in any other grasses, forbs, or shrubs between the two periods (Coughenour 1991; Coughenour et al. 1994; Singer 1994).

Diets were sampled with rumens from cropped animals during period 1 but from fecal analysis during period 2. Park management policies prohibited collections of animals for rumen analysis during period 2. We concluded that the two techniques did not obscure major diet shifts or invalidate comparisons between the two periods because: (*i*) forage groups changed independently amongst the ungulates between the two periods, suggesting no consistent bias, (*ii*) both techniques have the same bias: underrepresentation of forbs and overrepresentation of browse and grass (Anthony and Smith 1974; Johnson and Pearson 1981; Smith and Shadrunk 1979), (*iii*) the two techniques provide very similar results if sample sizes are large (McInnis et al. 1983; Casebeer and Koss 1970; Smith and Shadrunk 1979), as in our case, and (*iv*) underrepresentation of forbs is less critical during winter, when plants are dormant (Vavra et al. 1978), as in our study.

Niche Overlap

Increased competition might have been demonstrated by the increased habitat and diet overlaps for bison and bighorn sheep, but different mechanisms are inferred from their life histories. Bison numbers increased about 700% between the study periods, more than any other species, and intraspecific as well as any interspecific competition likely influenced bison niche occupation. The bighorn sheep population size was smaller during period 2, following the *Chlamydia*-caused dieoff, than during period 1, and interspecific competition (probably with elk) more likely explains their increased niche occupation. We observed high diet overlap (0.62–0.73), and high habit use (0.48–0.78) also indicated overlaps between bighorn sheep and elk, suggesting potential competition, as concluded by Keating (1985). Elk and bighorn sheep increased their vegetation overlap and diet niche overlaps from period 1 to period 2, the opposite of the prediction from competitive exclusion (Wiens 1977; Hudson 1976; McCullough 1980), primarily because of increases in occupied niches by bighorn sheep, not elk. Bighorn sheep used more grasses, and they made more use of mesic grasslands and sagebrush, where grass biomass is greater (Houston 1982). High diet overlaps during winter and likely interspecific competition between the two species have been reported by other workers (Constan 1972; Barmore 1980; McCullough 1980; Kasworm et al. 1984; Keating et al. 1985). Some authors, however, report less competition between bighorn sheep and elk, owing to differences in spatial segregation (McCullough 1980), topography (Constan 1972; Hudson et al. 1976), and diet (Hobbs et al. 1983).

As in previous studies, we observed low to moderate diet overlaps but high habitat overlaps between elk and bison (Telfer and Cairns 1979; Wydeven and Dahlgren 1985). We observed moderate vegetation type overlaps but low diet overlaps between elk and mule deer. Most studies report high habitat overlap between elk and mule deer (Hudson 1976; McCullough 1980; Hudson et al. 1976), but most studies also report large differences between the diets of elk and mule deer (Hansen and Reid 1975; Kufeld 1973; Mackie 1970; McCullough 1980; Hobbs et al. 1983). We observed only minor vegetation, snow depth, and diet overlaps between elk and pronghorns, as was also reported by Wydeven and Dahlgren (1985) and McCullough (1980).

We observed no significant correlations between the severity of winter weather and ungulate numbers or ungulate productivity. Picton (1984) concluded that climatic effects on ungulates were greatest when populations were at or near ecological carrying capacity (ECC). The lack of correlation between ungulate populations and climate over the 20 years 1968–1988 may be related to reduced densities of ungulates during most of this period. Elk and bison populations likely approached or exceeded ECC by 1988 (Merrill and Boyce 1991); however, most data were from years when elk and bison populations were well below ECC and therefore were probably less influenced by weather.

Intraspecific competition may have increased in the rapidly expanding populations of several of the ungulate species, especially elk, bison, and pronghorns, but increased habitat and dietary breadths, as predicted by Fretwell and Lucus (1969), were observed only for bison and bighorn sheep. Intraspecific competition was implicated for bison; in the case of bighorn sheep change was more likely due to interspecific competition.

How could total ungulate numbers increase nearly 3-fold without any evidence of dramatic diet or habitat overlap between the ungulate species? We propose 4 possible explanations.

First, several ungulates may not have reached ECC by period 2, so competition for resources had not become intense enough to allow the outcome of competition to be measured. Elk, bison, pronghorns, and bighorn sheep were at levels far below ECC during period 1. Elk were probably at or near ECC during period 2 and bison were probably close to ECC (Merrill and Boyce 1991), while the relation of the other ungulates to ECC is unknown. The mild winters of perod 2 may have delayed the critical period of resource limitation.

Second, stimulation of aboveground production of grasses and nutrient enhancement through elk and bison grazing could have effectively increased ECC and delayed the point of observed competition. In other words, some ungulate interactions might be mutualistic. Frank and McNaughton (1992) reported stimulation of aboveground grassland production (+58%) across several sites as a result of elk and bison grazing. Singer (1994) documented a 10%–36% higher protein content in grazed versus ungrazed grasses on the northern winter range.

Third, habitat-use patterns and resource partitioning could have occurred at a finer scale than we sampled (McNaughton 1984; Belsky 1986; Gordon and Illius 1989; Day and Detling 1990).

Fourth, the occupied winter range for bison and elk increased by 300 and about 25%, respectively, during period 2 (Singer 1991), thus effectively increasing ECC for bison and elk and delaying the point of observable competition. Shallower snows during period 2 permitted all ungulates to use a larger area of winter range, again effectively increasing ECC.

Lastly, fluctuating environments and nonequilibrium population dynamics (Wiens 1984; Chesson and Case 1986; DeAngelis and Waterhouse 1987) might obscure the evidence of competition between potentially competing species.

Conclusions

Two ungulate species exhibited evidence of possible increased intra- or inter-specific competition following release from artificial controls, but three other species showed no such evidence. Neither elk, pronghorns, nor mule deer exhibited any but the most minor changes in habitat use, habitat breadth, diets, or diet overlaps between periods 1 and 2. The bison population increased by about 700%, and its occupied range increased by about 300% during the study periods; however, increased intra- and inter-specific competition was likely for bison, which increased their habitat breadth, their habitat overlaps with all other ungulates from 25 to 39%, and their diet overlaps with two other grazing ungulate species, owing to their increased use of grasses. The bighorn sheep population was smaller during period 2, and its increased habitat and diet breadths more likely reflect increased interspecific competition due to large increases in those of the other grazers, elk and bison. Between periods 1 and 2, bighorn sheep increased their use of the sagebrush type, and they consumed more grasses, commonly found in the sagebrush type. Bighorn sheep do not prefer tall shrubs, and their increased use of the sagebrush type during period 2 might reflect interspecific competition with elk.

