ECOLOGICAL RESEARCH IN NATIONAL PARKS OF THE PACIFIC NORTHWEST

Compiled from Proceedings of the Second Conference on Scientific Research in the National Parks

San Francisco, California

November 1979

Copies available from:

National Park Service Cooperative Park Studies Unit
Forestry Sciences Laboratory
3200 Jefferson Way
Corvallis, Oregon 97331

Ecological Research in National Parks of the Pacific Northwest

An Oregon State University Forest Research Laboratory Publication
Corvallis, Oregon 97331

(Compiled from Proceedings of the Second Conference on Scientific Research in the National Parks, San Francisco, California, November 1979)

TECHNICAL COORDINATORS

Edward E. Starkey, Project Leader
Cooperative Park Studies Unit
National Park Service
Oregon State University
Corvallis, Oregon 97331

Jerry F. Franklin, Project Leader
U.S. Forest Service
Pacific Northwest Forest and Range Experiment Station
Forestry Sciences Laboratory
3200 Jefferson Way
Corvallis, Oregon 97331

Jean W. Matthews, Science Editor
Cooperative Park Studies Unit
National Park Service
Forestry Sciences Laboratory
3200 Jefferson Way
Corvallis, Oregon 97331

Published September, 1982

FOREWORD

Three main points emerge from this collection of papers...1) the value of natural areas for research into the workings of the natural systems, 2) the fiscal and informational benefits of interagency cooperation and cross disciplinary approaches to research, and 3) the importance of such research to managers of both manipulated and natural sites.

One of the most rewarding outcomes of this work has been the "serendipitous" insights that specialists, working together, have achieved. Specialization is absolutely basic to thorough, in-depth science; but the meshing of a number of disciplines in a concerted effort to understand one particular site or problem can result in unique flashes of insight. Those insights can come through papers assembled from various disciplines into a generally focused volume, or they can arise from the meshing of minds in an intensive interdisciplinary exercise like the Hoh River Pulse Study (from which seven of these papers were drawn).

Just as important as the excitement such sparks generate among individual scientists is the useful comparison the studies provide for managers of natural areas and for managers of manipulated areas. The store of information about how best to perform each task is considerably enhanced by findings of the kind presented here.

Natural areas, most notably National Parks, Research Natural Areas, and Biosphere Reserves, encompass a broad set of representative ecosystems operating today as nearly as possible in the pathways they would have taken if technology had not become such a decisive factor in, and on, the biosphere of Earth. To the extent that technology is an outgrowth of natural systems, it must be considered "natural." Volcanoes, however, are natural also; and we recognize that they have had devastating effects on the ecosystems in place when they erupted. By bringing together in one volume a cross section of scientific investigation into the functioning of the underlying natural systems that support our technology and our lives, we are documenting the state of our scientific investigation at this time. We are also demonstrating the way scientists from two federal agencies with different missions have worked together to provide additional light on the agencies' subject areas.

This volume then, represents a joint recognition on the part of two caretaker agencies that natural areas are the best remaining "libraries" for understanding the natural systems that brought us all to our present position as the prime manipulators in the history of Earth. It suggests that among the most immediate future roles for these areas may be as baseline "controls" against which to measure similar environments being manipulated. And finally, it provides a richer understanding of the Northwest's ecosystems and of the future possibilities for extending their uses, meanwhile preserving their on-going health and productivity.

PREFACE

The National Park Service and the American Institute of Biological Sciences sponsored the Second Conference on Scientific Research in National Parks, November 26-30, 1979, in San Francisco, California. More than 500 scientists and managers attended from local, State, and Federal organizations.

Presented at the Conference were 20 papers dealing with various aspects of the overall ecology of National Parks and a National Monument in the Pacific Northwest Region. These papers do not cover the breadth of research in this area, but are instead examples of current issues that concern researchers and resource administrators. The papers also reflect the growing base of knowledge acquired as a result of shared effort among a variety of research support agencies, organizations, and institutions.

The diverse range of research topics covered could only have been studied in relatively undisturbed areas such as National Parks. Examples are the papers dealing with climax forests, ungulate populations that are unhunted, and habitats ungrazed by domestic livestock, where air and water are clean enough to serve as a baseline for pollution measurements.

The USDA Forest Service, Environmental Protection Agency, Army Corps of Engineers, and several universities and private industries all provided principal investigators and cooperation. Without this support, most of the research reported herein would not have been initiated nor could this report have been published.

The papers are printed here essentially as submitted by the authors except for some minor copy editing to assure uniformity of style.

Jean Matthews
Science Editor
National Park Service

CONTENTS

Ecosystem Studies in the Hoh River Drainage, Olympic National Park

Jerry F. Franklin

Jerry F. Franklin, U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station, Forestry Sciences Laboratory, 3200 Jefferson Way, Corvallis, Oregon 97331.

Interdisciplinary, ecosystem-oriented research is essential to understanding complex, interlinked resource values. A project of this type was carried out in the South Fork of the Hoh River in the western Olympic Mountains. This wilderness drainage has outstanding examples of broad terraces with Picea sitchensis-Tsuga heterophylla rainforests, a major glacial-fed river, and fluvial processes. During an intense 11-day "pulse," relationships were examined between geomorphic processes, terrestrial communities, and aquatic systems. This paper discusses the rationale of the study, describes the objectives and approaches, and serves as introduction to seven papers that follow.

On September 5, 1978, a large group of scientists, technicians, and graduate students entered the South Fork of the Hoh River drainage. The research team included personnel from 11 different organizations and a broad range of disciplines. During the next 11 days, 46 technical personnel devoted 266 field days to an examination of landforms, geomorphic processes, and aquatic and terrestrial communities and their interrelationships.

My objective in this paper is to outline the rationale and objectives of this short-term intensive research effort which we refer to as a "pulse." I will also describe the essential features of the site. All of this serves as introduction to the seven papers that follow. Six of these papers are based on research conducted in the South Fork during the pulse. One paper (see Jenkins and Starkey in this report), based on work in the main Hoh River drainage, is included in this session because of the importance of the Roosevelt elk herds in these valley ecosystems.

RATIONALE

It is increasingly apparent that integrated studies of natural ecosystems are critical to solution of management problems as well as to the general progress of natural history research. Projects like the Coniferous Forest Biome have demonstrated both the practicality and value of integrated examinations of natural ecosystems (Edmonds 1980). In such studies emphasis is placed on linkages between ecosystem compartments, such as the interface between a forest and stream; linkages which are often avoided or not considered in traditional disciplinary research. There is increasing evidence of the necessity for focusing on linkages with many examples of difficulties encountered in considering problems in isolation, whether it be herbivores viewed outside of a habitat context or a stream analysis that fails to consider terrestrial inputs. Land managers are increasingly faced with problems involving multiple linkages and resource tradeoffs; and their needs often can only be met with integrated, ecosystem-level research.

A corps of interested scientists and associates with a tradition of integrated, ecosystem-oriented research has developed around programs centered at Corvallis, Oregon. Personnel include staff of Oregon State University and the USDA Forest Service Forestry Sciences Laboratory as well as "graduates" who have moved out into industry and other agencies. Joint research efforts are an essential factor in maintaining the interdisciplinary linkages and system-level perspective among the corps. Hence, the desire and need for periodic field exercises.

The south fork of the Hoh River represents a complete river drainage from 20 km from its headwaters to the Olympic National Park boundary. The drainage is essentially pristine with very light recreational use, one short trail, and no roads. Although the river is relatively small, fluvial processes are evident; and the valley bottom is broad with extensive alluvial landforms. Geomorphic-biologic interactions can, therefore, be viewed within a relatively compact but ecologically complete river drainage.

Baseline data are needed to serve managerial and scientific purposes on ecosystems within both Olympic National Park and the South Fork drainage. Basic resource information is, of course, welcomed by Park managers and interpreters. Management-related data on the fisheries resource are important in Olympic National Park. Recent designation of Olympic National Park as a Biosphere Reserve increases the need for expanded data bases and monitoring programs. Finally, the South Fork of the Hoh River is identified as a potential Research Natural Area because of the outstanding valley-bottom Picea sitchensis forests and need for further evaluation.

There also is a basic need for scientific data on ecosystems of the type found in the South Fork drainage. Substantial research exists on forest and stream interactions, but almost none has been done on northwestern rivers. Information is needed on natural fisheries and sediment levels in a pristine but natural sediment-rich river system; these data provide a baseline for comparison with adjacent Olympic Peninsula river systems that are being logged. Further, basic knowledge of western Olympic Mountain valley bottom forests (Fonda 1974) is still sparse and includes essentially little on population structure of the trees and on coarse woody debris.

Thus, a variety of factors combined to make desirable an integrated research project on the South Fork of the Hoh River. An interdisciplinary examination of Olympic rainforests and associated streams and rivers was needed. Appropriate methodology and perspectives were available along with a corps of personnel with a suitable mix of disciplines. An outstanding site existed in the South Fork drainage. Baseline data and permanent sample plots were generally needed for the National Park/Biosphere Reserve, and managers had current needs for specific types of data. Research in these coastal forests was also needed to advance basic ecosystem science in the Pacific Northwest.

STUDY AREA

The drainage of the South Fork of the Hoh River is located on the western slopes of the Olympic Mountains at about 47°47' N. latitude and 123°56' W. longitude (fig. 1). The South Fork is a glacial river arising from Hubert Glacier on the slopes of Mount Olympus and running for about 25 km to its confluence with the main fork of the Hoh River. Most of the drainage is located within Olympic National Park (fig. 2).

The South Fork drainage covers about 11,400 ha within the Park and is generally a broad, glacially carved, u-shaped valley. Adjacent mountain slopes are precipitous and composed largely of sandstones and shales. The floodplain in the lower valley is exceptionally wide, occupying nearly 25 percent of the total width of the valley at the primary study sites; the floodplain in the main fork of the Hoh River is, by contrast, only 10 percent of the width of the valley. The landforms in the lower valley are discussed by Swanson and Lienkaemper in this report.

Climatically, the study area is extremely wet and mild. The Spruce Weather Station is located along the Hoh River below the study area (U.S. Department of Commerce 1965). Precipitation there averages over 3 200 mm annually with 55 mm in the driest month (July). Snow is uncommon. Mean temperatures are probably around 10°C with January minima of around 1°C and July maxima of 21°C. Fog and low clouds often occupy the valley even when higher mountain areas are experiencing clear weather. Precipitation occurred every day between September 5 and 15, 1979, and totalled at least 200 mm. Rains in excess of 100 mm at the camp during a 2-day period resulted in water ponding on the lower terrace and a substantial increase in the height of the river.

Environmental stresses are obviously uncommon in these valley bottom forests. Snow, ice, and drought play little or no role. Windstorms do cause significant tree mortality, particularly from strong southwesterly winds associated with major winter storms. Catastrophic blowdowns do occur every few decades in localized areas. A major blowdown actually occurred in January 1979 and caused significant mortality of mature trees within the permanent sample plots. Fire appears to be an insignificant factor on the terraces themselves; the only charcoal found in soil pits appeared to have been transported to the site. Fire has been an important factor on the mountain slopes.

The research was confined primarily to the valley bottom environment with very little sampling of the mountain slope or river headwater environments. The major study sites are located 3 to 5 km upstream from the National Park boundary at about 215-m elevation. Forest sampling was confined to terraces and river bars except for anchor points of the two longest transects which were located on mountain slopes. Terrace habitats were generally not confounded with colluvial and alluvial deposits from sideslopes and alluvial fans from tributary drainages as is the case along much of the main Hoh River.

Figure 1.--Olympic Peninsula in Washington State showing general location of Olympic National Park and the Hoh River drainage; coastal strip of the National Park not shown.

LOGISTICS

The logistical arrangements were developed jointly by Olympic National Park and the research team leaders. Base camp was located 3.5 km upstream from the Park boundary on a river bar in order to minimize long-term impacts of a large group on the valley. Equipment and supplies necessary for base camp and the research were brought in by helicopter. Research personnel brought in their own gear over 5 km of trail from the road head.

A total of 46 persons contributed at least 1 day of field work. Organizations represented in the group included the National Park Service, USDA Forest Service, Oregon State University, Weyerhaeuser Company, University of Washington, Washington Department of Natural Resources, University of Alberta, University of Edinburgh, U.S. Geological Survey, and U.S. Fish and Wildlife Service. Not all personnel were present on any single day; average daily participation was 26, not including visitors. Teams were formed to do individual tasks with personnel leaving or being reassigned to new tasks upon completion of an activity.

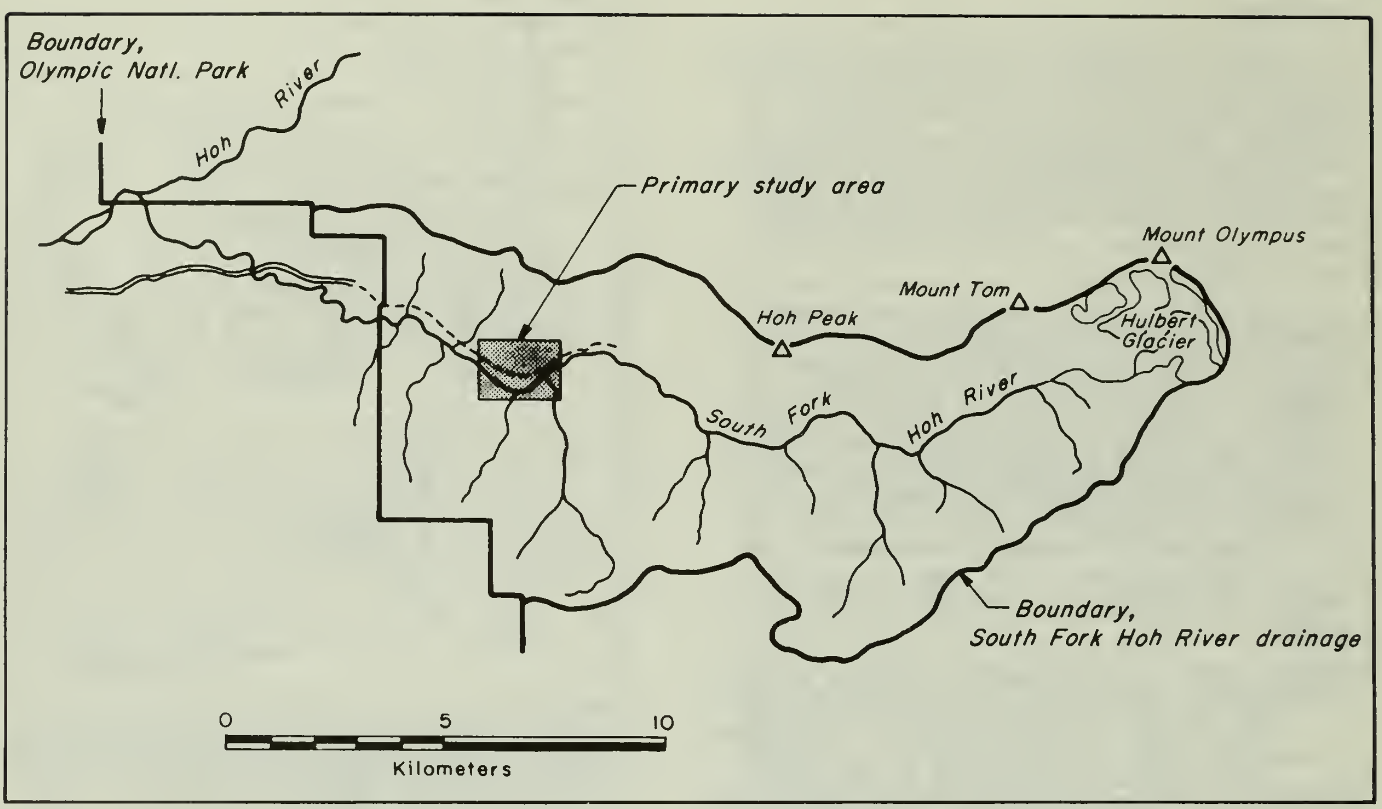


Figure 2.--The South Fork Hoh River drainage showing location of major study site.

A key feature of the pulse was the regular evening review session during which personnel presented and discussed that day's findings. These sessions were critical in modifying and sharpening the research effort as well as insuring an interdisciplinary exchange of viewpoints on features and phenomena of common interest. Such exchanges sometimes resulted in serendipitous discoveries. A large team project needs to provide for semi-structured exchanges of this type to get the desired communication and collaboration.