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Predicting Effects of 1988 Fires on Ungulates in Yellowstone National Park

Mark S. Boyce

College of Natural Resources
University of Wisconsin
Stevens Point, Wisconsin 54481

Evelyn H. Merrill

Department of Zoology and Physiology
University of Wyoming
Laramie, Wyoming 82071

Abstract. We used computer simulation to forecast the effects of the 1988 fires on bison (*Bos bison*) and elk (*Cervus elaphus*) in Yellowstone National Park, based on our studies of these two species before the fires. Few ungulates died as a direct result of the 1988 fires in Yellowstone National Park. The greatest effects of the fires are expected to be changes in the forage base for these animals. Most of the area burned was summer range. Only 9% of the grasslands normally used by elk and bison on the northern range during winter burned. Before the 1988 fires, factors were studied that influence population dynamics of elk and bison in Yellowstone. Three variables—summer herbaceous biomass, winter severity, and population size—accounted for most of the year-to-year variance in per capita population growth rates for both species. These three parameters were modeled into a stochastic difference equation for each species. According to the model, the population for both elk and bison at the beginning of winter 1988–89 was larger than average carrying capacity due to a series of mild winters. High overwinter mortality during spring 1989 was therefore largely a consequence of abnormally high populations and slightly more severe winter weather. According to other studies, drought during the summer of 1988 and the burned winter ranges further aggravated the situation. Vegetation succession was used to project consequences of the 1988 fires to elk and bison populations. Both elk and bison should have enhanced recruitment and population size for several years, gradually declining to long-term carrying capacities of approximately 3,000 bison and 20,000 elk overwintering in the park.

Key words: Bison, elk, fire ecology, population dynamics.

The 1988 fires in Yellowstone National Park (YNP) are touted by some to be the ecological event of the century—nearly 42% of the park surface was affected by fires to some extent. This was the largest area burned in the greater Yellowstone landscape in recorded history. High intensity fires are known to be an integral component of Yellowstone ecology, with extensive fires appearing infrequently, sometimes as long as 300 years between major fires (Romme 1982; Romme and Despain 1989a, 1989b).

One of our major concerns about fire is the consequence to large mammals, which are key attractions for seasonal visitors to the park. We believe that fires may be beneficial to most ungulate species because of an increase in the availability of high-quality forage, particularly in areas formerly dominated by lodgepole pine (*Pinus contorta*). Ungulates may also be benefited because the fires have altered the spatial pattern and juxtaposition of habitat types. The fires created a complex mosaic with an increase in the amount of edge (Knight and Wallace 1989). Elk prefer forest edge where they can feed in close proximity to cover (Thomas 1979; Bobek et al. 1984).

Surveys by the National Park Service (NPS) revealed that less than 2% of the ungulates in YNP were directly killed by the fires of 1988 (Singer and Schullery 1989; Singer et al. 1989). It appeared that most deaths were from asphyxiation. Most animals simply moved away from the fires.

Many elk and bison died during the winter of 1988–89, and it is unclear whether some of these deaths were attributable to reduced forage availability because of fire. The winter was near average for snowfall and temperature, but ungulate populations were substantially above average carrying capacity because of several mild winters during the 1980's (Merrill and Boyce 1991). Considering the high elk population at the beginning of winter 1988–89, heavy losses were not unexpected, irrespective of the fires. Also, drought during summer 1988 was responsible for a reduction in winter range forage production—22% below normal (Singer and Schullery 1989). Elk and bison populations were further reduced by hunting outside the park during winter 1988–89 (Meagher 1989). Montana Department of Fish Wildlife and Parks hosted a late-season hunt in which 2,400 elk were killed, and 569 bison were killed in another, highly controversial hunt.

Studies of ungulates in the western United States have generally shown that diet quality and foraging efficiency of ungulates is enhanced as a consequence of fires (Hobbs and Spowart 1984; Urness 1985; Canon et al. 1987). Both elk and bison are attracted to burned areas where new forage is highly nutritious (Penfound 1968; Coppock and Detling 1986). In this paper we extrapolate from our studies on ungulate population dynamics in Yellowstone National Park (Merrill and Boyce 1991) to construct computer projections of the probable consequences of the 1988 fires on the size of future elk and bison populations.

Background

We used LANDSAT satellite imagery to characterize summer ranges on the northern range of northeastern Yellowstone National Park from 1972 through 1987. During summer 1987, we sampled vegetation in 1,300 plots at 25 sites scattered across the northern range. Linear combinations of 3 Multi-Spectral Scanner (MSS) wave lengths were used to estimate the average amount of green plant material (green herbaceous phytomass) over a 300-km study area. Only grasslands were sampled. Based on the among-site variation for 1987, we then estimated green herbaceous phytomass for LANDSAT images from 1972–87. Details of methods are given by Merrill et al. (1988).

Estimates of green herbaceous phytomass exhibited a strong pattern dependent upon the date of the satellite pass. We suspect this is largely attributed to annual variations in the seasonal pattern of drying of the plants (phenology). To standardize for this effect, we calculated the residuals from an average seasonal decline in green phytomass represented by a maxima function (as in Fig. 1). Deviations from this phenological pattern were a quadratic function of winter precipitation, implying that winter snowpack influences forage greening and thereby alters the timing of available green forage for ungulates, particularly at higher elevations. Therefore, we will define the negative of these residuals to be an index of range quality.

After accounting for density dependence and winter severity (Houston 1982), variation in summer range quality was significantly correlated with recruitment rates, calf survival, and per capita population growth rates for elk on the northern range. With the addition of spring precipitation, a similar relation was documented for bison. These relations allowed us to construct population models to extrapolate effects of changes in summer range on future dynamics of elk and bison.

Modeling Forage Dynamics

Our projections of forage responses are based primarily on patterns in plant succession in lodgepole pine (Basile 1975), sagebrush grasslands (Harniss and Murray 1973; West and Hassan 1985), and sedge meadows after clear-cutting or burning. We acknowledge that forage on burned sites may be higher in nutrients after burning (Coppock and Detling 1986) but these changes are likely short lived (3 years).

Diet quality also can increase initially because burning removes senescent vegetation which hinders diet selectivity (Wilms et al. 1980; Hobbs and Spowart 1984; Coppock and Detling 1986; Cannon et al. 1987). However, litter cover will return within a few years because summer ranges in Yellowstone are highly productive and do not receive the heavy ungulate use that is evident on winter range. Studies of *Stipa comata* in North Dakota found a return to prefire mulch structure after 4 years, although stands of *Agropyron smithii* took longer to restore mulch structure (Dix 1960).

We submit that the major change after fires will be in relative availability of various forage species. Forb diversity will increase and forb production will peak 5–10 years after the disturbance in lodgepole pine communities. Diversity and production decline thereafter (Basile 1975), possibly because of the chemical content of needles of lodgepole pine trees and canopy closure. Elk are expected to benefit from the increase in forbs because forbs are highly nutritious (Cook 1972), have high breakdown rates (Spalinger et al. 1986), and afford greater foraging efficiency (Canon et al. 1987; Merrill 1987). Bison do not make as extensive use of forbs, relying more on grasses and sedges (Meagher 1973). Sedges and grasses are expected to increase, primarily in wet meadows and sagebrush–grasslands (Old 1969; Coupland 1973; Harniss and Murray 1973).

Most anticipated changes in plant communities will enhance the forage available for ungulates. For example, some areas will be converted from tree cover to meadow. Forest encroachment onto these meadows may require a long time. Furthermore, burned aspen stands should undergo extensive suckering and vigorous regrowth (Bartos and Mueggler 1979; Boyce 1989). Burned sagebrush stands will be dominated by grasses and forbs until sagebrush plants become established and grow to maturity—we also anticipate an increase in open woodlands and savannas (Knight and Wallace 1989).

To simulate the effects of the fires on summer range forage, we modeled range quality, $Q(t)$, in t years after the fires as a maxima function, which is written

$$Q(t) = At\,e^{nt} \qquad (1)$$

where A is a positive constant and n is a negative constant which together scale the peak in range quality and the number of years postfire at which the peak will occur, and e is the base of natural logarithms.

The year of peak forage quality for the maxima function was scaled relative to variation in available green herbaceous biomass which we documented on the northern range of Yellowstone National Park during the period 1972 through 1987 (Merrill et al. 1988; Merrill and Boyce 1991). We have computed the function with a maximum at one and two standard deviations above average forage (Figs. 1 and 2). Peak forage quality for elk occurs 6 years after the fires (i.e., in 1994) with forage remaining average in the first year after the fire (Basile 1975; Bartos and Mueggler 1979). Although we do not know how to estimate the actual magnitude of response in forage quality, we propose that the two maxima curves may encompass the range of probable responses.

Population Projections

Ungulate response to summer range variation was estimated by fitting the per capita growth rate to a linear combination of effects attributable to population size in year t, $K(t)$, winter severity (Lamb's Index, see Houston 1982), $S(t)$, and summer range quality, $Q(t)$:

$$ln[N(t+1)/N(t)] = r - (r/K)N(t) - aS(t) + bQ(t) \qquad (2)$$

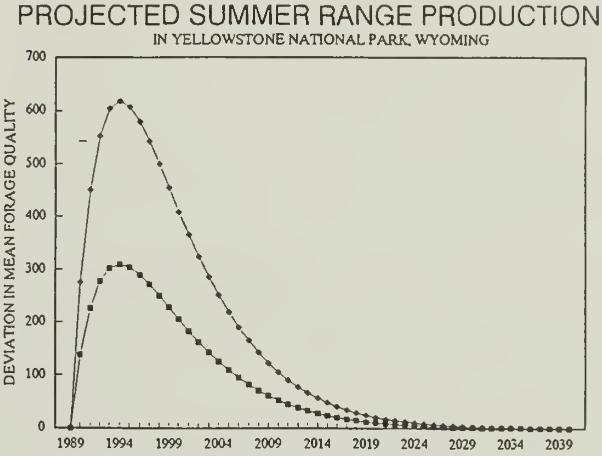

Fig. 1. Predicted postfire response in range quality for elk after the 1988 fires in Yellowstone National Park. Curves are generated using the maxima function—$y = 336te^{-0.2t}$ for the higher curve and $y = 168te^{-0.2t}$ for the lower curve.

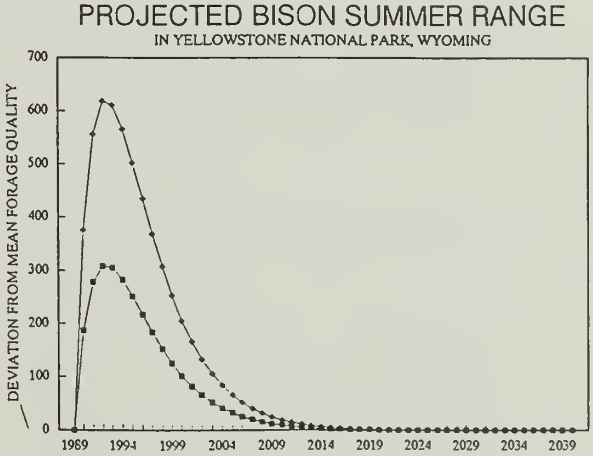

Fig. 2. Predicted postfire response in range quality for bison subsequent to the 1988 fires in Yellowstone National Park. Curves are generated using the maxima function—$y = 507te^{-0.3t}$ for the higher curve, and $y = 253te^{-0.3t}$ for the lower curve.

r is the logistic potential growth rate, and *K* is the carrying capacity where $N(t+1)/N(t) = 1$. Multiple regression coefficients, *r*, (*r/K*), *a*, and *b*, were estimated by least squares (Merrill and Boyce 1991).

This model can be rewritten as a difference equation to project future population size:

$$N(t + 1) = K(t)\,exp[r - (r/K)N(t) - aS(t) + bQ(t)] \qquad (3)$$

We used this model to project a stochastic (random) time series by defining $S(t)$ and $Q(t)$ to be independent random variables with normal distributions with variances equal to those observed during the period 1972 through 1987.

In Fig. 3, we present the results of deterministic projections of the number of elk wintering in Yellowstone National Park for the next 52 years, based upon range quality functions in Fig. 1. In Fig. 4, we show a stochastic simulation to illustrate the magnitude of fluctuations attributable to climatic unpredictability.

For bison, the projected population sizes are presented in Figs. 5 and 6. Again, stochastic fluctuations, especially due to severe winters, cause substantial unpredictability in future population sizes.

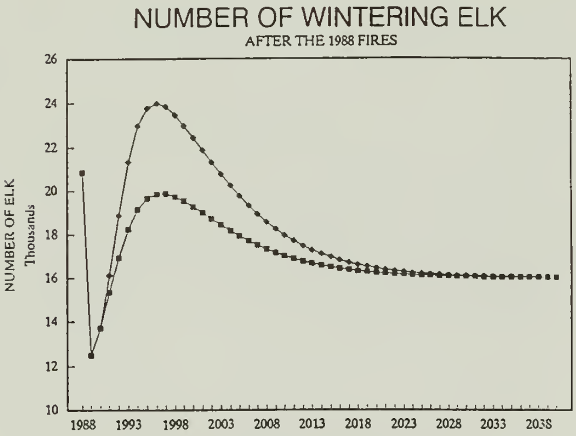

Fig. 3. Predicted population size for elk wintering in Yellowstone National Park for each of the range quality response scenarios suggested in Fig. 1.

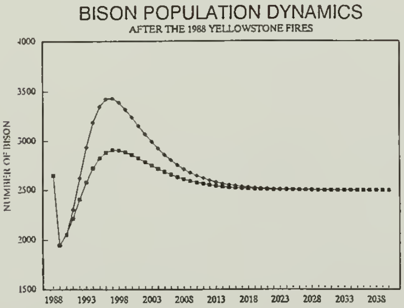

Fig. 5. Predicted population size for bison wintering in Yellowstone National Park for each of the range quality response scenarios suggested in Fig. 2.