OBJECTIVES AND APPROACHES

The major objectives of the studies in the South Fork of the Hoh River are outlined in table 1. Many of the tasks appear relatively independent although all relate to the overall objective of describing and better understanding the valley bottom ecosystems found on the western slopes of the Olympic Mountains. Interdisciplinary efforts often break down into component tasks, some of which are strongly discipline oriented. The overall design provides the context which makes the parts fit into a whole. In fact, in the Hoh studies each objective is linked to at least one other objective, generally by a requirement for information. Several objectives, such as the definition of aquatic habitats and their relation to geomorphic processes and terrestrial vegetation, obviously require interdisciplinary collection and synthesis of data.

The basic geomorphic analysis of the valley bottom landforms and processes is covered by Objective I (table 1). Fonda (1974) had developed a model of vegetation-landform relationships for the main fork of the Hoh River, and the research team wanted to test its application in the South Fork. Special interest centered on interactions of landforms, and geomorphic processes with terrestrial vegetation and major reciprocal effects do exist (see Swanson and Lienkaemper in this report). Geomorphic processes and vegetation also link to produce certain aquatic habitats. The major approaches to Objective I were mapping of elevation-vegetation profiles along permanent transects laid out across the valley floor (see Swanson and Lienkaemper in this report).

Objectives II, III, and IV focus on descriptions of the valley bottom forests with special attention to a key structural component (dead wood) and the reproductive population dynamics of the two major tree species--*Picea sitchensis* and *Tsuga heterophylla*. The research team was interested in obtaining data on amounts and decomposition rates of coarse woody debris in coastal environments to compare with a large data base collected from Cascadian conifer forests. The team also hypothesized that reproductive behavior would be influenced by down logs although the overwhelming importance of logs (see McKee et al. in this report) was not appreciated at the outset of the study. The relative reproductive success and presumed ecological role of *Picea* and *Tsuga* in the Olympic rainforests has been an unresolved topic of discussion (Franklin and Dyrness 1974, Fonda 1974).

Since Objectives II, III, and IV (table 1) generally utilized the same data base, the sampling techniques are detailed here to avoid repetition. Sampling of the forest communities began with reconnaissance and systematic sampling at intervals along four line transects run perpendicular to the river and across several landforms. The line transects were also used by the geomorphic research team. The transect data are incorporated into the general compositional and structural descriptions of the valley forests in the study area (see McKee et al. in this report).

Reconnaissance and the transect sampling revealed two distinct, mature forest communities of Picea sitchensis and Tsuga heterophylla. These are described in detail by McKee et al. in this report but generally consist of an open Picea sitchensis/Acer circinatum/herb forest on lower terrace surfaces (fig. 3) and Picea sitchensis-Tsuga heterophylla/Vaccinium sp./moss forest on high or upper terraces (fig. 4).

Permanent hectare (100- x 100-m) sample plots were established in typical segments of these two forest types to facilitate sampling of coarse woody debris and tree regeneration and collection of additional compositional and structural data on mature forests. Two continuous plots were established in each forest for a total of 4 hectares. The basic layout of the plots followed the procedures developed for reference stands at the H. J. Andrews Experimental Forest (Hawk et al. 1979). Plot boundaries were surveyed with staff compass and tape. Plots were then temporarily gridded with string into segments as small as 5 m to ease ocular mapping of all live trees $\geq$ 5 cm, snags $\geq$ 15 cm, and logs $\geq$ 10 cm in diameter. Since these were permanent plots, all live trees over 15 cm diameter were tagged with numbered metal tags at breast height. Galvanized steel pipe approximately 1.5 m in height and 4 cm in diameter were installed at the corners, center, and quarter corners of each plot. Live trees and snags were subsequently

Table 1--Major objectives of South Fork Hoh River ecosystem studies

---

I. Describe the valley landforms with some specific interests
   - A. Role of vegetation in landform development
   - B. Formation of different aquatic habitats

II. Develop baseline descriptions of the valley-bottom forest including
   - A. Live, standing dead, and down trees
   - B. Relationships of forest types to landform
   - C. Descriptions developed as a permanent sampling system

III. Analyze the amounts and role of dead and down wood in the valley-bottom forests

IV. Analyze the regeneration dynamics of forest trees in the valley-bottom forests

V. Describe and analyze aquatic habitats in the lower valley
   - A. Define aquatic habitats and determine their relation to geomorphic and terrestrial processes
   - B. Determine biology of habitats, energy base, and invertebrate communities
   - C. Baseline data on sediments

VI. Analyze use of aquatic habitats by fish
   - A. Species distributions
   - B. Habitat use by anadromous fish
   - C. Overall importance to total fishery

VII. Examine interactions between Roosevelt elk and vegetation

---

Figure 3.--Mature forests on the lower terrace are typified by large, widely spaced Picea sitchensis, a tall shrub layer of Acer circinatum, and a dense herbaceous ground layer that is rich in grasses.

Figure 4.--Well-stocked stands of Picea sitchensis and Tsuga heterophylla typify mature forests on upper terraces along with understories dominated by Vaccinium sp., ferns, and mosses.

measured for height. Areas of standing water and elk trails also were mapped. The resulting stand maps for two of the hectare plots are shown in figures 5 and 6. Additional sampling of down logs (see Graham in this report) and regeneration (see McKee et al. in this report) was done on these permanent plots.

Objectives of the aquatic research involved definition of distinct aquatic habitats with the assistance of the geomorphologists followed by a thorough characterization of their biology--energy sources, invertebrate communities, and type and level of usage by various fish (table 1). The habitat classification scheme is discussed by Swanson and Lienkaemper and Ward and Cummins both in this report. The aquatic biologists and fisheries researchers selected representative areas of each habitat for their sampling (see Ward and Cummins and Sedell et al. in this report). The research on sediments and anadromous fish also involved extensive sampling along nearly 10 km of the South Fork.

The objective (VII) on Roosevelt elk-vegetation interactions is listed last because little was accomplished as part of the South Fork pulse; not because it is unimportant. Roosevelt elk are a significant component of these ecosystems and several hypotheses have been proposed about their effects on plant composition and tree reproduction (see McKee et al. in this report). We are grateful that Jenkins and Starkey agreed to include their paper in this report, which is based on research in the main Hoh River valley, with this series from the South Fork. Dr. D. Boersma, of the Environmental Research Institute of the University of Washington, has initiated a study on effects of elk grazing on tree reproduction. This research, along with the planned establishment of 0.5-ha exclosures around portions of the permanent sample plots on both the upper and lower terraces, should begin providing some quantitative information on elk-vegetation interactions.

CONCLUSION

This paper introduces and places in perspective a series of seven papers on valley-bottom ecosystems in the Hoh River drainage. The concluding paper (see Franklin et al. in this report) is a brief summary emphasizing the major conclusions and reiterating the interrelationships between ecosystem components.

LITERATURE CITATIONS

Edmonds, Robert L., editor.
1980. The natural behavior and response to stress of western coniferous forests. US/IBP Synthesis Series. Dowden, Hutchinson & Ross, Inc., Stroudsburg, PA. In Press.

Fonda, R. W.
1974. Forest succession in relation to river terrace development in Olympic National Park, Washington. Ecology 55(5):927-942, illus.

Franklin, Jerry F., and C. T. Dyrness.
1973. Natural vegetation of Oregon and Washington. USDA Forest Service Gen. Tech. Rep. PNW-8, 417 p., illus. Pac. Northwest For. and Range Exp. Stn., Portland, OR.

Hawk, G. M., J. F. Franklin, W. A. McKee, and W. B. Brown.
1979. H. J. Andrews Experimental Forest reference stand system: establishment and use. Coniferous Forest Biome Bull. 12, 79 p., illus. Univ. of Wash. Seattle, WA.

U.S. Department of Commerce.
1965. Climatic summary of the United States--supplement for 1951 through 1960. Washington, D.C. Climatography of the United States No. 86-39. 92 p.

SOUTH FORK HOH UPPER TERRACE
PLOT 1

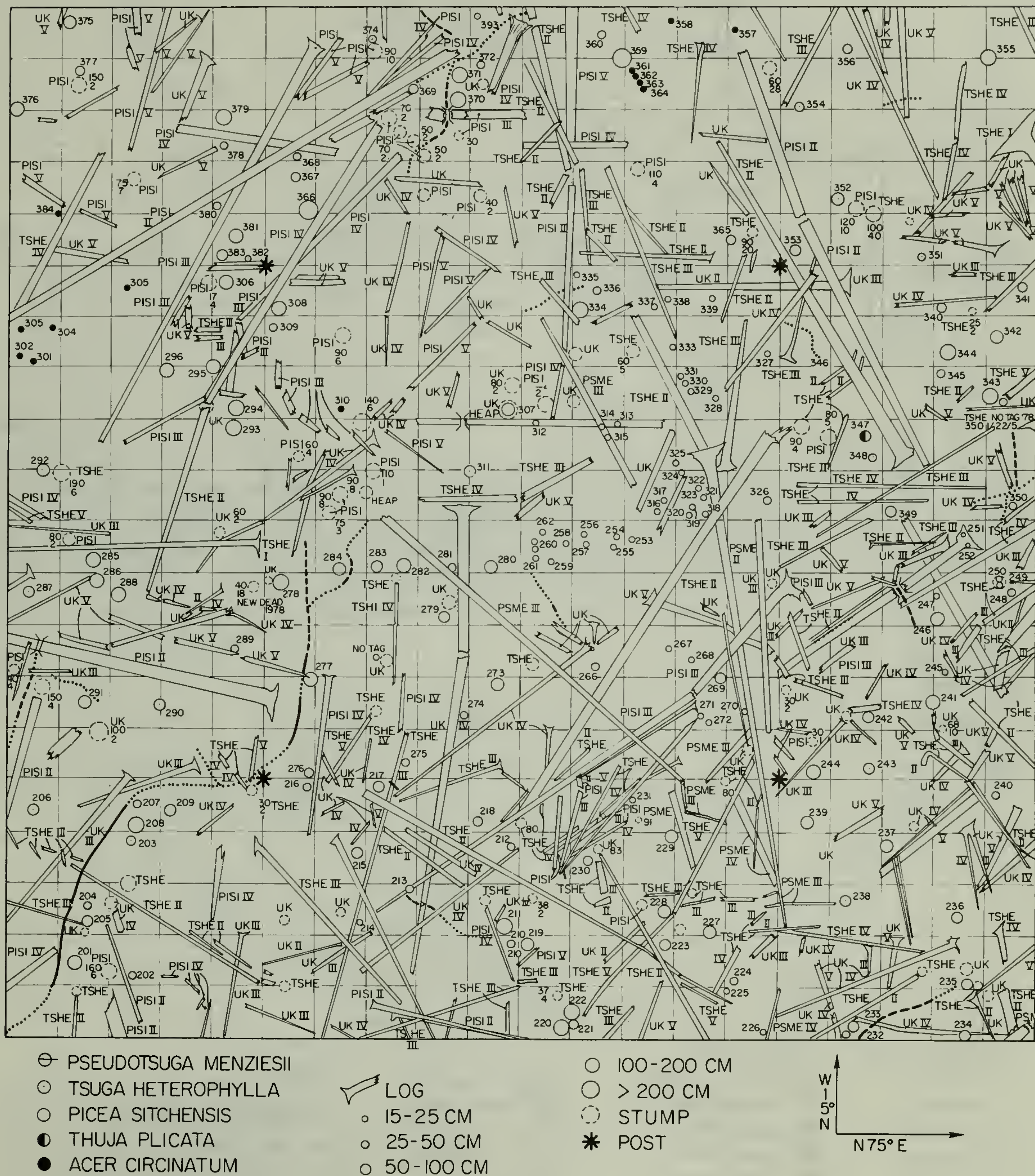


Figure 5.--Stem map of permanent sample plot 1 located on the upper terrace.

SOUTH FORK HOH LOWER TERRACE
PLOT 4

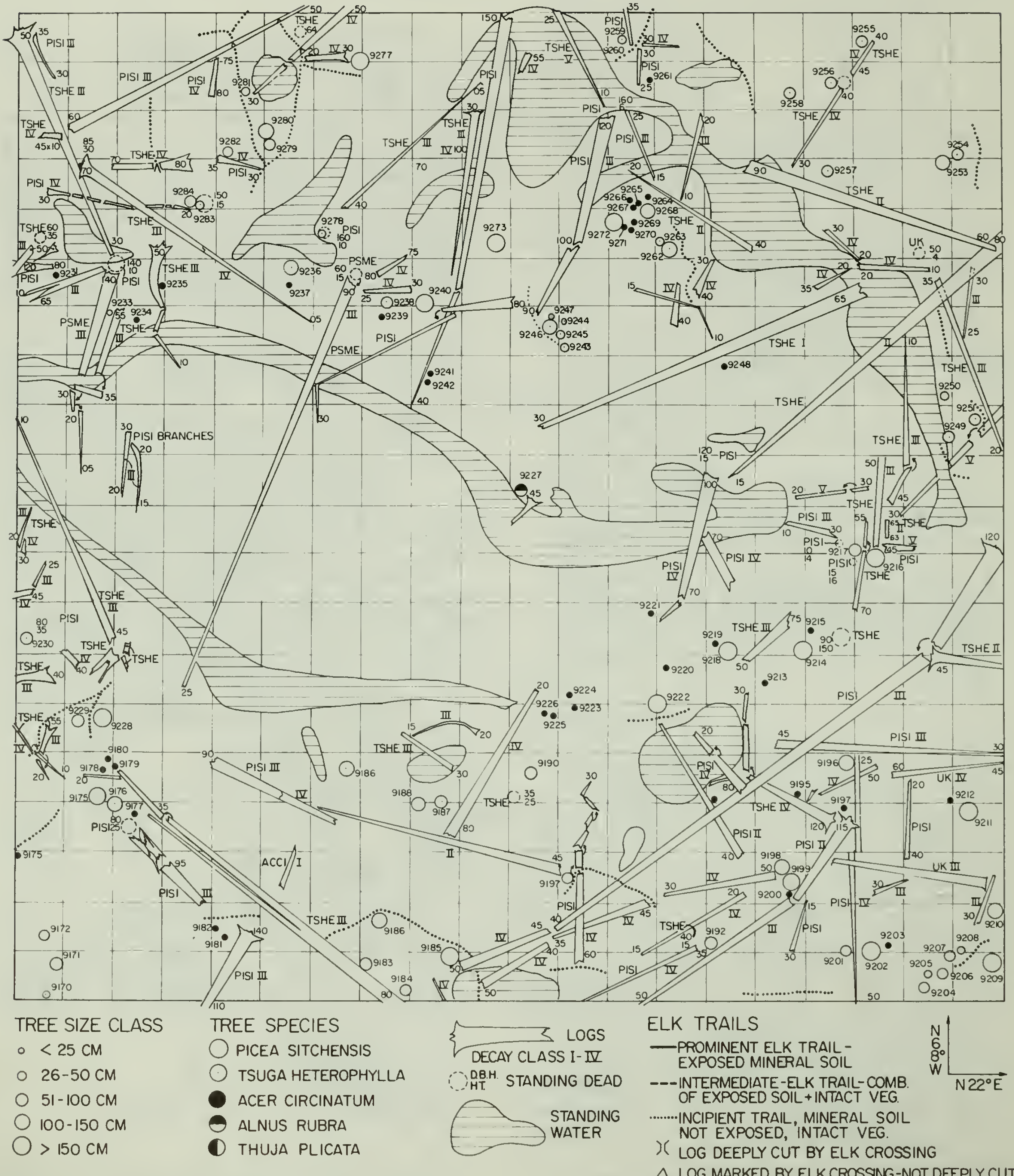


Figure 6.--Stem map of permanent sample plot 4 located on the lower terrace; note the reduced density of logs and stems and the extent of standing water.