Discussion

Population growth rates for ungulates in Yellowstone National Park are mostly determined by winter severity, population density, and summer range quality. Our simulations presume that the effects of the 1988 fires will be manifested primarily through the consequences to summer forage composition and therefore forage quality. Previous studies have

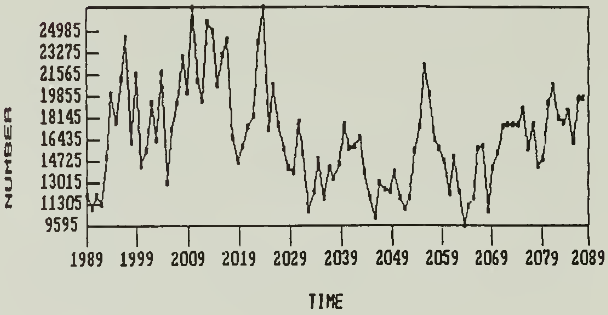

Fig. 4. A stochastic simulation of the future population size for elk wintering in Yellowstone National Park.

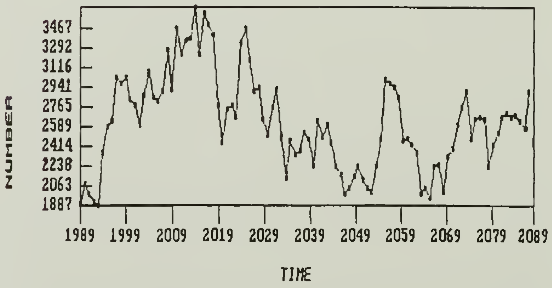

Fig. 6. Stochastic simulation of the future population size for bison in Yellowstone National Park after the 1988 fires.

demonstrated that diet quality and foraging efficiency will be enhanced by fire, but we cannot know the extent to which ungulates will use the burned areas and how much better diets will be, compared to prefire diets.

Therefore, the scales presented on the *y*-axis in Figs. 1 and 2 are tenuous. We suspect that our projections are conservative and the magnitude of population response is probably greater. Note that our projections are only within the normal range of variation that has occurred during the 15 years before the fires.

The simulations presented in this paper represent hypotheses based upon our current understanding of factors influencing elk and bison populations in Yellowstone National Park. Our projections are reasonably consistent with patterns of elk population dynamics following fires in the western United States (Leege 1968; Wright and Bailey 1982). Likewise, the curves presented in Fig. 3 are largely consistent with observations of Lowe et al. (1978) that maximum elk use of burned sites occurred 7 years after fire, although little preference for burned sites could be seen 20 years after burning. We hope that we will have an opportunity to evaluate our forecasts during the next 25 years.

Large fires in the greater Yellowstone ecosystem during the summer of 1988 offer a unique opportunity to study the role of fire in the ecology of ungulates in the Rocky Mountains. Numerous monitoring programs have been initiated to document the changes occurring since the fires. The fires, however, will have multiple consequences to the vegetation and the animals. In addition to monitoring studies, therefore, experimental work will be necessary to untangle the mechanisms causing responses by ungulates. Experimental manipulations that are heavy on the land may not be appropriate for Yellowstone National Park; it may be necessary to conduct such experiments on National Forest lands adjacent to the park. Certain experimental studies, however, may be conducted within the park; current investigations include use of exclosures and tame animals within the boundaries of the park.

The population projections presented in this paper form the basis for a model to anticipate the consequences of wolf recovery in Yellowstone (Boyce 1990). Beneficial effects of the fires on ungulates in Yellowstone may enhance the probability for success of proposed wolf recovery in Yellowstone National Park.

Acknowledgments

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Estimation of green herbaceous phytomass from Landsat MSS data in Yellowstone National Park

EVELYN H. MERRILL, MARY K. BRAMBLE-BRODAHL,
RONALD W. MARRS, AND MARK S. BOYCE

Authors are assistant professor, Department of Zoology and Physiology, University of Wyoming, Laramie 82071-3166; research associate, Department of Zoology and Physiology, University of Wyoming, Laramie 82071-3166; professor, Department of Geology, University of Wyoming, Laramie 82971-3006; and professor, Department of Zoology and Physiology, University of Wyoming, Laramie 82071-3166.

Abstract. Green herbaceous phytomass was measured in August 1987 in grassland and sagebrush–grassland communities of Yellowstone National Park and related to August 1987 Landsat MSS data. A linear model using MSS band 7 and the ratio of MSS bands 6 to 4 accounted for 63% of the variance in green herbaceous phytomass on ground-truth plots ($n = 25$). Error in estimates of green herbaceous phytomass was influenced by the relative amount of bare ground and the proportion of green to green plus dead herbaceous vegetation present at a site. The model was used to predict average green herbaceous phytomass in grassland and sagebrush–grassland communities across a 600 km portion of ungulate summer range in Yellowstone National Park for 11 years during 1972–1987 using additional Landsat MSS imagery. Green herbaceous phytomass declined seasonally from late July to early September. Annual deviations in green herbaceous phytomass from the 11-year average, corrected for date of satellite overpass, were not significantly related to precipitation or temperatures during the growing season but were related quadratically to December–March precipitation. Below-average green herbaceous phytomass in years of low and high winter precipitation may be related to the effects of snow accumulation and melt on phenological development (green wave) of plants across the summer range. Models based on MSS spectral data can provide useful descriptions of broadscale patterns of plant phenology may confound the interpretation of results when spectral models are used to compare vegetation yield of forage availability among years.

Key Words: biomass, Landsat, multispectral scanner, Yellowstone National Park, ungulate summer range

Traditional methods for estimating forage availability to ungulates such as elk and bison are not practical for application over large geographic areas. Yet such estimates are necessary if we are to understand the dynamics between wide-ranging ungulate populations and their habitat (Strong et al. 1985). Spectral values recorded by the Landsat multispectral scanner (MSS) can be used to estimate vegetative characteristics, because foliage of plants differentially absorbs and reflects energy in the visible and near infrared regions of the spectra

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(Knipling 1970, Tucker and Sellers 1986, Tueller 1989).

Previous estimates of green phytomass made using spectral data have used near infrared and red wave bands in ratio (Colwell 1974, Pearson et al. 1976a, Boutton and Tieszen 1983) or linear combinations to form vegetation indices (Tucker et al. 1981, Richardson and Wiegand 1977, Weaver 1986). Richardson et al. (1983) found a nonlinear relationship between a perpendicular vegetation index (PVI) and biomass of *Cynodon* spp. in Texas. Kauth and Thomas (1976) combined 4 MSS bands to form the soil brightness index (SBI), which establishes the expected reflectance of soils, and the green vegetation index (GVI) which is orthogonal to the soil index.

Although Landsat multispectral information can provide useful indices to range vegetation, relationships for 1 site may not apply at other sites due to variation in range and soil conditions (Boyd 1986). Therefore, reliable estimates require that the procedures be tailored to site-specific conditions. The purpose of this paper is (1) to describe a spectral model designed to estimate green herbaceous phytomass in grassland and sagebrush communities of Yellowstone National Park using Landsat MSS spectral data, and (2) to evaluate the model for detecting annual trends in forage availability on ungulate summer range.

Methods

Study Area

The study was conducted in the northeast portion of Yellowstone National Park with major focus on the upper Lamar, Cache, and Calfee River drainages and the Mirror Plateau (Fig. 1). Geology of the park has been described by Keefer (1972) and topography, vegetation and soils have been described by Meagher (1973), and Houston (1982), Despain (1990). Climate data from Cook City, Montana (Fig. 1) were used to characterize weather patterns. Annual precipitation at Cooke City averaged 67.0 cm and daily temperature in January and July at Cooke City averaged −10.3° C and 13.9° C, respectively (U.S. Dep. Commerce 1970– 1987).

Our work focused on the sagebrush and grassland portions of the study area at elevations of 2,000–2,780 m. Sagebrush areas were dominated by big sagebrush (*Artemisia tridentata* Nutt.) communities with understories of bluebunch wheatgrass [*Agropyron spicatum* (Pursh) Scribn. & Smith] in dry areas and Idaho fescue (*Festuca idahoensis* Elmer) in mesic areas. Silver sagebrush (*Artemisia cana* Pursh)/ Idaho fescue communities were associated with stream banks and seeps. Idaho fescue/wheatgrass [*Agropyron spicatum* and *A. caninum* (L.) Beauv.] communities dominated at intermediate elevations. Grasslands occurred at high elevations and were dominated by Idaho fescue/tufted hairgrass [*Deschampsia cespitosa* (L.) Beauv.] and tufted hairgrass/sedge (*Carex* spp.). Elk (*Cervus elaphus*) and bison (*Bison bison*) are the most abundant ungulates in this area of the Park (Houston 1982).

Model for Estimating Green Phytomass

In 1987, we assessed regression models to estimate green phytomass from vegetation data collected 9–21 August 1987 at 25 ground-truth sites (Fig. 1) and Landsat imagery for 5 August 1987. Ground-truth sites comprised at least 2.7 ha (about 6 pixels of Landsat 5) of homogeneous vegetation. Phytomass was estimated using a double sampling approach (Wilm et al. 1944, Carande and Jameson 1986). At each ground-truth site, green herbaceous phytomass was estimated within fifty 0. 18-m^2 microplots using either a capacitance meter (Neal et al. 1976), or, in remote areas into which the capacitance meter could not be transported easily, measurements of forb and grass volume (canopy coverage × average plant height). Ten of the 50 microplots on each site were clipped to ground level and clippings were separated into standing dead herbaceous material, green forbs, and green graminoids. A criterion of ≥25% "green" was used to differentiate green from senesced plants. Current growth of shrubs, consisting of new growth of twigs and all green leaves, was estimated with a capacitance meter. Readings of the capacitance meter were taken before and after shrubs were removed from the microplots (Morris et al. 1976). Shrubs removed from the plot were clipped of current growth.

Clipped plant material was oven-dried at 100° C for 48 hours and weighed to the nearest 0.1 g. An average dry to wet weight ratio of 0.70 (n = 50) was used to convert wet weight of standing dead herbaceous plants in each microplot to dry weight Oven-dried weights of phytomass were regressed on capacitance or volume measurements and regressions were used to predict the dry weight of phytomass in the nonclipped microplots. Regressions of phytomass weights from capacitance meter readings explained more of the variation in green herbaceous phytomass (grasses plus forbs) ($r^2 = 0.73$) than regressions of green forb ($r^2 = 0.45$) and green grass ($r^2 = 0.63$) phytomass based on plant volume. Regressions of

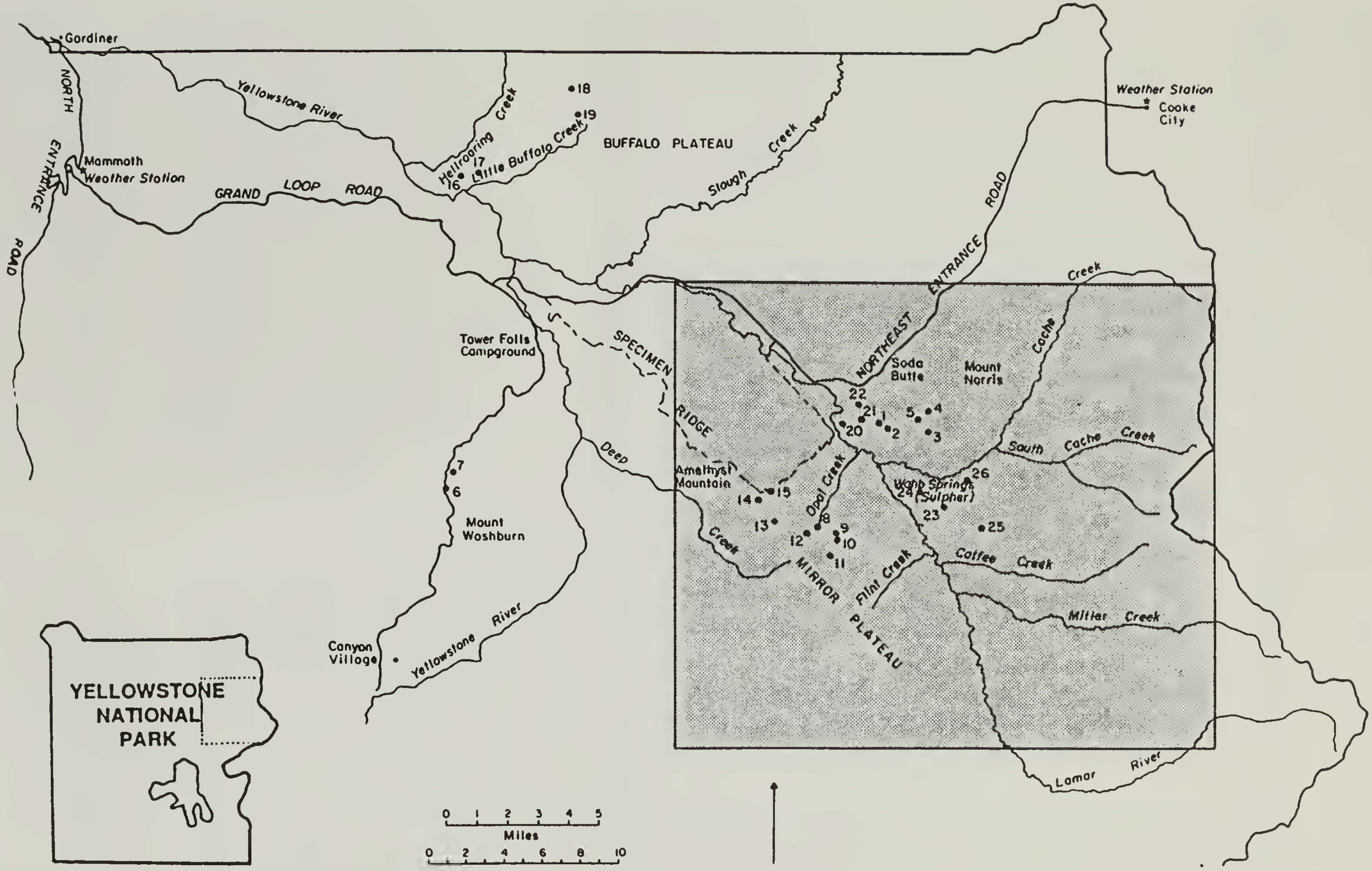

Fig. 1. Location of field plots in Yellowstone National Park sampled to determine relationships between green phytomass and reflectance values remotely sensed by Landsat multispectral scanner and the Cache/Calfee–Mirror Plateau study area (shaded) for which average green herbaceous phytomass was estimated during 1972–1987. See text for details.

current growth from the difference in capacitance readings before and after shrubs were removed from a microplot, explained 68% of the variance in shrub current growth.