Habitat and Food Resources for Invertebrate Communities in South Fork Hoh River, Olympic National Park, Washington

G. Milton Ward, Kenneth W. Cummins, Robert W. Speaker,
Amelia K. Ward, Stanley V. Gregory, and Thomas L. Dudley

ABSTRACT

The morphological and biological structure of four aquatic habitats in the valley of the South Fork Hoh River are described, and the potential effect of naturally occurring inorganic sediments (glacial flour) is discussed. The main river habitat was heavily impacted by the hydrologic regime of the river, compounded by the scouring action of a large suspended inorganic sediment load. River off-channel and terrace tributary habitats were less affected by these events, and they developed relatively larger invertebrate communities. Small, high gradient streams draining valley side slopes were not affected by main river processes but possessed a potentially flashy hydrologic regime. River off-channel and terrace tributary habitats seemed to provide the optimal aquatic habitat in this river system.

G. Milton Ward, Kenneth W. Cummins, Robert W. Speaker, Amelia K. Ward, Department of Fisheries and Wildlife, Oregon State University, Corvallis, Oregon 97331; Stanley V. Gregory, U.S. Fish and Wildlife Service, Columbia National Fishery Research Laboratory, Field Research Station, Oregon State University, Corvallis, Oregon 97331; and Thomas L. Dudley, Department of Entomology, Oregon State University, Corvallis, Oregon 97331.

INTRODUCTION

For the few remaining pristine watersheds in the Pacific Northwest, there exists a need for documentation of the types of aquatic habitats present and a description of their physical and biological structure. An example of one such watershed is the South Fork Hoh River, Olympic National Park, Washington. This system was of interest because of its size, relatively undisturbed state, and the presence of large quantities of naturally occurring inorganic sediment. Finely ground rock, generated by glacial activity in the headwaters, was found throughout the main river channel, backwater areas, and in the downstream reaches of many tributaries.

As a result of current grazing and forestry practices in the Western United States, erosion of valley slopes and stream banks has been greatly accelerated in recent years.

Descriptive data on the South Fork Hoh River system, with its natural, long-term sedimentation patterns may be useful in assessing the impacts of recent sedimentation in other streams.

The interplay of geomorphic processes and terrestrial vegetation in the South Fork basin has created four major aquatic habitats. Two of these, the main river and river off-channel areas, lie in the lowest section of the river valley at or below the level of winter base flows. The two other habitats are tributary systems, one that drains steep valley walls and a second that flows across the elevated terraces occurring along the north side of the river.

The objective of this investigation was to establish physical and biological descriptions of the aquatic habitats in the South Fork Hoh River Valley and to examine the influence of naturally occurring inorganic sediment on these habitats. Two specific objectives were communities and the food resources available to them.

Invertebrate communities were examined from both a taxonomic and ecological standpoint. Based on insect feeding habits, Cummins (1974) classified aquatic insect groups according to their ecological role in stream ecosystems. Within a system, four basic groups of organisms could be recognized: species that feed on fine particle detritus; scrapers, whose main diet is periphyton; shredders, who feed primarily on coarse particulate organic matter; and predators, who feed on organisms in other functional groups. Insect species composition in stream habitats vary geographically; but in all areas, representatives of these ecological groups can be found.

Figure 1.--River channel and off-channel habitats in South Fork Hoh River, Olympic National Park, Washington.

DESCRIPTION OF AQUATIC HABITATS AND INVERTEBRATE COMMUNITIES

River Channel

Fed by cold glacial headwater streams, the main stem of the South Fork Hoh River flows along a wide, shallow, and unstable channel containing rocks, small boulders, and considerable easily transported inorganic matter (fig. 1). Much of this fine inorganic sediment is generated by glacial activity in the headwaters and then transported in high concentrations throughout the downstream reaches, even into terrace tributaries during major flood events. This sediment (glacial flour), which imparts a milky color to the water when suspended and a greyish-white color to the benthos, was very prevalent in river channel, off-channel, and terrace tributary habitats, where it often completely fills intergravel spaces along stream margins.

For many other river channels equal in size to that of the South Fork Hoh River, primary production by attached algae is a major source of energy and carbon for the system; however, here that energy source was greatly reduced, being only 10 percent as great as has been measured in a comparable system, the McKenzie River, Oregon (Naiman and Sedell 1980) (table 1). The large amounts of suspended inorganic sediment reduce productivity by scouring algal cells from the rock surfaces, and deposited sediments may bury many potential algal sites. The large size of the main channel did not allow terrestrially produced energy sources to play a prominent role, and the movement and deposition of the glacial flour prevented much autochthonous production. As a result, the system possessed a meager food base, with little organic detritus and low algal production.

The resulting invertebrate community in the main channel was of generally low density and biomass (tables 2 and 3). Fine particle feeding detritivores, composed mostly of two mayflies, Baetis and Rithrogena, were the dominant organisms (table 4). Algavores, which might typically inhabit the upper surfaces of rocks in streams of this size, were noticably missing, perhaps due to constant scouring action of suspended glacial flour.

Table 1--Organic matter content in aquatic habitats, South Fork Hoh River

Habitat	TOM		BOM		Allochthonous inputs:		Algal
	mg/m³	% org	g/m²	% org	leaf litter	wood	chla
River channel	116	8	13	2	+	+	6
River off-channel	--	--	15	2	+++	++	34
Terrace tributaries	106	14	37	5	+++	+++	12
Valley wall tributaries	209	33	21	12	++	++++	11

TOM = Transported Organic Matter, BOM = Benthic Organic Matter.

Table 2--Density of insect functional groups on aquatic habitats, South Fork Hoh River

Habitat	Number of taxa	Sediments (#/m² of rock)					Leaf litter (#/g)				
		Sh	Col	Scr	Pred	Total	Sh	Col	Scr	Pred	Total
River channel	22	22	390	0	75	487	0.65	3.79	0	0.06	4.50
River off-channel	15	8	202	0	16	228	5.81	8.51	0	.20	14.52
Terrace tributaries	26	38	395	67	59	559	4.83	2.56	0	.17	7.56
Valley wall tributaries	23	13	411	182	20	626	8.87	6.21	.30	.30	15.68

Sh = Shredders, Col = Collectors/gatherers, Scr = Scrapers/grazers, Pred = Predators.

Table 3--Biomass of insect functional groups in aquatic habitats, South Fork Hoh River

Habitat	Sediments (mg/m² of rock)					Leaf litter (mg/g)				
	Sh	Col	Scr	Pred	Total	Sh	Col	Scr	Pred	Total
River channel	5	114	0	100	219	.53	2.18	0	.05	2.76
River off-channel	3	365	0	653	1022	2.23	3.63	0	.10	5.96
Terrace tributaries	9	301	84	35	429	4.45	2.05	0	.29	6.79
Valley wall tributaries	< 1	70	48	11	130	1.94	1.93	0	.20	4.07

Sh = Shredders, Col = Collectors/gatherers, Scr = Scrapers/grazers, Pred = Predators.

Table 4--Taxonomic distribution of the most abundant invertebrates in aquatic habitats, South Fork Hoh River

Habitat	Sediments (#/m^2)		Leaf litter (#/g)	
River channel	Baetis	164	Alloperla	.89
	Rithrogena	71	Baetis	.71
			Ecclisomyia	.53
River off-channel	Baetis	54	Capnia	3.11
	Alloperla	54	Nemoura	2.49
			Ecclisomyia	2.28
Terrace tributaries	Baetis	59	Ecclisocosmoecus	2.31
	Alloperla	46	Nemoura	1.94
	Chronomidae	193	Alloperla	.87
Valley wall tributaries	Glossosoma	162	Nemoura	3.87
	Limnephilidae	88	Epeorus	2.38
	Chironomidae	175	Peltoperla	1.49
	Baetis	81	Lepidostoma	1.49

River Off-Channel

A second habitat, lying within the geomorphically active portion of the river channel (Surface 2, Swanson and Lienkaemper in this report) was comprised of areas previously part of the main river channel. Because of deposition behind large debris accumulations or because of the shifting river bed, parts of the river were isolated (fig. 1). Although they may carry water during summer storm flows and during winter base flows, these secondary and tertiary channels, comprising the major portion of off-channel habitats, are isolated from direct contact with the main river channel during low flow periods. A connection between the main river and these quiet off-channel pools can be maintained, however, through inter-gravel flow. This subsurface flow carries little suspended glacial silt, since the gravel acted as an efficient filter. Large amounts of glacial flour were present in the sediments of these areas (table 1), however, supporting the idea that river and off-channel habitats often are connected.

During periods of moderately high flows when main river and off-channel habitats are connected, large debris accumulations are important in protecting back-water habitats from severe scouring (fig.1). The reduced flow rates in protected areas create drop zones, however, where suspended particles collect and settle out.

The organic energy inputs to this habitat appeared to be greater than those to the main river channel. There is greater potential for leaf litter and wood input due to increased contact between the habitat and the land; and at the time of our observations, these habitats exhibited relatively large standing crops of algal chlorophyll a (table 1). As with the main river channel, standing crops of organic detritus were very low; and the percent of glacial silt in the sediments of these habitats was very high.

In spite of the potential impacts of the main river during high discharges, these habitats supported sizable invertebrate communities. The predominantly inorganic sediments demonstrated low insect densities but a high total biomass comprised mostly of predacious species (tables 2 and 3). Insects inhabiting leaf litter were relatively abundant, the shredders Capnia, Nemoura and Ecclisomyia among the more numerous (table 4).

Terrace Tributaries

Upon reaching the flat river terraces, valley wall tributaries encounter a significant change in slope. Water from these streams spreads out over the terrace surface, often standing several inches deep over a wide area. It seems likely that much of this water percolates into the porous terrace soil and reappears later as spring and seep water. The flow in these terrace streams is derived from valley wall tributaries and terrace springs, as well as from the main river during times of extremely high discharge (fig. 2).

These clear-water, sand- and gravel-bottomed streams typically had a low suspended inorganic load; benthic areas contained a relatively large amount of organic detritus. Sediments still contain substantial amounts of glacial flour, reflecting occasional contact with the main river. The nearly closed canopy and the presence of shrubs along the stream margins made the potential for allochthonous inputs quite high. Large woody debris also was a common feature of this habitat. The potential for algal production, while not as high as in the off-channel habitats, was intermediate between the main river and the off-channel habitats. A number of stream reaches had very high overstory canopies, and were well lighted. The potential for algal activity in these areas was quite good.

Invertebrate communities in the habitats were well developed, especially so in the gravel bottom areas, and exhibited wide taxonomic and functional diversity (tables 2, 3, and 4). Terrace tributaries appeared to offer a stable and relatively productive area for aquatic invertebrate activity. Due to the considerable spring activity, flow rates were relatively stable and the trauma for insect communities that might be associated with a large suspended inorganic load was relatively infrequent. It would seem that this was a very important aquatic habitat in the Hoh River valley.

Valley Wall Tributaries

Streams draining valley side slopes represent the fourth aquatic habitat examined in the South Fork Hoh River basin (fig. 3). These habitats, like many similar first- and second-order streams throughout the western Cascades, were characterized by steep gradients, large accumulations of woody debris, and heavy canopy cover. Average channel slopes were large, but much of the drop occurs in short steep falls over wood debris and rocks. Downstream reaches of these steams flow out into the river terraces, where water may stand for a time before percolating into the soil.

These habitats appear to be heterotrophic, the vast majority of the energy inputs comprised of wood debris and coniferous needle litter (Sedell and Triska 1975). Suspended loads and sediments in the habitats contain relatively little glacial flour, and total organic loading is the highest of any of the four habitats examined (table 1). Algal densities, as measured by chlorophyll a concentrations (table 1), were typical of similar habitats in the Cascades.

Densities of invertebrates in both benthos and leaf litter were high, although biomass was not (tables 2 and 3). Despite the heterotrophic nature of this habitat, a relatively large population of Glossosoma, a scraper, was present. All functional groups of aquatic insects were represented, including those species associated with woody debris. Particularly abundant species in the sediments and leaf litter were lepidostomatid and limnephilid caddisflies, as well as neumourid and peltoperlid stoneflies and the mayfly Epeorus (table 4).

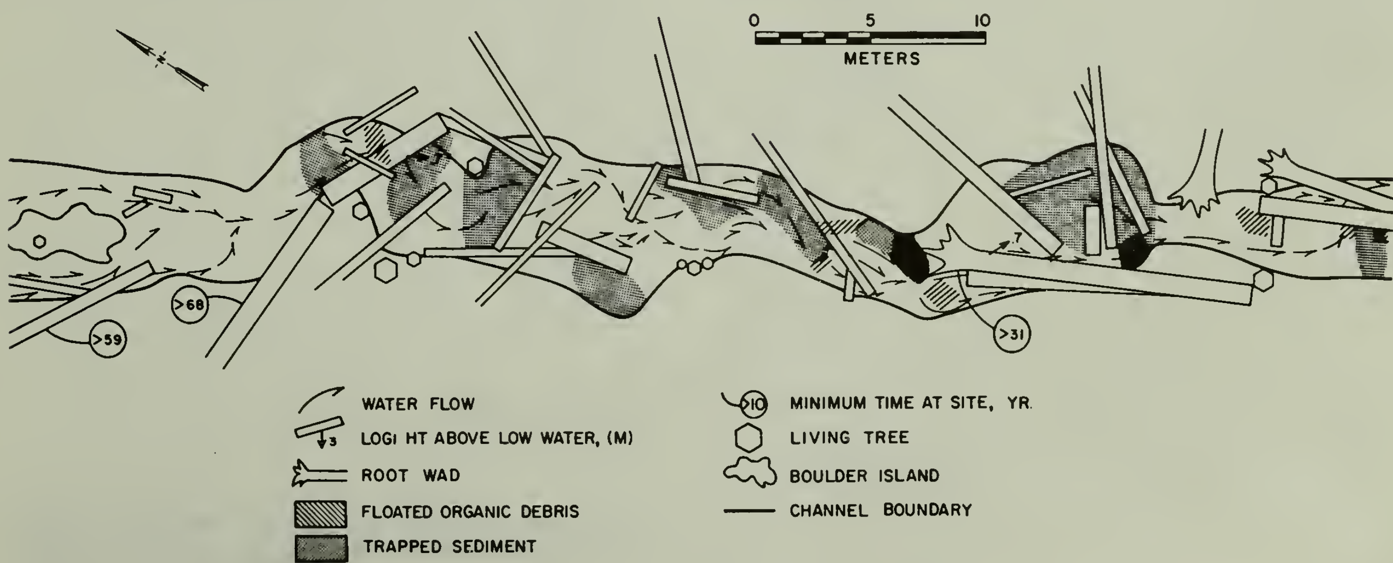
CONCLUSIONS

Of the four aquatic habitats examined in the South Fork Hoh River, the off-channel and terrace tributary habitats were the most favorable for aquatic invertebrates. Algal and invertebrate communities were not as affected by suspended glacial flour as were the river channel and valley wall tributary communities, nor were they as often subjected to hydrologic events capable of rearranging and destroying habitat. Food resources, too, were more available. The major organic inputs to river off-channel and terrace tributary habitats were leaf litter and algae; inputs to the river channel were extremely low and those to the valley wall tributaries were comprised mainly of refractory woody debris. The biomass of invertebrates in the terrace tributary and river off-channel areas also was higher than in the other two habitats. Total biomass and the groups of organisms present reflected both the increased physical stability of the habitats and the continual inputs of high quality food resources.

Presence of glacial flour was noted in terrrace tributary habitats as well as in river channel and

Figure 2.--Schematic drawing of terrace tributary systems in valley of South Fork Hoh River.

Figure 3.--Debris map of a small Cascade mountain stream very similar in physical and biological structure to valley wall tributaries in the South Fork Hoh River.



off-channel areas. At times of extremely high water, even the elevated terraces were inundated by flood waters. Glacial flour was detected both in the sediment and suspended in the water column; but effects of suspended sediment seemed to be greatest, particularly, in the main river channel. In the absence of suspended sediment, a river the size of the South Fork Hoh should be very productive, yet the main river channel habitat appeared to be quite the opposite. It is likely that wherever suspended and deposited inorganic sediments are comparatively high, stream communities change in response to their presence; however, those habitats which maintain a natural food base and a stable relationship with the terrestrial environment will maintain a diverse and stable invertebrate community.

LITERATURE CITATIONS

Cummins, K. W.
1974. Structure and function of stream ecosystems. Bioscience 24:631-641.

Naiman, R. J., and J. R. Sedell.
1980. Relationships between metabolic parameters and stream order in Oregon. Can. J. Fish. Aquat. Sci. 37:834-847.