Landsat data for 5 August 1987 were transferred from computer-compatible tape to the Map and Image Processing System (MIPS) for data processing and display. Ground-truth plots were mapped on orthophoto quadrangle maps in the field and transferred to 1:58,000-scale color infrared aerial photographs in the lab. Plot locations on the photographs were digitized using a Panasonic video display camera which allowed the image processor to capture spectral information from the 3 spectral bands (red, green, IR). The computer image was aligned with the Landsat image to establish plot locations on the Landsat scene. Digital values of the 4 Landsat MSS bands were recorded for the plot location (2 pixels) and 4 adjacent pixels within the same vegetation community. The 6 values (2.7 ha) for each band were averaged to represent the spectral signature of the ground-truth plot.

Relationships between green phytomass at the 25 ground-truth sites and the MSS spectral values, linear combinations of the spectral values, and vegetation indices (Rouse et al. 1974, Kauth and Thomas 1976) for the sites were evaluated using least squares regression analysis (Kleinbaum and Kupper 1978). Three criteria were used to select the most appropriate regression model for estimating green phytomass from Landsat spectral data: a significant F value ($P \leq 0.05$), an explanation of at least 50% of the variance in the phytomass data, and the lowest standard error of the estimate.

Annual Estimates of Green Herbaceous Phytomass

Annual estimates of average green herbaceous phytomass were derived for the grassland and sagebrush–grassland portions of a 600 km (Fig. 1) area of ungulate summer range during 1972–1986 using additional Landsat imagery for 10 years and the 1987 phytomass model. This procedure followed a 3-step process. First, Landsat data for previous years were calibrated to 1987 imagery conditions. Adjustments included corrections for machine differences in detector sensitivity and electronic gain among Landsat satellites (Markham and Barker 1987) and for environmental differences, such as sun angle and haze. Corrections for environmental differences were made by selecting 4 reference areas that had little to no vegetation (e.g., bare rock, lakes, and travertine deposits near a hot spring) and regressing spectral values in 1987 against the values for the same areas in other years (Merrill et al. 1988).

The second step involved the elimination of forests and clouds so that average estimates of green herbaceous phytomass for the study area represented only grassland and sagebrush–grassland areas. A principal component analysis (PCA), using spectral values for all 4 MSS bands, was performed on a "training area" within the study area to distinguish between forested and nonforested pixels. An appropriate threshold value, below which areas were classified as forests, was determined by visually comparing the display of the PCA index to forested areas on Yellowstone Park cover maps. The PCA index was then calculated for each pixel within the 600 km area. All pixels with a PCA value below the threshold were omitted from our estimate of average green herbaceous phytomass. Similarly, pixels with a PCA value above a designated threshold were covered by clouds and were omitted from the estimate of average green herbaceous phytomass.

Finally, calibrated spectral values were used in the model to obtain a pixel-by-pixel estimate of green herbaceous phytomass in the sagebrush–grassland and grassland portions of the study area for the 11 years for which we had Landsat imagery. Pixel values were then averaged across the study area to obtain an annual estimate of average green herbaceous phytomass for the same grassland and sagebrush–grassland portions of the study area.

Results

Phytomass at Ground-truth Sites

Estimates of total green phytomass (herbaceous phytomass plus current growth of shrubs) on the 25 ground-truth sites sampled in 1987 ranged from 482 to 3,154 kg/ ha (Table 1). At sites dominated by sagebrush, new twigs and leaves of shrubs averaged 28% of the total green phytomass. In grassland communities, grass comprised over 70% of green herbaceous phytomass, on average. Highest green herbaceous phytomass occurred on site 3, which was dominated by timothy (*Phleum pratense* L.). Forbs predominated only on the Buffalo Plateau where they comprised 79% of green herbaceous phytomass on 1 site. Percentage of senesced material in the standing crop averaged 20% (5–48%) of total phytomass (Table 1).

Table 1. Green phytomass (kg/ha), standing dead herbaceous phytomass (kg/ha), current growth of shrubs (CG), and bare ground (% cover) at 25 sites sampled in Yellowstone National Park on 9–21 August 1987.

Plot Number	Total[1] Green	Green[2] Herbaceous	Shrub CG	Green Forb	Green Grass	Standing Dead	Bare Ground Cover
	kg/ha						%
1	616.7	580.2	36.5	167.1	413.1	40.8	22.2
2	1978.7	1193.6	785.1	366.1	827.5	104.2	10.6
3	3153.9	3153.9	0.0	297.8	2856.2	165.7	3.3
4	885.0	638.7	246.3	183.7	455.0	59.0	34.4
5	960.2	960.2	0.0	267.6	692.6	121.4	31.7
6	673.4	638.1	35.3	203.5	434.6	39.0	2.6
7	1032.2	1032.2	0.0	138.9	893.3	79.9	2.1
8	1077.4	1077.4	0.0	269.6	807.8	380.2	3.9
9	694.8	694.8	0.0	178.5	516.3	101.6	7.1
10	1087.3	1087.3	0.0	323.7	763.6	226.2	6.0
11	838.6	838.6	0.0	276.6	561.7	123.2	12.0
12	1521.5	1521.5	0.0	182.8	1338.7	555.3	6.0
13	1536.8	1536.8	0.0	371.0	1165.9	369.9	2.4
14	1020.3	1020.3	0.0	249.8	770.5	302.8	2.9
15	1627.9	1627.9	0.0	481.5	1146.0	289.0	6.3
16	576.8	530.8	46.2	60.8	469.9	107.4	46.5
17	1180.8	964.7	216.1	224.4	740.3	208.9	11.9
18	907.5	907.5	0.0	714.0	193.2	371.8	47.7
19	946.0	946.0	0.0	260.9	685.1	232.4	3.0
20	481.9	363.5	118.4	80.2	283.3	130.6	6.4
21	1030.5	963.4	67.2	143.3	820.1	294.1	1.6
23	684.9	684.9	0.0	212.2	472.7	510.6	6.2
24	526.5	526.5	0.0	202.3	324.2	474.7	2.6
25	778.5	778.5	0.0	236.8	541.7	316.7	4.5

[1] Total Green = green herbaceous phytomass plus current shrub growth (new twigs and all green leaves).
Green Herbaceous = green grass plus green forb phytomass.

Green Phytomass Model

Correlations between spectral bands, band ratios, or vegetation indices and green phytomass were generally weak (Table 2). Among the linear models we tested, no combination of MSS spectral bands or band ratios explained more than 50% of the variation in total green phytomass, current growth of shrubs, or green forb phytomass, while several indices explained 50% of the variation in green grass and green herbaceous (grass plus forb). The equation which best met our criteria for model selection was:

$$GHP = 2687\ (MSS6/MSS4) - 87.68\ MSS7 - 396.79 \qquad (1)$$

where GHP is green herbaceous phytomass (grass plus forbs), $r^2 = 0.63$, $P < 0.001$, S.E. = 350.5 kg/ha. Logarithmic transformations of our data did not account for more than an additional 1% of the variation in any of the models and were avoided due to additional complexity of those transformations in our image processing system.

Potential sources of error in our model are illustrated in Fig. 2. Green herbaceous phytomass predicted by equation 1 is frequently overestimated when the ratio of green herbaceous phytomass to total standing herbaceous phytomass (green plus dead) is low and tends to be underestimated when bare ground is high.

Annual Estimates of Green Herbaceous Phytomass

Average green herbaceous phytomass in the grassland and sagebrush–grassland portions of the study area ranged from 633 kg/ha in 1974 to 1,806 kg/ha in 1979 (Table 3). A seasonal decline in green herbaceous phytomass was observed in relation to date of satellite overpass (Fig. 3). The following

Table 2. Linear correlation coefficients (r) between selected vegetation measurements and Landsat MSS bands values, band ratios, and vegetation indices (n = 25). NS indicates $P \geq 0.05$.

Parameter	Total green	Green herbaceous	Green forb	Shrub CG	% Cover[1] bare ground
MSS Band 4	−0.55	−0.64	NS	NS	NS
MSS Band 5	NS	−0.46	NS	NS	NS
MSS Band 6	NS	0.42	0.53	−0.42	NS
MSS Band 7	NS	NS	0.51	−0.45	NS
Ratio MSS6/MSS4	0.42	0.57	0.50	−0.42	NS
MSS6/MSS5	0.42	0.56	0.44	−0.40	NS
MSS7/MSS4	NS	0.52	0.49	−0.45	NS
VI[2]	NS	0.51	0.44	−0.43	NS
TVI[3]	NS	0.51	0.44	−0.43	NS
GVI[4]NS	NS	NS	NS	NS	
PVI[5]	NS	0.31	NS	NS	NS

[1] Correlations are based on arcsine-square root transformations of percentage values.

Vegetation index: VI = (MSS7-MSS5)/(MSS7+MSS5), Rouse et al. 1974.

[3] Transformed vegetation index: TVI = SQRT(VI+0.05), Rouse et al. 1974.

[4] Green vegetation index: GVI = −0.42305 (MSS4) - 0.5054 (MSS5) +0.25689 (MSS6) +0.7068 (MSS7)

[5] Perpendicular index: PVI = 1.08 (MSS7)/1.03 (MSS5–6)

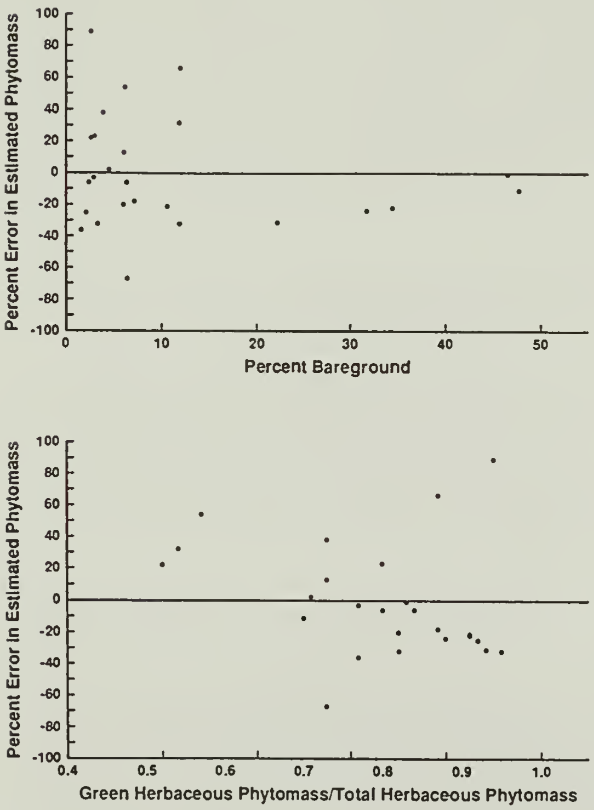

Fig. 2. Effects of bare ground (a) and plant senescence (b) on the percent of error in estimating green herbaceous phytomass of field plots in August 1987 using Equation 1.

maxima function curve (Spain 1982) was fit to the 11 annual estimates:

$$\text{GHP} = \text{A x exp (nx)} \qquad (2)$$

where GHP = green herbaceous phytomass (kg/ha) − 600, x = julian date of sampling − 100, A = 17,206, n = 0.068, ($r^2 = 0.61$, $P < 0.05$, n = 11). The equation represents the average seasonal decline in green herbaceous phytomass from the end of July to the beginning of September for the 11-year period of the study (Fig. 3). Deviations in our annual estimates of green herbaceous phytomass from this average were quadratically related to December–March precipitation ($r^2 = 0.81$, $P < 0.01$, Fig. 4). No significant relationship was found between deviations in annual estimates of green herbaceous phytomass from the average and temperature or total precipitation during the growing season.

Discussion

Our estimates of green herbaceous phytomass in northeastern Yellowstone National Park are well within values reported for the habitat types we sampled (Mueggler and Steward 1980) suggesting that canopy spectro-reflectance in grassland and sagebrush–grasslands of Yellowstone National Park can be a useful estimator of green herbaceous phytomass.

Table 3. Year and date of Landsat satellite overpass, Landsat satellite, total number of pixels within the Cache/Calfee-Mirror Plateau study area, total number non-forested pixels for which average green herbaceous phytomass (GHP) was estimated, number of pixels covered by clouds, and annual estimates of average green herbaceous phytomass (kg/ha).