Sedell, J. R., and F. J. Triska.
1975. Biological consequences of large organic debris in northwest streams. 1st Debris in Streams Workshop, September 1975, Oregon State University, 10 p.

The Biomass, Coverage, and Decay Rates of Dead Boles in Terrace Forests, South Fork Hoh River, Olympic National Park

Robin Lee Lambert Graham

ABSTRACT

A two part study examining: (1) the quantity and spatial distribution of dead boles, and (2) the decay rate of fallen boles by species and diameter was done in the terrace forests along the South Fork Hoh River in the Olympic National Park. On the upper terrace, dead boles occupied 11 percent of the forest floor and accounted for 165 tonnes/ha. The exponential decay rate for Sitka spruce was 0.0107 yr^{-1}; for western hemlock it was 0.0124 yr^{-1}. In both species, smaller diameter boles decayed more rapidly.

Robin Lee Lambert Graham, Department of Botany and Plant Pathology, Oregon State University, Corvallis, Oregon 97331.

The importance and ecosystem function of large woody debris only recently has been explored (Grier 1978, Franklin and Waring 1980, Lambert et al. 1981). In forest ecosystems in the Pacific Northwest, where dead boles typically account for 200 tonnes/ha of biomass and occasionally as much as 500 tonnes/ha, they represent an enormous pool of carbon, nitrogen, and mineral elements (Franklin and Waring 1980). In addition, these dead boles may persist for centuries; Douglas-fir typically lasts over 300 years. Because of their longevity and massive quantity, dead boles have been hypothesized to function as ecosystem stabilizers carrying the nutrients and stored energy of an ecosystem through disturbances (O'Neill et al. 1975).

Not only does abundant dead wood persist for long periods of time, it also accumulates nitrogen, phosphorous, and sometimes calcium and magnesium. Nitrogen fixation also has been shown to occur in dead boles (Roskowski 1977, Larsen et al. 1978). The rates are low but the enormous quantities of dead wood make the net input to the system substantial. The effect these nitrogen-fixing, nutrient-accumulating boles may have on the forest floor is largely unknown but could be considerable as the boles frequently occupy 10 percent of the floor area.

Because boles accumulate nutrients and their moisture and temperature regimes are more stable than those of the soil, they are often sites for germination and subsequent tree development (Berntsen 1960, Minore 1972). Certain species particularly prefer down wood as a substrate. These nurse logs, as they are commonly called, play an important role in determining the spatial distribution and species composition of trees in the forest.

The effect of large woody debris is not limited to the vegetative nutrient sphere of the ecosystem. The presence of boles profoundly affects the insect, bird, small mammal, and ungulate populations of the forest. Foresters have long known that survival of many of the so-called forest insect pests depends on the presence of dead wood in varying stages of decay. Members of the Cerambycidae, Buprestidae and Sesiidae are all dependent on the availability of dead wood, as are many members of the Hymenoptera. Although they may damage timber, these insects also serve to break down and recycle the carbon and nutrients in the wood and in some cases to rid the forest of suppressed or unhealthy trees.

Small mammals use the logs as runways and for protection. These mammals may be critical for the transport of mycorrhizal spores essential for tree development (Maser et al. 1978). The movement of ungulates is often controlled by impassable down boles. Thus the presence of down boles may determine where they feed and travel which in turn may modify their grazing pressure. In forests such as the rainforest of the Olympic Peninsula where grazing pressure by elk is intense and may control the vegetative structure, boles which impede elk travel have the potential of determining forest structure.

Birds are particularly affected by the presence of both dead standing and down boles. Many species will nest only in snags and some only in very particular types of snags (McClellan et al. 1979). The snags also are used as a source of grubs, beetles, and other insects. Down boles rarely provide nesting sites, but the grubs, ants, and beetles which inhabit them are an important source of food to birds and mammals alike.

Down logs and snags exert a profound influence on the ecosystem function of a forest. For this reason, I chose to study the quality, quantity, and longevity of down boles and snags as part of a larger project on the ecosystem function of streams and forests in the valley bottom of the South Fork Hoh River on the west side of the Olympic National Park. My objectives were: (1) to determine the quantity and quality of dead wood in the mature valley forests and (2) to measure decay rates of logs of the two dominant tree species--Sitka spruce (Picea sitchensis (Bong.) Carr.) and western hemlock (Tsuga heterophylla (Raf.) Sarg.).

METHODS

Study Area

The study area was located 5 km inside the Olympic National Park along the South Fork of the Hoh River. The valley bottom of the river is quite flat, fairly broad--often a mile or more across--and flanked by steep ridges. On these flat, wet bottoms a series of terraces with associated forests has developed (see Swanson and Lienkaemper in this report). Three general terraces can be described sequentially away from the river. Adjacent to the river are narrow bands of red alder (Alnus rubra Bong.) flats. Next, on what will be called the lower terrace in this paper, is an open, grassy, park-like forest of massive Sitka spruce with occasional vine maples (Acer circinatum Pursh) and hemlocks. Between this terrace and the sidewall of the valley, lies the third or upper terrace. The forest occupying this terrace has a closed canopy, a moss and fern floor, and little to no vine maple. Hemlock is more important on this forest than on the lower terrace. Because the upper and lower terraces occupy most of the valley, I chose to study these rather than the alder flats. A more detailed description of the forests along the South Fork on the Hoh is found in McKee et al. in this report.

Field Work

After examining the logs on the forest floor, I classified them into five types analogous to decay types developed by Fogel and Cromack (1977) for Cascade Range Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco), but modified for the forest species and conditions found on the South Fork Hoh River. Type 1 boles were those with no decay, fine twigs remaining, and complete bark coverage. When sliced, the sap and heartwood were clear. This was the only class that was moss free. Type 2 boles were slightly decayed with most of the bark present but no fine twigs. When sliced, the sapwood was rotted but the heartwood sound. Type 3 boles were moderately decayed with some bark present but only stubs of branches remaining. When sliced, both the sapwood and the heartwood showed signs of rot; but the bole could still support itself. Type 4 differed from Type 3 boles in that Type 4 boles could no longer support themselves. Frequently, all the bark was gone. When sliced, the sapwood was often absent and the heartwood was a deep red brown and would crumble into chunks. Type 5 logs were boles noticeable only by their moss outline on the forest floor. Bark was entirely absent, and the shape of the bole was no longer round but oval. When sliced, the wood was like red powder with little discernible structure or sign of rings. Often a bole would be a different decay type at opposite ends, in which case I chose the decay class occupying the most volume in the log.

In conjunction with other researchers (see Franklin in this report), two adjacent hectare plots were laid out on the upper and lower terraces, respectively. All dead boles greater than 10 cm in diameter were mapped and their species and decay class recorded on these plots. Further description of these hectare plots is found in McKee et al. in this report. Using these large maps, I counted the number of windthrows on the hectares by the number of rootwads present and the number of windbreaks by the number of snags with a long intact bole radiating from them. Trees that died as snags were those snags with no apparent associated down log.

Four subplots were selected in each hectare plot for detailed analysis of their dead boles. The plots were chosen randomly with the stipulation that no more than two of the subplots could be contiguous. In each subplot, the length and end diameters of the down logs were measured, the species and decay class determined, the coverage of bark and moss estimated, and the activity of birds noted. Only bole portions within the plot were considered. Snags were measured for height and diameter; characteristics such as bark coverage, crown presence and bird activity were noted. On the basis of these characteristics, snags were later assigned to five decay classes analogous to those of the boles.

From these data, I calculated the number, volume, and surface area of down logs and snags by decay classes and tree species in each of the plots. Data were then pooled by terrace level.

The segment of the study concerning decay rates was conducted in areas adjacent to the hectare plots; 12 Sitka spruce boles and 11 western hemlock boles were selected. Each bole was a windthrow or windbreak that had scarred a live tree when it fell, recording its death date in the scar. The number of rings laid down since the scar was determined by cutting a small wedge. The 23 boles covered the range of decay classes except for Type 5. I had selected five Type 5 boles which had trees growing on them that I could date and thus could get a minimum estimate of the bole age. Upon later microscopic examination, each of these boles turned out to be a Douglas-fir, a species no longer of any significance in these forests.

Three samples of wood and bark were taken from each down log, taking care to get proportional samples of sapwood, heartwood, and bark. These samples were either entire narrow cylinders if the bole was small or portions of a cylinder if the bole was large. The samples were cut 4 m from either end of the bole and at the center. The sample volume was estimated in the field using similar geometric forms if it were likely that the sample would crumble in the process of returning it to the laboratory. At each sampling point, the decay state, amount of bark, amount of moss, type of rot, and diameter of the log were noted.

Lab Work

The samples were taken to a laboratory in Corvallis, Oregon, and weighed. Samples whose volumes had not been computed in the field were either measured and their volume determined assuming a geometric form or they were placed in plastic bags, immersed in water, and their volume determined by water displacement.

After determining volume, wet weights were measured. The samples were dried at 60°C for 4 weeks prior to dry weight determinations. Using the dry weight and volume of each sample, I calculated the density of the wood. The means of the density of each species and decay class were calculated from these samples. Mean densities were multiplied by volume measurements of appropriate decay classes for each of the terraces in order to calculate the biomass of dead boles on a per hectare basis. Snag biomass was likewise calculated.

To determine the linear and exponential decay rates of Sitka spruce and western hemlock boles, the density or logarithm of the density of the sample was regressed against the sample's age as determined by the scar. This was done by species for (1) all the samples, (2) all the samples with large diameters, and (3) all the samples with small diameters. The break between large and small was 60 cm for spruce and 30 cm for hemlock. The slope of the regression gave the decay rate for either the linear or exponential model. In all cases the r^2 was calculated.

RESULTS

Maps of two of the four hectare plots are in Franklin in this report. These maps, which were made in September 1978, were used successfully the next year to identify subsequent tree mortality. Continuing annual surveys are planned.

From these maps, I was able to determine the percent mortality due to windthrow or windbreak. This varied between upper and lower terrace and between tree species (table 1). As expected, windthrow or break was more frequent than snag formation in the open lower terrace forest. On the closed canopy upper terrace, wind related death and snag formation were about equal. Hemlock boles were unlikely to become snags on either terrace although the upper terrace data are ambiguous due to the large number of unidentifiable logs and snags. On either terrace, Sitka spruce was more likely to become a snag than was hemlock.

Table 1--Numbers of trees that appeared to have died standing (snags) and been wind killed (windthrow/windbreak), by terrace level and species; area sampled was 2 ha on each terrace

Species	Upper terrace		Lower terrace	
	Snag	Windthrow/ windbreak	Snag	Windthrow/ windbreak
Sitka spruce	31	21	11	14
Western hemlock	14	33	3	11
Unknown	40	40	1	2
Total	85	94	15	27

The biomass of snags and down wood was markedly different between the two terraces as was the relative importance of the two species (fig. 1). On both terraces, snags represented 20 to 25 percent of the total dead bole biomass. Hemlock and spruce were of similar importance on the upper terrace while spruce was more important on the lower terrace.

Because of the large volume of a single spruce log on the lower terrace, the surface area occupied by spruce was low in comparison to its mass (fig. 2). Thus the lower terrace, which had three-fourths of the upper terrace's dead wood mass, had only half its surface area. Eleven percent of the forest floor was covered by dead wood on the upper terrace and six percent on the lower. On both terraces, snags occupied a negligible area.

The decay rates of spruce and hemlock are shown in table 2 and figures 3 and 4. In addition to the traditional exponential model, a linear model was also tried as previous investigators have found that often the linear model describes bole decay as well as the exponential model (Grier 1978, Lambert et al. 1981). None of the models fit well due to the highly variable data, but some trends do emerge. For both species, bole wood taken from large diameter logs had decayed more slowly than that taken from small diameter logs. On the average, hemlock decayed more quickly than spruce, though this may have been due only to its smaller size. The linear model, using all the samples, predicts that a 54-cm spruce bole would be totally decayed in 141 years and a 37-cm hemlock in 130 years. The exponential model predicts 95 percent disappearance of spruce in 280 years and hemlock in 241 years.

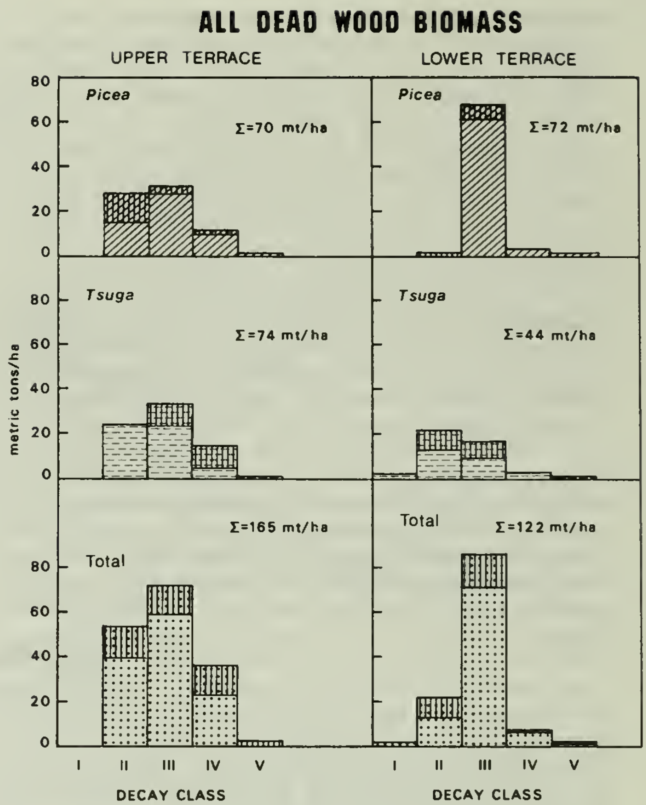


Figure 1.--The total biomass of dead wood. The vertical hatching represents snag biomass.

Figure 2.--The total surface area of the forest floor occupied by dead wood. The vertical hatching represents snag area.

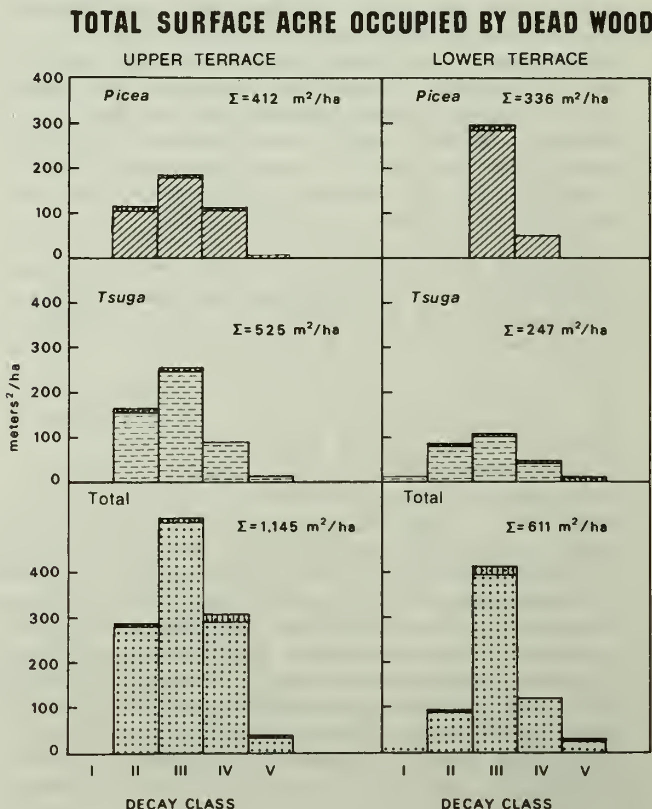


Table 2--The decay models for Sitka spruce and western hemlock; x = number of years since death and y = density

WESTERN HEMLOCK		
Logs > 30 cm (n = 18)	Logs < 30 cm (n = 10)	All logs (n = 28)
$y = -.00251x + .373$ ($r^2 = .150$)	$y = .00690x + .399$ ($r^2 = .878$)	$y = -.00310x + .374$ ($r^2 = .227$)
$y = .375e^{-.0122x}$ ($r^2 = .160$)	$y = .368e^{-.0177x}$ ($r^2 = .609$)	$y = .363e^{-.0124x}$ ($r^2 = .203$)
SITKA SPRUCE		
Logs > 60 cm (n = 16)	Logs < 60 cm (n = 19)	All logs (n = 35)
$y = -.00201x + .321$ ($r^2 = .345$)	$y = -.00284x + .378$ ($r^2 = .464$)	$y = -.00251x + .356$ ($r^2 = .421$)
$y = .310e^{-.00881x}$ ($r^2 = .269$)	$y = .383\ e^{-.0119x}$ ($r^2 = .534$)	$y = .354e^{-.0107x}$ ($r^2 = .415$)

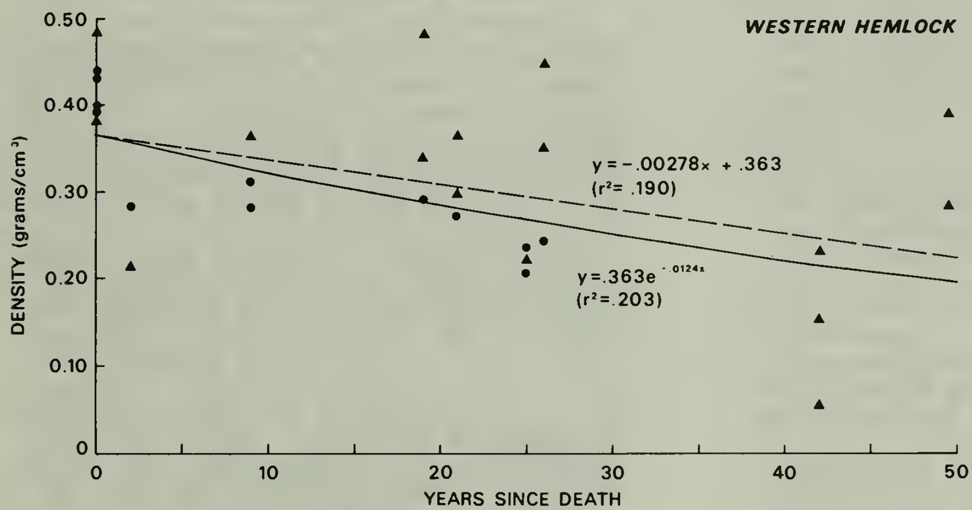


Figure 3.--The density of western hemlock plotted against its age; triangles are large boles (>30 cm) and circles are small boles.