	Date of	Landsat	Total Area		Grasslands		Cloud Cover		
Year	Over	satellite	Pixels[1]	Area	Pixels	Area	Pixels		GHP
			(no)	(km²)	(no)	(km²)	(no)	(%)	(kg/ha)
1972	8/07	1	148992	671	57375	258	0	0	1409
1973	8/20	1	148772	670	46671	210	4867	10	722
1974	9/02	1	148480	669	42286	190	0	0	633
1975	8/10	1	146432	659	46949	211	0	0	1707
1976	9/09	1	147456	664	52902	238	0	0	913
1978	7/25	3	145290	654	49173	221	0	0	1050
1979	7/29	2	204800	665	68632	223	1917	3	1806
1991	8/23	2	204800	665	58361	190	0	0	915
1984	8/12	5	204800	665	70246	228	13813	20	964
1986	8/02	5	204800	665	68726	223	1834	3	1592
1987	8/05	5	204800	665	60529	197	3072	5	1204

[1] Geometrically uncorrected pixel size (57 × 79 m): 1972–1978
Geometrically corrected pixel size (57 × 57 m): 1979–1987

Although the precision of our model is comparable to those for other grassland communities (Boutton and Tieszen 1983, Weaver 1986), errors can be large and would limit the use of this technique in investigations requiring precise estimates. Boutton and Tieszen (1983) found that average percent error of the estimate increased as the proportion of live biomass of the standing biomass declined. Pearson et al. (1976b) found estimates of green phytomass from spectral models were unreliable when live or green vegetation comprised less than 30% of the total phytomass (green plus standing dead). We had no plots in 1987 on which green herbaceous phytomass was less than 50% of the total herbaceous vegetation (green plus standing dead) but found that green herbaceous phytomass was overestimated when the proportion of green to total (green plus standing dead) phytomass in a plot was less than 60%. Green herbaceous phytomass was underestimated in plots with greater than 20% bare ground. Soil background signals can have an overriding effect on predicting vegetative conditions (Huete et al. 1984, Elvidge and Lyon 1985). We did not collect data on the spectral characteristics of soils at our ground-truth sites and in the future it may be possible to improve these estimates with corrections for soil reflectances.

Estimates of green herbaceous phytomass indicated a rapid seasonal decline in green herbaceous phytomass from late July to early September in the Cache-Calfee/Mirror Plateau area (Fig. 3). Most studies have reported positive, linear relationships between winter–spring precipitation and herbaceous yield in grassland and sagebrush–grassland communities (Craddock and Forsling 1938, Blaisdell 1958, Whysong 1973). In this study, we found that green herbaceous phytomass in late summer was below the seasonal average when December–March precipitation was low or high (Fig. 4). Because spectral models like ours predict green, rather than total phytomass, we suggest that average green herbaceous phytomass was influenced by annual variation in phenology (green wave) which is determined by winter snow accumulation and timing of

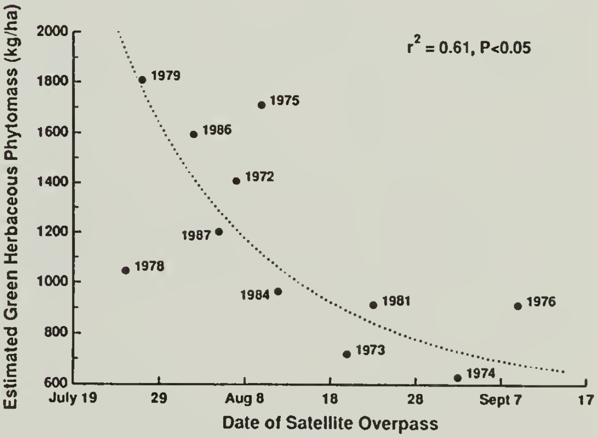

Fig. 3. Average green herbaceous phytomass (GHP) (kg/ha), estimated from Landsat MSS spectral data, for the grassland and sagebrush–grassland portions of the Cache/Calfree–Mirror Plateau study area during 11 years from 1972–1987. The dotted line represents the average seasonal decline in green herbaceous phytomass for the years of the study.

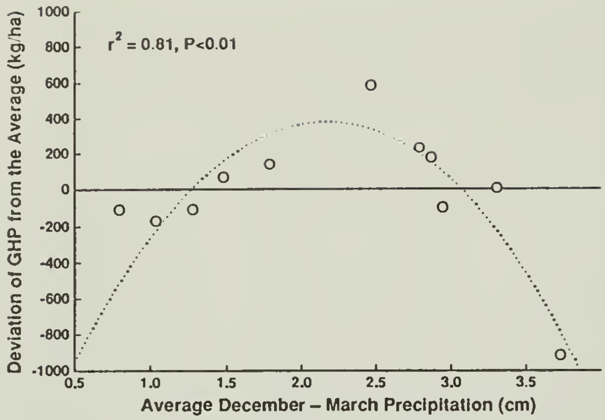

Fig. 4. The deviation in green herbaceous phytomass (GHP) (kg/ha) from the average seasonal decline in green herbaceous phytomass in relation to average December–March precipitation (cm).

snowmelt. When winter snow accumulations were low, snowmelt and spring green-up occurred early and plants cured early so that less green herbaceous phytomass was available in late summer than in years of average snow accumulation. Likewise, in years of heavy snowfall, the amount of green herbaceous phytomass measured in late summer was below average because snow melt occurred late, delaying phenological development. The quadratic relationship between variation in green herbaceous phytomass and winter precipitation we present is highly dependent on a few data points and it needs to be substantiated further. Yet, because we found no significant relationships between green herbaceous phytomass and precipitation or temperatures during the growing season, we hypothesize that the pattern of snow accumulation and melt is the dominant factor influencing phenological development in these high elevation grasslands. This hypothesis is consistent with the results of Frank (1990), who found that concentration of green biomass (mg cc^{-1}) at his field sites on the Cache-Calfee summer ranges was significantly related to days after snowmelt. Timing of snowmelt has been shown to influence phenology of plants in other high elevation grasslands of this region (Canaday and Fonda 1974, Weaver 1974).

Snow accumulation and melt also may influence total yield, but this relationship does not seem to be a simple one. For example, in Montana, Weaver and Collins (1977) found a decline in herbaceous yield of *Festuca idahoensis/Agropyron caninum* vegetation under snowbanks relative to driftless areas. They attributed reduced yield under the snowbank to a shortened growing season caused by late snowmelt, but similar ending dates to the growing season. Knight et al. (1979), however, found that prolonged snow cover, due to artificial augmentation of snow in subalpine grasslands in southeast Wyoming, decreased yield in wet meadows but increased yield in dry meadows. They suggested that additional water in dry meadows may have wet the soil to a greater depth than normal, thereby providing a greater supply of water for plant growth via deeper plants roots or capillary movement from below.

In addition to climatic factors, Frank (1990) found that ungulates in this area can stimulate aboveground plant growth. During the period of our study, ungulate numbers increased to record highs (Singer et al. 1989). However, we did not find a correlation between ungulate population numbers and the deviation in green herbaceous phytomass from the mean in the years of the study, implying that ungulates were not affecting green herbaceous phytomass.

We conclude that Landsat MSS data can provide estimates of green herbaceous phytomass in Yellowstone National Park that are useful for landscape questions (e.g., Merrill and Boyce 1991) but may not be precise enough for other purposes. It is possible that Landsat thematic mapper data may improve the precision of the phytomass estimates because more band options are available for model development. Nonetheless, annual variation in phenology may confound the interpretation of results when spectral models are used to examine trends in vegetation production or forage availability across years.

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