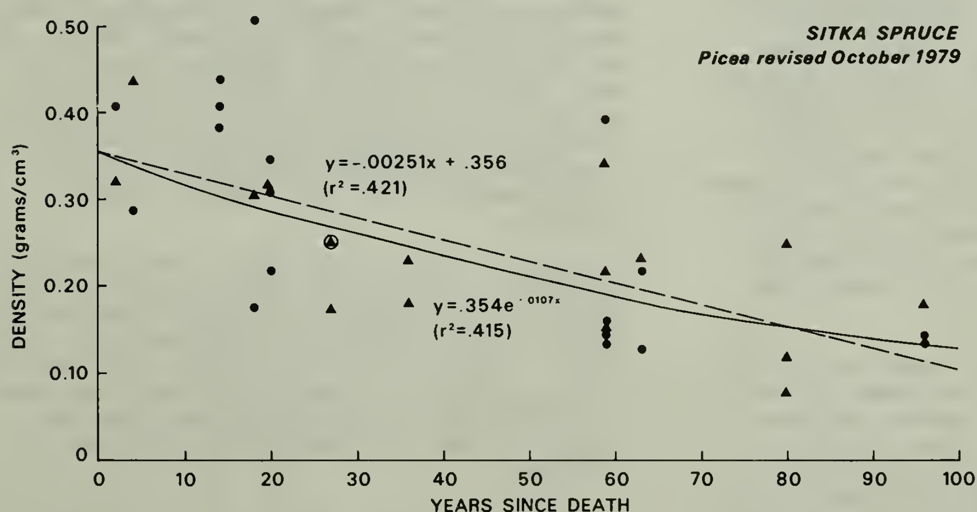


Figure 4.--The density of Sitka spruce plotted against its age; triangles are large boles (>60 cm) and circles are small boles.

DISCUSSION

The biomass of dead wood on both terraces was low but within the 118 to 251 tonnes/ha found in a chronosequence of 10 mid-elevation forests in the Cascade Range (Franklin and Waring 1980). Grier (1978) found 211 tonnes/ha of fallen boles in a 140-year-old Sitka spruce-western hemlock stand at Cascade Head, Oregon. His value is much higher than mine, though the forest types are superficially similar. The Olympic valley bottom spruce-hemlock forests have low densities relative to other coastal forests (see McKee et al. in this report).

Dead bole biomass in excess of 100 tonnes/ha seems representative of coastal and Cascadian forests of the Pacific Northwest. For contrast, in the Northeastern United States, second-growth deciduous forest has only 28 tonnes/ha (Aber et al. 1978) and virgin subalpine coniferous forest has 35 to 70 tonnes/ha (Lambert et al. 1981).

The area dead wood occupies (6 and 11 percent) is very significant in the Hoh valley forests because regeneration occurs only on dead boles and root wads (see McKee et al. in this report). These Hoh forests seem to be an extreme example of Sitka spruce and western hemlock's preference for organic substrate (Minore 1972, Berntsen 1960). The areal coverage of the forest floor by wood in either terrace is much lower than the 16 percent mean areal coverage for the 10 previously cited Cascadian forests. This is probably due to the immense Sitka spruce boles present in the Hoh forests, the low numbers of live stems in the upper and lower terrace (143 ha^{-1} and 64 ha^{-1}, respectively), and the more rapid decay rates of hemlock and spruce relative to Douglas-fir (see McKee et al. in this report). Although snags occupy only about 30 m^2/ha, they are among the few sites for successful hemlock regeneration as their height offers protection from elk grazing.

Measuring bole decay rates is an inaccurate process at best. Other authors have found low correlations with linear and exponential decay models, probably because bole decay is so variable (Grier 1978, Lambert et al. 1981, Means, personal communication). One end of a bole may be red pulp, the other merchantable saw timber. Within a single disc, I found essentially sound wood next to fluffy cellulose which, in turn, was adjacent to cubical brown rot. To minimize this problem, I took 1 to 9 liters of wood for each sample and obtained proportionate amounts of the various types of wood. As the bole diameter becomes larger, the problem of variable decay becomes increasingly significant. This is reflected in the lower r^2 values for the decay rates of large hemlock and spruce.

Determining decay rates by the change in density is conservative as it assumes no change in the original volume. In reality, sapwood may decompose to the point that it disappears or sloughs off, and heartwood may compact as it loses its structure. Either case results in an exaggerated density value and thus a slower decay rate. In this study, none of the samples was decayed to the point of compaction, but some had lost their sapwood. Thus my rates are probably slightly low.

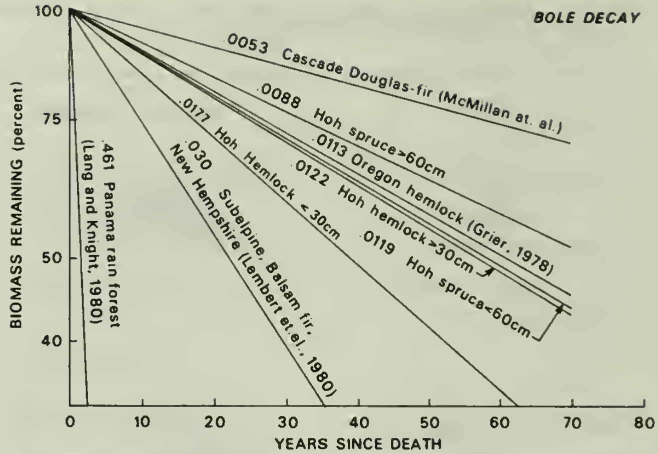


Figure 5.--The decay rates of boles in several forests. Value for Cascade Douglas-fir is from: MacMillan, P. C., J. E. Means, K. Cromack, and G. M. Hawk. 1979. Douglas-fir decomposition, biomass, and nutrient capital in the Western Cascades, Oregon. Unpublished manuscript on file at Forest Research Laboratory, Oregon State University, Corvallis, Oregon.

Very few decay rates for boles have been published. Figure 5 is a compilation of rates found in the literature compared with those of the Hoh forests. The Hoh boles decayed more quickly than the Douglas-fir boles but more slowly than the balsam fir or tropical rainforest boles. Grier's (1978) value for Oregon coastal hemlock is quite similar to the Hoh values for larger hemlock. The forests of the west side of the Olympics have often been called temperate rainforests (Franklin and Dyrness 1973), yet they differ in bole decay rates from those in a true tropical rainforest (Lang and Knight 1979), a difference due primarily to the presence of termites in the tropical rainforest. In the Olympics, insects are a minor component in the process of bole decay. Insects are also inconsequential in the subalpine forest, yet the decay rate is rapid, because of the small size of the boles (15-cm diameter). In fact, the rate represents the weight loss of all dead boles standing and down. Standing boles appear to decay more quickly than down boles in moist forests such as the Olympic or Pacific Northwest coastal forests (Cline et al. 1980). The Cascadian forests are drier than the Hoh forests and Douglas-fir is denser and more resistant to decay (Boyce 1923). Therefore, although the large spruce boles can match Douglas-fir for size, they decay more quickly.

Wood decay, though long a topic of wood products scientists, has only just begun to show up in the forest ecology studies. In the Hoh valley forest where decay occurs quickly, boles represent a huge pool of biomass, and provide the only site for regeneration despite their small area of occupancy. It is essential that we come to understand and appreciate their interactions with the entire ecosystem.

ACKNOWLEDGMENTS

I wish to thank Dr. Kermit Cromack for his cheerful advice and help in setting up this study, Ted Thomas for being my able sawyer and field assistant, and Joe Means for providing me his log computer programs and even more for running them.

LITERATURE CITED

Aber, J. D., D. B. Botkin, and J. M. Milillo.
1978. Predicting the effects of different harvesting regimes on forest floor dynamics in northern hardwood. Can. J. For. Res. 8:306-315.

Berntsen, C.
1960. Planting Sitka spruce and Douglas-fir on decayed wood in coastal Oregon. USDA For. Serv. Res. Note PNW-197, 5 p. Pac. Northwest For. and Range Exp. Stn., Portland, Oreg.

Boyce, J. S.
1923. Deterioration of windthrown timber on the Olympic Peninsula, Washington. U.S. Department of Agriculture Tech. Bull. No. 104. 28 p.

Cline, S. P., A. B. Berg, and H. M. Wight.
1980. Snag characteristics and dynamics in Douglas-fir forests, western Oregon. J. Wildl. Manage. 44:773-786.

Fogel, R., and K. Cromack.
1977. Effect of habitat and substrate quality on Douglas-fir litter decomposition in western Oregon. Can. J. Bot. 55:1632-1640.

Franklin, Jerry F., and C. T. Dyrness.
1973. Natural vegetation of Oregon and Washington. USDA For. Serv. Gen. Tech. Rep. PNW-8, 417 p., illus. Pac. Northwest For. and Range Exp. Stn., Portland, Oreg.

Franklin, J. F., and R. H. Waring.
1980. Distinctive features of the northwestern coniferous forest: development, structure and function. In Richard Waring, ed. Proceedings, 20th Annual Biology Colloquium. Oreg. State Univ. Press. Corvallis, Oreg.

Grier, C. C.
1978. A Tsuga heterophylla-Picea sitchensis ecosystem of coastal Oregon: decomposition and nutrient balances of fallen logs. Can. J. For. Res. 8:198-206.

Lambert, Robin L., Gerald E. Lang, and William A. Reiners.
1981. Loss of mass and chemical change in decaying boles of a subalpine balsam fir forest. Ecology 61(6):1460-1473.

Lang, G. E., and D. K. Knight.
1979. Decay rates for the boles of tropical trees. Biotropica 11(4):316-317.

Larsen, M. J., M. F. Jurgensen, and A. E. Harvey.
1978. N_2 fixation associated with wood decayed by some common fungi in western Montana. Can. J. For. Res. 8:341-345.

Maser, C., J. Trappe, and D. Ure.
1978. Fungal-small mammal interrelationships with emphasis on Oregon coniferous forests. Ecology 59(4):799-809.

McClellan, B. R., S. S. Frissell, W. C. Fischier, and C. H. Halvorson.
1979. Habitat management for hole-nesting birds in forests of western larch and Douglas-fir. J. For. 77:480-484.

Minore, D.
1972. Germination and early survival of coastal tree species on organic seed beds. USDA For. Serv. Res. Pap. PNW-135, 6 p. Pac. Northwest For. and Range Exp. Stn., Portland, Oreg.

O'Neill, R. V., W. F. Harris, B. S. Ausmus, and D. E. Reichle.
1975. A theoretical basis for ecosystem analysis with particular reference in element cycling. Pages 28-40 in Mineral Cycling in Southeastern Ecosystems. F. G. Howell, J. B. Gentry and H. H. Smith, eds. ERDA Symposium Series (CONF-74013).

Roskowski, J. P.
1977. Nitrogen fixation in northern hardwood forests. Ph. D. thesis, Yale Univ. New Haven, Conn. 112 p.

Structure, Composition, and Reproductive Behavior of Terrace Forests, South Fork Hoh River, Olympic National Park

Arthur McKee, George LaRoi, and Jerry F. Franklin

ABSTRACT

Mature forests of Picea sitchensis and Tsuga heterophylla varied with terrace level. Upper terraces had denser stands, greater numbers of Tsuga, and understories of Vaccinium, ferns, and mosses. Lower terraces had open stands with understories of Acer circinatum and grasses. Tree reproduction occurred primarily on down logs. Less than 1 percent occurred on ground humus. Picea reproduction numbers and survival rates were superior to Tsuga. Tsuga reproduction may have exceeded that of Picea earlier. Both similarities and differences exist with Fonda's Hoh River model. Picea was apparently climax in these terrace forests in contrast to other coastal types.

Arthur McKee, Department of Forest Science, Oregon State University, Corvallis, Oregon 97331; George LaRoi, Department of Botany, University of Alberta, Edmonton, Alberta, Canada T6G 2E9; and Jerry F. Franklin, U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station, Forestry Sciences Laboratory, 3200 Jefferson Way, Corvallis, Oregon 97331.

Franklin (in this report) has described the relationships of the vegetation studies to the other portions of the South Fork Project. Plant community analyses in the South Fork were directed toward collecting baseline vegetation data in a manner that would facilitate their interpretation relative to topographic position and proximity to aquatic habitats. Previous studies by members of the research team had shown the importance of woody debris in mediating erosional processes (Swanson 1980). Information was sought to examine these interactions in a coastal ecosystem and the results are presented by Swanson and Lienkaemper in this report.

From research in the main valley of the Hoh River, Fonda (1974) proposed a successional model for river terrace forests that interpreted successively higher terraces as a series of seral stages tending toward a climax forest of Tsuga heterophylla. Terrace formation occurs by meandering of the river and periodic flooding. The wide valley floor of the South Fork of the Hoh River with its extensive terraces seemed an appropriate place to test the generality of Fonda's (1974) model.

More knowledge of the successional roles of Picea sitchensis and Tsuga heterophylla was needed to further evaluate the above model. In mature forests of the coastal fog belt (Franklin and Dyrness 1973) and on alluvial terraces bordering the lower reaches of coastal rivers (Cordes 1972), the two species compete strongly for dominance. In some habitats P. sitchensis seems unable to co-exist indefinitely with T. heterophylla in the absence of disturbances because it is less shade tolerant (Fowells 1965). P. sitchensis succeeds Alnus rubra in alluvial terraces for some distance inland, becoming the dominant tree species (Cordes 1972, Fonda 1974). It may be more tolerant of seasonal flooding in these sites than T. heterophylla. As one of the major attractions of the Olympic National Park, the stability and successional fate of the terrace forests is of extreme interest. Therefore, regeneration behavior of P. sitchensis and T. heterophylla was a major part of the vegetation studies.

This paper discusses the vegetation of the South Fork terraces in terms of upper versus lower terrace stands, but the collation of our terms with those of the geomorphologists is critical. At least six terrace surfaces have been recognized in the study area (see Swanson and Lienkaemper in this report). Surfaces 1, 2, and 3 range from fresh gravel bars to low terraces with young A. rubra stands. Their surfaces 4, 5, and 6 are occupied by mature, conifer-dominated forests and are the locale of the studies reported here. Data from surfaces 5 and 6 are combined for our "upper terrace" values. Surface 4 is our "lower terrace." Although it is difficult to draw exact comparisons between the adjacent river valleys, our lower terrace is believed roughly equivalent to Fonda's (1974) first terraces, and our upper terrace is roughly equivalent to his second terrace.

METHODS

Two different vegetation sampling procedures were employed in this study to accommodate the diverse needs of the group (see Franklin in this report). Transects allowed us to examine the interactions between topographic position, vegetation, and aquatic habitats. A point-quarter sampling method was used at 50-m intervals on these transects. Herbaceous cover was estimated in eight microplots (20- x 50-cm) around each point. Shrub cover was estimated by line intercept along the transects.

The remainder of the vegetation sampling was conducted on the four large (1-ha) permanent plots (see Franklin in this report). Detailed sampling of down logs for dimensions and decay class is described by Lambert, in this report, who provided the basic data utilized here on log numbers and surface area.

Restricted random sampling was performed on each of the two terrace stands of the immature tree subpopulations (stem $\leq$ 8 m tall). Five major substrate types were sampled: ground duff and humus, tree stumps and uprooted tree bases ("root wads"), P. sitchensis logs, T. heterophylla logs, and logs unidentifiable as to species. The three log substrates were further subdivided by a decay class scheme (see Lambert in this report). A logarithmic height classification system was used in tallying seedlings and saplings in which the height range of each taller class is doubled: e.g., (1) < 0.125 m; (2) 0.125 - 0.25 m; (3) 0.25 - 0.5 m, etc. This was done to achieve a greater resolution in smaller size classes.

Biomass estimates were made from data collected on the four permanent plots using allometric equations developed by the Coniferous Forest Biome (Gholz et al. 1979). Heights of selected trees were measured on the permanent plots. Ages of overstory dominants were determined by increment cores taken along the transects.

RESULTS

Structure and Composition

Forests on the valley floor of the South Fork of the Hoh River were dominated by P. sitchensis and T. heterophylla except for recently created, relatively narrow terraces along the main river channel, which were dominated by A. rubra. Much of the valley floor of the South Fork consists of two relatively distinct terraces, however, and most of the following discussion is a comparison of these upper and lower terraces. Although there are similarities, the data from the transects and permanent plots are evidence that different terrace levels were occupied by stands that differ substantially in structure and composition.

Both upper and lower terraces had similar ages and heights of the overstory Picea and Tsuga. Mean and maximum ages at 1.5 m above ground were 220 and 266 years on the upper and 205 and 258 years on the lower terrace. The tree strata on both terraces consisted of a tall tree layer of P. sitchensis 75 to 80 m in height and a medium tree layer of T. heterophylla and P. sitchensis of 45 to 55 m. Maximum heights measured on both terraces exceeded 85 m. Mean heights and ages were slightly greater on the upper terrace, but sampling was insufficient for a test of significance.

Table 1--Mean densities, basal areas, and diameters by species for upper and lower terrace forests of the South Fork of the Hoh River

Species[1/]	Density		Basal area		Mean diameter	
	Upper	Lower	Upper	Lower	Upper	Lower
	Number per hectare		Square meter per hectare		Centimeters	
PISI	57.8	33.1	61.9	52.8	90.4	118.4
TSHE	79.9	24.7	15.8	10.3	45.8	64.9
THPL	2.1	[2/]0.3	1.0	[2/]0.8	73.0	[2/]176
PSME	1.7	--	2.9	--	114.0	--
ALRU	[2/]0.3	5.3	[2/]0.03	1.9	[2/]28.0	64.9
ACMA	--	0.7	--	0.4	--	84.0
ABAM	[2/]0.3	--	[2/]0.1	--	[2/]51.0	--
All species	142	64	81.8	66.3	65.6	93.3

[1/]Species are: PISI = Picea sitchensis, TSHE = Tsuga heterophylla, THPL = Thuja plicata, PSME = Pseudotsuga menziesii, ALRU = Alnus rubra, ACMA = Acer macrophyllum, and ABAM = Abies amabilis.

[2/]Only one individual in the sample.

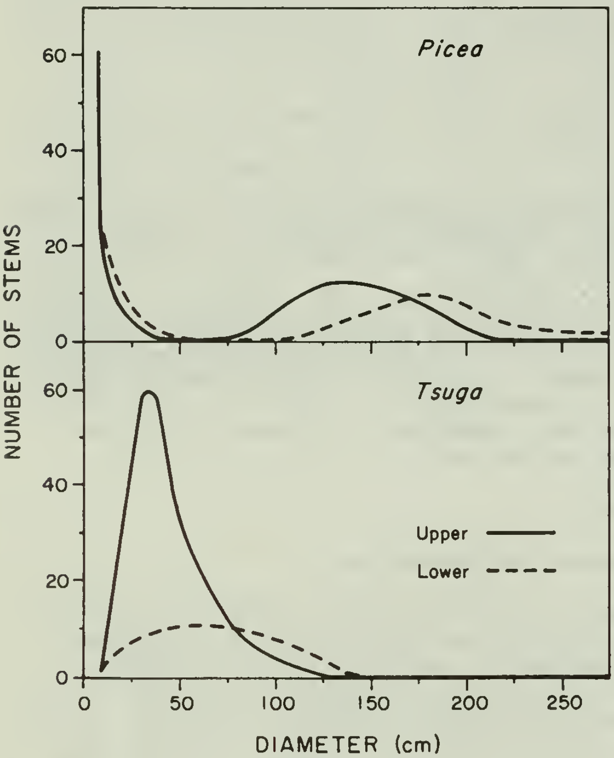


Figure 1.--Diameter distributions for all Picea sitchensis and Tsuga heterophylla sampled which were over 5 cm in diameter on upper and lower terraces.

Upper and lower terrace stands differed substantially in several structural and compositional features (table 1 and fig. 1). Total density and basal area were greater in upper terrace than lower terrace stands: 142 vs. 64 stems/ha and 81.8 vs. 66.3 m^2/ha. Mean diameters, on the other hand, were greater on the lower than the upper terrace. P. sitchensis averaged 118-cm d.b.h. on the lower and 90-cm d.b.h. on the upper terrace, while T. heterophylla averaged 65- and 46-cm d.b.h. respectively. The larger diameters on the lower terraces may have been due to wider spacing which results in reduced competition or to better site conditions or both. Diameter distributions of P. sitchensis and T. heterophylla showed that, except for the smallest size class, P. sitchensis had peak densities at substantially larger size classes than T. heterophylla on both terraces (fig. 1). The bimodal nature of the P. sitchensis diameter distributions on both terraces should be noted. The implications of this distribution will be discussed later in the section on regeneration.

The biomass estimates in table 2 reflect some of the structural variation encountered in upper and lower terrace stands. Total biomass was measured in metric tonnes per hectare (t/ha) and averaged more in the upper terrace permanent plots than in the lower terrace. Considerable variation existed, however, in the biomass of P. sitchensis in the upper terrace plots and in T. heterophylla in the lower terrace plots. Total biomass was quite high on both terraces for 200- to 250-year-old stands, indicating the productive nature of the Picea-Tsuga forests.

Composition differs dramatically between upper and lower terrace forests. T. heterophylla was of much greater importance in upper terrace stands as shown by the density and basal area values (table 1). Minor tree species such as Pseudotsuga menziesii and Abies amabilis seemed confined to upper terraces. Alnus rubra was much more important on the lower terraces (tables 1 and 2).

Understory composition also differed between the two terraces (table 3). Composition of the shrub layer shifted from Acer circinatum-dominated to Vaccinium-dominated. Cover of Acer circinatum dropped from 28.2 to 2.4 percent as one went from lower to upper terrace stands, while Vaccinium cover went from 0.6 to 10.8 percent. Total shrub cover was twice as great on the lower terrace. The herbaceous layer of lower terrace stands was dominated by grasses and forbs with 25.4- and 37.3-percent cover, respectively. As with Acer, grass cover dropped dramatically in upper terrace stands. Mosses and ferns became much more important in the upper terrace forests. Total cover of forbs decreased slightly in upper terrace forests. Species composition of the forbs was quite similar on both terraces.

Table 2--Biomass estimates (metric tonnes per hectare) for four permanent 1-ha plots established September 1978 in upper and lower terrace forests of the South Fork of the Hoh River, Olympic National Park. Calculated for stems ≥ 15-cm d.b.h.

	Bole and bark		Branches		Foliage[2]		Total	
Species[1]	Upper	Lower	Upper	Lower	Upper	Lower	Upper	Lower
PISI	442.4	428.4	50.7	51.7	4.2	4.0	497.3	484.1
	740.5	446.8	86.2	53.4	6.9	4.2	833.6	504.3
TSHE	110.6	36.4	33.6	12.8	6.3	2.1	150.4	53.3
	62.7	154.6	18.3	56.8	3.6	8.1	84.6	219.4
THPL	2.6	10.8	0.5	1.9	0.2	0.7	3.3	13.4
	0.3	--	0.2	--	0.1	--	1.1	--
PSME	17.2	--	0.8	--	0.2	--	18.3	--
	22.9	--	1.1	--	0.3	--	24.2	--
ALRU	--	5.0	--	0.6	--	0.03	--	5.6
	--	4.1	--	0.5	--	0.02	--	4.6
Total	572.8	482.6	85.6	67.0	10.9	6.9	669.3	556.4
	829.7	605.4	106.1	110.6	11.1	12.3	946.8	728.3
$\bar{x}$	701.2	544.0	95.8	88.8	11.0	9.6	808.0	642.4
s_d	181.7	86.8	14.5	30.8	0.1	3.8	196.2	121.6

[1] Species are: PISI = Picea sitchensis, TSHE = Tsuga heterophylla, THPL = Thuja plicata, PSME = Pseudotsuga menziesii, and ALRU = Alnus rubra.

[2] Foliar biomass estimates for Picea are conservative because the equations used (Gholz et al. 1979) are partially based on wind-trimmed trees.

Table 3--Mean composition of shrub and herbaceous layers of forest communities on the upper and lower terraces of the South Fork of the Hoh River

	Shrub layer[1], % Cover					Herbaceous layer, % Cover			
	ACCI	VAsp	RUSP	MEFE	$\sum$	Forbes	Grasses	Mosses	Ferns
Upper terrace	2.4	10.8	1.9	.03	15.1	29.8	4.8	64.3	13.5
Lower terrace	28.2	0.6	1.8	0.0	30.6	37.3	25.4	42.4	6.8

[1] Shrub species abbreviations are: ACCI = Acer circinatum, VAsp = Vaccinium species, RUSP = Rubus spectabilis, and MEFE = Menziesia ferruginea.

Table 4--Picea sitchensis and Tsuga heterophylla subpopulation density (stems ≤ 8 m tall/m^2) on the 5 major substrate types and 4 major log decay classes in the upper and lower terrace forests, South Fork Hoh River, Olympic National Park

Substrate type and log decay class	Upper terrace		Lower terrace	
	Picea	Tsuga	Picea	Tsuga
Substrate type:				
Picea logs	36.0	15.3	19.3	6.6
Tsuga logs	29.9	9.6	11.3	4.3
Unknown logs	30.0	7.5	11.5	5.1
Stumps and root wads	5.1	1.6	7.7	2.9
Ground humus	0.08	0.01	0.08	0.01
Log decay class:				
2. Early	24.8	15.5	8.3	2.0
3. Middle	38.5	10.7	21.7	7.7
4. Late	28.6	9.2	11.9	5.4
5. Very late	28.2	8.2	11.9	4.7

One interesting aspect of species composition concerned the naturalized Eurasian weeds. These exotic species were confined almost entirely to lower terrace stands and recently formed terraces and gravel bars. The only exotic species encountered in the upper terraces were Agrostis alba and Prunella vulgaris, and these were rare. The other exotic species--Poa trivialis, Ranunculus repens, Rumex acetosella, Rumex crispus, Trifolium repens, and Lactuca serriola--seem restricted to the lower terraces. Agrostis alba, Poa trivialis, and Ranunculus repens were important components of the lower terrace herbaceous layer with covers frequently exceeding 20 percent. The other species tended to be locally important or rare. Fonda's (1974) data show these Eurasian weeds similarly distributed on the terraces in the main stem of the Hoh River. Historically, traffic of both humans and livestock has been heavier in the more open lower terraces. These factors and the more frequent disturbance by flooding on the lower terraces were probably the reasons for the current distribution of exotics.

Forest Tree Reproduction

Regeneration on Different Substrates

The density of seedlings and saplings less than 8 m tall growing on the five major substrate types on the two terraces is given in table 4. Both P. sitchensis and T. heterophylla obviously had difficulty establishing on ground humus in the two terrace stands. Down logs are a much more favorable site for establishment. P. sitchensis logs are better recruitment sites than T. heterophylla logs for both tree species. This difference is confirmed by chi-square tests and also has been observed by Minore (1972).

Total recruitment densities of P. sitchensis were higher than those for T. heterophylla on all five substrates in both terrace stands. Environmental conditions during the life span of these seedlings and saplings have clearly favored P. sitchensis over T. heterophylla.

Regeneration on Different Log Decay Classes

Densities of seedlings and saplings on four different log decay classes also are tabulated in table 4. Both terraces lacked sufficient logs in class 1 to provide good tree seedling density estimates. P. sitchensis density was highest on class 3 logs on both terraces. The maximum density of T. heterophylla regeneration, however, was on class 2 logs in the upper terrace stands and class 3 logs in the lower terrace stands.

Chi-square tests support two conclusions: (1) tree recruitment potentials of fallen logs in the study area change significantly with decomposition stage and (2) the off-log environments of the two terraces exert a strong influence on the recruitment potential of different log decay classes. Seedling and sapling density is almost always greater on the upper than lower terrace for a given substrate type and species.

Total Regeneration

The data on densities on different substrates and decay classes reveal much about the behavior at the two tree species but do not show regeneration in the two terrace stands. Total density per hectare is the product of the above densities and the amount of surface area per hectare occupied by the different substrate types and decay classes. These calculations show P. sitchensis regeneration was approximately three times more abundant than T. heterophylla in both upper and lower terrace stands (table 5).

The importance of logs as a recruitment site is dramatically shown in table 5. Logs provided 96 and 88 percent of the P. sitchensis recruitment on the upper and lower terraces, respectively. Proportions of T. heterophylla were 97 and 93 percent. Class 3 logs are obviously of special importance (table 5). On a per hectare basis, they supported the largest number of seedlings and saplings less than 8 m tall for both species on both terraces.

Survivorship

Total densities (table 5) are interesting but do not reveal differences between species in abundance of different size classes. The abundance of P. sitchensis might be largely restricted to the smallest size classes, T. heterophylla to the largest, which would have vastly different implications for successional trends. Abundance data are presented in figure 2 as height-based survivorship curves for the two species on the two terraces. The regeneration sampling provided data for the first seven height classes, and the transect and permanent plot samples provided data for larger height classes.

Table 5--Calculated densities (stems $\leq$ 8 m tall) of Picea sitchensis and Tsuga heterophylla (ha^{-1}) on 5 major substrate types and 4 major log decay classes in the upper and lower terrace forests, South Fork Hoh River, Olympic National Park

Substrate type and log decay class	Upper terrace		Lower terrace	
	Picea	Tsuga	Picea	Tsuga
Substrate type:				
Picea logs	14,500	6,170	5,810	1,980
Tsuga logs	15,300	4,910	2,420	930
Unknown logs	4,920	1,230	600	260
Stumps and root wads	550	170	440	160
Ground humus	700	90	750	90
Total	35,970	12,570	10,020	3,420
Log decay class:				
2. Early	7,030	4,340	500	116
3. Middle	19,000	5,250	7,530	2,660
4. Late	7,800	2,500	1,730	780
5. Very late	820	170	80	30

The survivorship curves show P. sitchensis to be more abundant than T. heterophylla on both terrace forests for the first eight height classes ($\leq$16 m tall) (fig. 2). The environmental conditions during the recent past have clearly favored P. sitchensis recruitment and survival. Such has not always been the case, however.

The survivorship curves for both terraces show an increase in T. heterophylla abundance in the larger size classes with a concomitant reduction of P. sitchensis (fig. 2). The diameter distributions shown in figure 1 revealed a greater abundance of T. heterophylla in the intermediate size classes, sandwiched between the peaks of the bimodal distribution of P. sitchensis. Hence, T. heterophylla regeneration was favored over P. sitchensis at some time in the past. The relative position of the survivorship curves for that period would have been reversed for both terraces, with T. heterophylla more abundant than P. sitchensis in the smaller size classes.

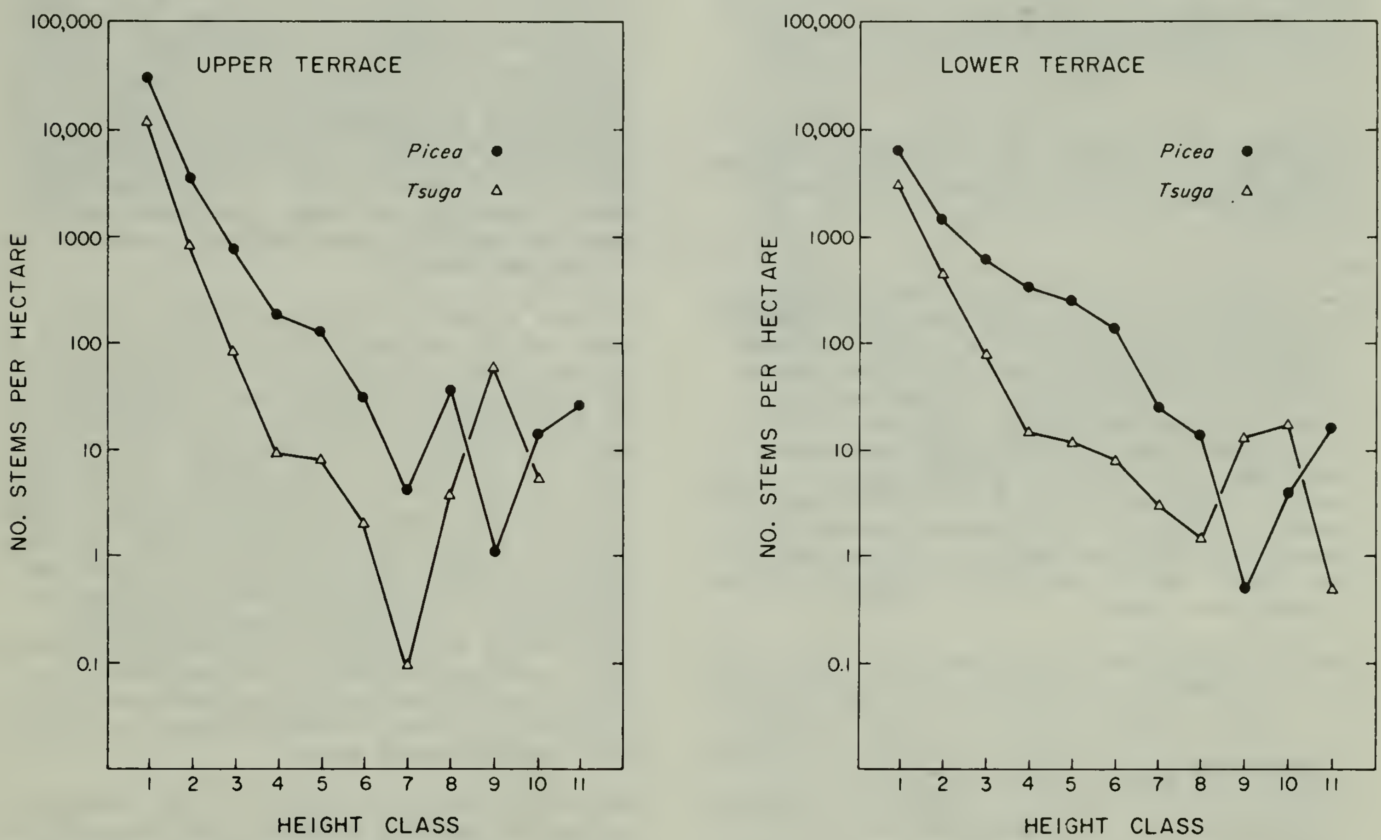


Figure 2.--Survivorship curves for Picea sitchensis and Tsuga heterophylla on lower and upper terrace forests in the South Fork of the Hoh River; each height class is twice as large as its predecessor (i.e., 1 = < 0.125 m, 2 = 0.125 to 0.25 m, 3 = 0.25 to 0.5 m, 4 = 0.5 to 1 m, 5 = 1 to 2 m, 6 = 2 to 4 m, 7 = 4 to 8 m, 8 = 8 to 16 m, 9 = 16 to 32 m, 10 = 32 to 64 m, and 11 = > 64 m tall).

DISCUSSION

The composition and structure of the terrace forests of the South Fork of the Hoh River have both similarities and differences with Fonda's (1974) terrace-based model developed for the main Hoh River drainage. The higher terraces supported increasing amounts of T. heterophylla in both the South Fork and the main Hoh River valleys. Grasses were an important component of the lower terraces in both systems; mosses increased in cover on the upper terraces. Forb cover remained relatively constant on all the terraces, and naturalized Eurasian weeds were confined almost entirely to the lower terraces in both valleys.

There were slight differences in the terrace forests between the two valleys, however. Alnus rubra is present in the lower terrace forests in the South Fork valley as well as on recent alluvium. The lower terrace forests in the South Fork appeared to be a much older version of Fonda's (1974) first terrace forest and lacked Populus trichocarpa. The upper terrace stands of the South Fork appeared to be intermediate to the second and third terrace forests of Fonda (1974). The upper and lower terrace stands of the South Fork had lower densities and higher basal areas than their analogs in the main Hoh River valley. Shrub cover was higher in the South Fork terraces with Acer circinatum much more abundant on the lower terraces and Vaccinium species more abundant on the upper terrace.

More important differences concerned the ages of the terrace forests and the role of P. sitchensis in the South Fork stands. In contrast to Fonda's (1974) model, the forests of the upper and lower terraces had dominants of about the same age and thus cannot be viewed as seral stages in a sequence of forest development. As shown by the survivorship curves, P. sitchensis regeneration was currently favored over T. heterophylla on both terraces. This is in contrast to what Fonda (1974) reports for even his third terrace forests which average two-thirds the basal area of our upper terrace stands, and thus should favor Picea by virtue of being less shaded.

Franklin and Dyrness (1973) suggest a climax role for P. sitchensis on alluvial habitats, in contrast to its seral role throughout most of the coastal zone. Fonda (1974), on the other hand, indicates T. heterophylla is the climax species on the older terraces. No evidence exists in our data for a directional change from P. sitchensis to T. heterophylla dominance in the South Fork valley. P. sitchensis was currently replacing itself on both terraces and should maintain, if not actually increase, in importance relative to T. heterophylla. A successional shift to Tsuga dominance is not apparent. This is consistent with Cordes' (1972) findings in valley Picea-Tsuga stands in British Columbia.

Several factors could be responsible for the persistence of Picea in these alluvial forests. Many of the stands were park-like with widely spaced stems and numerous openings ranging up to several hectares in size. Such conditions would be more favorable for Picea which is less shade tolerant than Tsuga. An often-cited factor is grazing by Roosevelt elk which are believed to feed selectively on the Tsuga. The importance of browsing has yet to be demonstrated, however, and could not account entirely for the better survival of Picea reproduction. Picea currently demonstrated superior survival from the smallest size classes, presumably below the size of material typically taken by elk.

It is important to note, however, that within the ages of the stands in the South Fork, T. heterophylla regeneration has been favored relative to that of P. sitchensis. The survivorship curves for both upper and lower terraces show a curious reversal in the abundances of pole-sized individuals of the two species. The reasons for this oscillation in regeneration of the two species is not clear. It could be related to climatic fluctuation or to changes in the population of Roosevelt elk. Elk populations were low early in this century, which might account for the wave of larger-sized T. heterophylla. Age data collected for Tsuga do not support this hypothesis, however (i.e., trees sampled did not originate uniformly in the period 1890 to 1910). Fluctuations of either climate or elk herds could create unstable size structures with oscillations in abundance due to time-lag effects.

The lack of correlation between Fonda's (1974) model and the terrace forests of the South Fork is not surprising. Each terrace valley has had its own history of disturbances since the retreat of the glaciers from the valleys. Flooding patterns have not been identical. Moreover, the South Fork valley is distinctive in the breadth of the valley floor relative to the total width of the drainage. Colluvial and alluvial depositions from the valley walls and tributaries, which might alter the basic patterns in these terrace forests, are much less important in the South Fork than in the main Hoh River valley. For example, Acer macrophyllum groves which were confined to colluvial fans (Fonda 1974) were almost absent in the South Fork. The fire history of the two valleys could also be very different, creating an array of seral stand conditions that correlate poorly.

Results of this study clearly show the importance of logs and decaying wood for forest perpetuation. Recruitment would be sparse, indeed, but for these substrates. The superiority of P. sitchensis logs as a regeneration site remains to be explained. The factors which severely limit regeneration on the forest floor are doubtless many, including competing vegetation and possibly disease. The consequences are clear, however, from the extremely rare seedlings not associated with down logs, stumps, or root mounds. Removal of these materials from terrace stands would clearly limit regeneration.

Implications for lands managed for timber production in the vicinity of the Park are clear. Rotten wood is an important substrate for seedling establishment on cutovers, especially where shrub competition is severe. Rotten logs, stubs, and root wads which are potential sites for seedling establishment should be viewed as assets in regeneration problem areas on the west side of the Olympic Peninsula.

CONCLUSIONS

The mature forests described on terraces in the South Fork of the Hoh River provide an outstanding sample of the valley-bottom stands sometimes referred to as Olympic rainforest. Details of composition and structure do vary in other parts of the South Fork and in the main river drainages of the western Olympic Mountains--main Hoh, Quinault, Queets, and Bogachiel Rivers. Nevertheless, some general conclusions about the valley-bottom forests are possible. Landform is, as indicated by Fonda (1974), of major importance in forest composition and structure. The mature Picea-Tsuga forests are often relatively open. Logs are of overwhelming importance for recruitment of new conifers; nurse logs are an essential structure rather than an interesting novelty. A variety of factors appears to make Picea as much a potential climax species as Tsuga. Roosevelt elk intuitively appear important influences on vegetative composition and dynamics, but quantitative data still are absent.

LITERATURE CITED

Cordes, Lawrence D.
1972. An ecological study of the Sitka spruce forest on the west coast of Vancouver Island. Ph.D. thesis, Univ. of British Columbia, Vancouver, Canada. 452 p., illus.

Fonda, R. W.
1974. Forest succession in relation to river terrace development in Olympic National Park, Washington. Ecology 55(5):927-942, illus.

Fowells, H. A.
1965. Silvics of forest trees of the United States. USDA Handb. 271. 262 p., illus.

Franklin, Jerry F., and C. T. Dyrness.
1973. Natural vegetation of Oregon and Washington. USDA For. Serv. Gen. Tech. Rep. PNW-8, 417 p., illus. Pac. Northwest For. and Range Exp. Stn., Portland, Oregon.

Gholz, H. L., C. C. Grier, A. G. Campbell, and A. T. Brown.
1979. Equations for estimating biomass and leaf area of plants in the Pacific Northwest. Oreg. State Univ., For. Res. Lab. Res. Pap. 41, 37 p.

Minore, Don.
1972. Germination and early growth of coastal tree species on organic seed beds. USDA For. Serv. Res. Pap. PNW-135, 18 p., illus. Pac. Northwest For. and Range Exp. Stn., Portland, Oregon.

Swanson, Frederick J.
1980. Erosion as an ecosystem process. In Richard Waring, ed. Proceedings 20th Annual Biology Colloquium. Oreg. State Univ. Press. Corvallis, Oregon. In Press.

Interactions Among Fluvial Processes, Forest Vegetation, and Aquatic Ecosystems, South Fork Hoh River, Olympic National Park

Frederick J. Swanson and George W. Lienkaemper

ABSTRACT

Interactions among fluvial processes and forest vegetation created a variety of landforms, plant communities, and aquatic habitats in the South Fork Hoh River. We distinguished six geomorphic surfaces based on differences in vegetation and elevation relative to low water level. Relations between high flows and forest vegetation vary from one surface to another. Flood effects included inundation, bank cutting, surface scour, deposition, and transport of large organic matter. Geomorphic processes have created four distinctive aquatic habitats in the valley: main river channel, off-channel areas along the main stem, and valley-wall and valley-floor tributary streams.

Frederick J. Swanson and George W. Lienkaemper, U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station, Forestry Sciences Laboratory, Corvallis, Oregon.

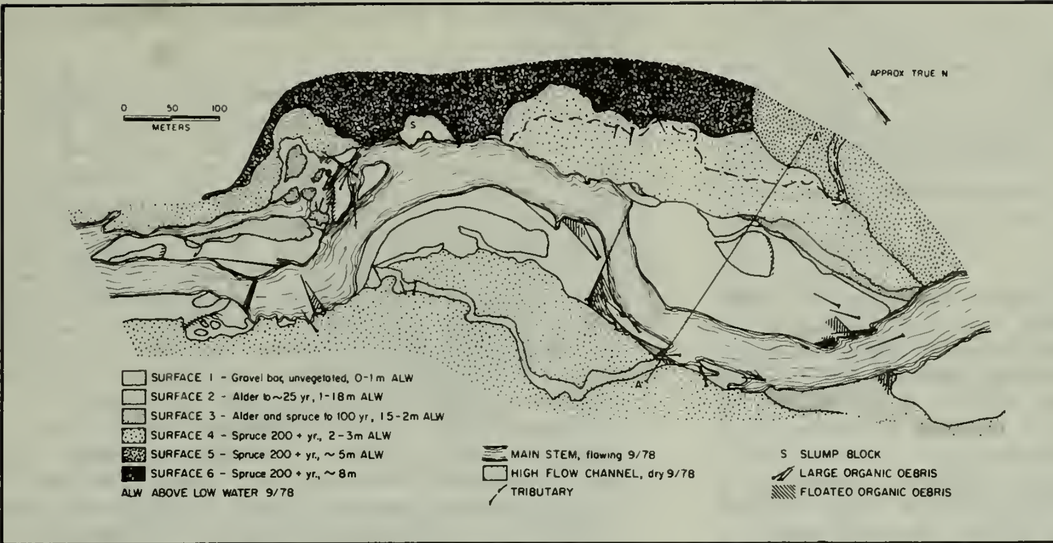


Figure 1.--Geomorphic surfaces, channel position, and large organic debris in a section of South Fork Hoh River. Mapped by pace and compass by G.W. Lienkaemper.

INTRODUCTION

Landforms and geomorphic processes are important factors in development of most terrestrial and aquatic ecosystems. Interactions between physical and biological features and processes are especially well developed along glacier-fed rivers flowing through heavily forested, glacially carved valleys such as the Hoh River. On the broad valley floor of the Hoh River system, fluvial geomorphic processes create landforms providing sites for terrestrial and aquatic ecosystem development that contrast markedly with valley-wall sites. Fluvial processes regulate the development of these ecosystems in areas subject to flooding and sedimentation.

In the geomorphology phase of the interdisciplinary South Fork Hoh River study, we examined these relationships by addressing three specific objectives:

1. Map valley-floor geomorphic surfaces and channel features and age associated trees.

2. Examine relations among fluvial processes and vegetation along the main river channel.

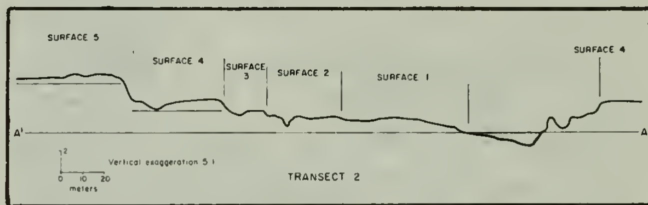
3. Define relations among fluvial processes and vegetation along the main river channel.

We briefly report results of each of these study phases to provide the physical environmental context within which to view the study results.

FLUVIAL SURFACES AND CHANNELS OF THE MAIN STEM

At low and moderate flow conditions, the main stem of the South Fork Hoh River meanders within its broad, gravel-floored, flood channel. Within the study reach, about 2.5 km east of the western Olympic National Park boundary, the unvegetated flood channel is about 100 m wide, less than 10 percent of average valley-floor width. The steep (60-percent) valley side slopes, carved by glaciers as recently as the latest Wisconsin advance (Crandell 1965, Heusser 1974), end abruptly at the valley floor. The valley bottom is partially filled with younger outwash gravels that form a complex set of terraces.

Figure 2.--Surveyed cross section of valley bottom along transect A-A' (see fig. 1).



The 1 000-m study reach contained six geomorphic surfaces distinguishable on the basis of vegetation and elevation above river level (figs. 1 and 2). Successively higher surfaces up to Surface 5 bore forest communities in progressively more advanced stages of development and greater amounts of large woody debris produced by forests on the surface. Emergent, unvegetated gravel bars of Surface 1 extended to 1 m above the late summer river level at the time of the study (mid-September 1978). Surface 2 had alder, Alnus rubra, thickets of trees up to 30 years old. Alder and spruce, Picea sitchensis, trees on Surface 3 were up to more than 100 years in age. Old-growth, open-grown spruce and western hemlock, Tsuga heterophylla, on Surface 4 ranged in age up to 258 years, based on a sample of about 20 trees (see McKee et al. in this report). Individual spruce and hemlock trees on Surface 5 did not appear to be significantly older. McKee et al. (in this report) observed a maximum age of 266 years in a sample of about 20 trees. Unlike Surface 4, however, many large, down boles in advanced stages of decay littered the forest floor of Surface 5, suggesting that the community might have been much older than the oldest living individuals. This hypothesis was favored by the occasional occurrence of well-rotted Douglas-fir logs on Surfaces 5 and 6 (see Graham in this report). An alternative hypothesis is that greater biomass of down logs on higher surfaces was a consequence of higher stand densities. Forests of Surface 6 were not readily distinguished from those of Surface 5.

Tree ages only roughly bracket the age of geomorphic surfaces. Oldest trees on Surfaces 2 and 3 may well date the time the geomorphic surface was formed as a fresh substrate for vegetation establishment. Old-growth trees on higher surfaces simply provided minimum estimates of surface ages. Estimates of minimum ages of Surfaces 5 and 6 will be improved with better understanding of stand development and age and decay rate of pieces of dead wood.

The mapped reach and adjacent areas examined only in reconnaissance revealed some consistent patterns of backwater channels and zones of addition and accumulation of large organic debris. Whole trees fell into the river where Surface 4 and higher surfaces were undercut on the outside of bends in the river. These trees accumulated at the heads of the downstream gravel bars (Surface 1) which are persistent sites for accumulation of large debris. In many instances, these debris accumulations regulated water movement into high water channels that occurred regularly along the back edges of Surfaces 1, 2, and, in some cases, 3 on the inside of bends in the river.

Many small tributary channels flow directly toward the river over Surfaces 5 and 6, but then turn downstream and parallel the river by flowing along the back edge of Surfaces 3 or 4. The tributary stream in the east portion of figure 1 took such an indirect route. The net effect was to increase the area of low gradient, valley-floor tributary streams. The cause of this channel pattern was not clear. The back edges of many surfaces were wet areas, and surveys across the valley floor revealed some tendency for surfaces to slope away from the main channel (fig. 2). This could be a product of a type of levee formation due to preferential accumulation of sediment on the margin of the surface along the river during periods of overbank flow. Low areas at the back edges of Surfaces 3 and 4 also might originate by the same processes that form and maintain high flow channels along the back edges of Surfaces 1 and 2. These types of gravel bars with high centers in the axis of the main channel have been observed in other sediment-laden rivers (R. J. Janda, pers. comm.). In some instances along the South Fork of the Hoh, accumulations of large organic debris on the prows of gravel bars may aid sediment accumulation along the axis of the bar and direct high flows into a channel along the back edge of the bar. As the river continually changes its course, these high water channels may be largely abandoned by the main stem only to be occupied later by a tributary stream.

INTERACTIONS OF FLUVIAL PROCESSES, LANDFORMS, AND VEGETATION

Interactions between high flow events and forest vegetation vary from one geomorphic surface to another (fig. 3). Flooding by the main stem affected Surfaces 1 through 4. This inundation might affect plant community composition. One effect was localized deposition of fine sediment which might provide seed bed for species such as alder that otherwise might not become established in the stand. Surface 3 and higher surfaces were subject to bankcutting while surface scour was the more important erosion process on lower surfaces. Floated large organic debris has both positive and negative effects on live vegetation. Debris carried by flood flow can severely batter living plants on lower surfaces. Stabilized, large, down debris provided protected sites where alder and other pioneering species became established. Once established, living vegetation in turn began to stabilize geomorphic surfaces by developing root systems and reducing water velocity by the flow resistence of stems.

Some of these interactions between fluvial processes and vegetation could be interpreted from analysis of the alder thicket ("camp thicket") on Surface 2 along transect A-A' in figure 1. This thicket appeared to have developed after floods in 1962, 1966, and 1968 (fig. 4). Tree ages varied over more than a decade, suggesting occurrence of repeated disturbance and opportunity for establishment. The main body of the stand was protected by several large logs partially buried in sediment (fig. 5). Alder stems in bordering areas not protected by the down logs had been repeatedly and heavily abraded by floating organic debris and moving bedload sediment. The major down logs protecting the thicket and trees in the thicket itself created a localized quiet water environment where fine sediment was deposited during high flows. This process, coupled with litter production by the stand, accelerated soil development and growth of the stand. The large, down debris helped the stand reach a stage of structural development where it could better withstand most floods.

Age analysis of sapling and small trees at the camp thicket and other sites in the mapped area provided additional insight into the role of flooding on vegetation establishment (fig. 4). The camp-alder thicket appeared to postdate the flood of November 1962, but the broad spread of ages indicated that subsequent high flows provided new opportunities for establishment. Some other areas mapped as Surface 2 had trees nearly 30 years old which could have been established after the second highest flow on record in November 1949. Trees sampled on Surfaces 3 and 4 had a broad range of ages, some of which clustered following years with high flows (fig. 4). The group of 23- to 28-year-old trees on Surface 4 appeared to postdate the high flow of November 1949. The forest floor of this surface was well covered with litter and herbaceous vegetation, suggesting that establishment of these alder trees may have occurred on overbank deposits.

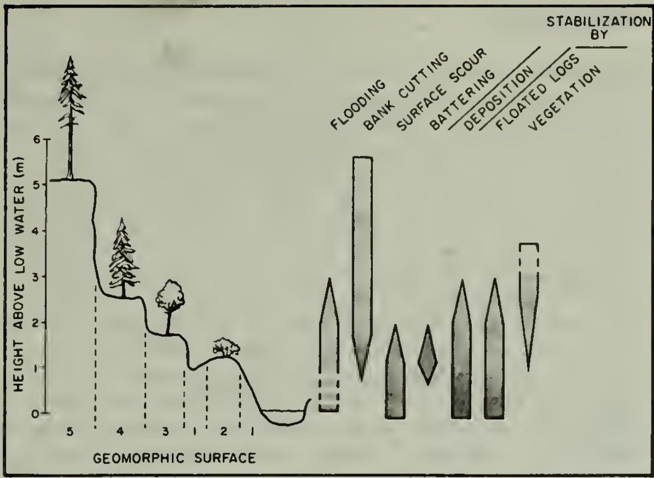


Figure 3.--Types of effects of fluvial processes on geomorphic Surfaces 1 through 5.

In general, the lower geomorphic surfaces are repeatedly affected over a period of at least several centuries by high flows which damage vegetation and create new opportunities for establishment. Forests on Surface 4, for example, contained trees over 250 years old, and these stands were still affected by flooding. Consequently, forests on these surfaces were not simple single-aged stands dating from single floods.

AQUATIC HABITAT

Geomorphic processes had created and maintained four broadly defined classes of aquatic habitat in the valley. The main river channel was characterized by fast, turbid water and shifting channel position. Glaciers at the river's head are a source of abundant silt and clay-sized sediment during the spring, summer, and fall months. Riparian vegetation had only moderate influence over the wide river, and overall abundance of large organic debris was low relative to the other three classes of stream environment.

The broad valley floor allowed development of a variety of back-water and high-flow channels we term "off-channel" sites. These sites ranged from ephemeral high flow channels to secondary river channels that carried water much of the year. In some cases, log jams regulated flow into off-channel areas. Compared with the main channel, flow velocity was moderate, and large organic debris and riparian vegetation were more important. However, this environment was quite varied with flow conditions ranging from fast and turbid to slow and clear to no flow at all.

Tributary streams originating from springs at the back edges of valley-floor surfaces or from streams draining the valley walls were termed "terrace tributaries". These streams were typified by low gradients, quiet, clear water, and strong influence of surrounding forest vegetation.

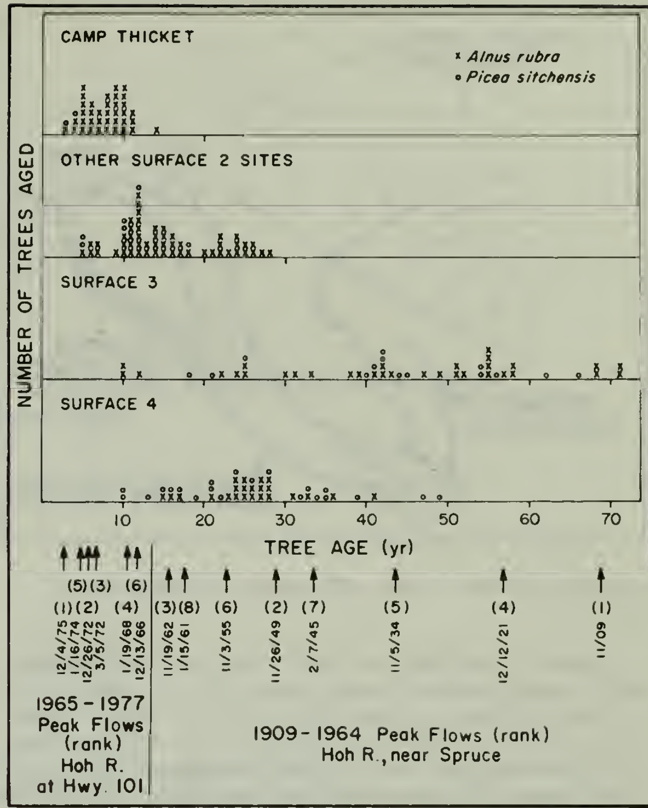
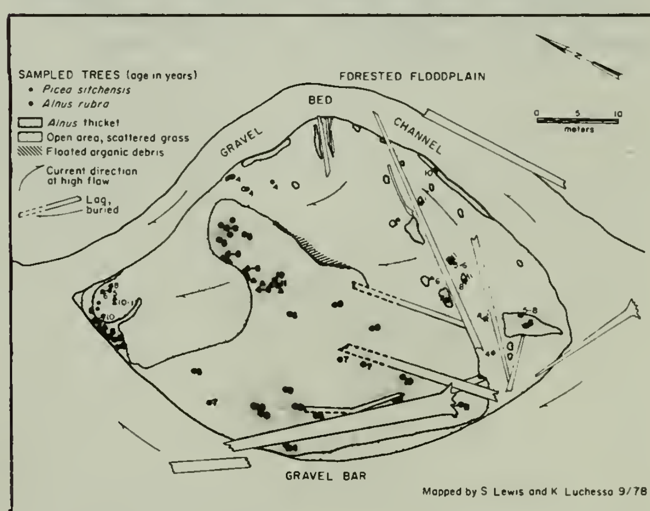


Figure 4.--Age distribution of alder and spruce saplings and small trees on Surfaces 1 through 4 and peak flows since 1909. Peak-flow data for 1927-57 for Hoh River and earlier peaks for Quinault River from Bodhaine and Thomas (1964). More recent data from annual U.S. Geological Survey reports of Surface Water Supply of the United States, Part 12, and Water Resources Data for Washington.

Figure 5.--"Camp" alder thicket on Surface 2 located on transect A-A' (see figs. 1 and 2).



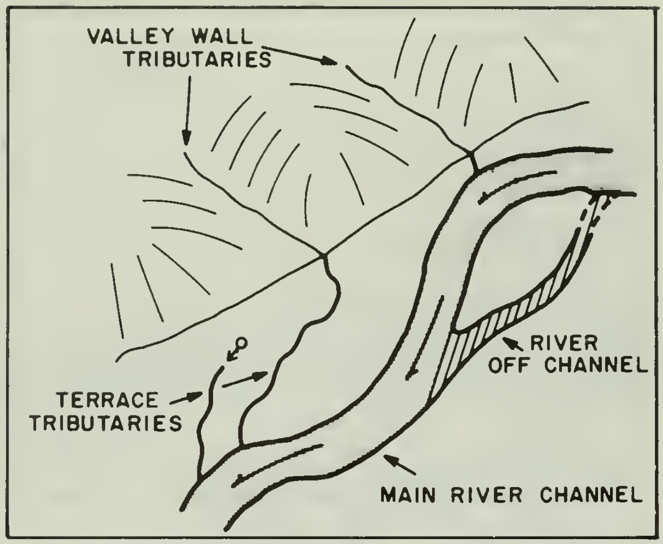


Figure 6.--Four types of stream environments.

Valley-wall tributaries were rigorous environments with steep gradients and flashy flows. Since these streams are not glacier fed and heavy forest vegetation on the valley walls minimizes soil erosion, stream water was clear except during periods of high flow. Forest vegetation strongly influences valley-wall tributaries, particularly in the case of large organic debris which forms a stair-step profile along streams. Falls and plunge pools formed in this fashion dissipate stream energy, store sediment, slow removal of fine organic detritus which is the food base of the aquatic ecosystems, and shape microhabitats within the stream.

The influences of forest vegetation on aquatic ecosystems and geomorphic forms and processes increased across this range of stream types from main river channel to valley-wall tributary. Structure and productivity of aquatic communities varied across these types in response to geomorphic factors and degree of forest influence (see Sedell et al. and Ward et al. in this report).

CONCLUSIONS

Geomorphic features set the stage for development of terrestrial and aquatic ecosystems of the South Fork Hoh River. Geomorphic processes regulate the types and rates of ecosystem development. Structure, age distribution, abundance of dead wood, and other characteristics of forest communities varied from one geomorphic surface to another in response both to the time period available for forest development and to degrees and types of flood influences. Successively higher surfaces were less influenced by fluvial processes of the main river. For example, vegetation on Surface 2 was subjected to a variety of destructive and beneficial influences of high flows, while higher surfaces were mainly affected by bankcutting and overbank deposition of sediment. Alder establishment in spruce forests on Surface 4 may have occurred on seedbed provided by deposits of fine overbank sediment. Thus, this surface appeared to have been affected by fluvial processes for at least several centuries.

Geomorphic processes have created and maintained four distinctive types of aquatic environments in the valley (fig. 6): (1) the main river channel with fast, turbid water and only moderate influence of forest vegetation; (2) off-channel areas of the main stem with flows that vary from fast to quiet and turbid to clear and may dry up part of the year; (3) terrace tributaries characterized by quiet, clear water; and (4) valley-wall tributaries that have fast, generally clear water. Forest influences increase across this array of stream types.

Understanding geomorphic setting, both in terms of landforms and processes, is essential to interpreting terrestrial and aquatic ecosystems of the Hoh valley.

LITERATURE CITED

Bodhaine, G. L., and D. M. Thomas.
1964. Magnitude and frequency of floods in the United States. Part 12. Pacific slope basins in Washington and upper Columbia River basin. U.S. Geol. Surv. Water-Supply Pap. 1687. 337 p.

Crandell, D. R.
1965. The glacial history of western Washington and Oregon. In The Quaternary of the United States. p. 341-353. H. E. Wright, Jr., and D. G. Frey, eds. Princeton Univ. Press, Princeton, N.J.

Heusser, C. J.
1974. Quaternary vegetation, climate and glaciation of the Hoh River valley, Washington. Geol. Soc. Am. Bull. 85:1547-1560.

Ecology and Habitat Requirements of Fish Populations in South Fork Hoh River, Olympic National Park

J.R. Sedell, P.A. Bisson, J.A. June, and R.W. Speaker

ABSTRACT

Four distinct running water habitats are defined and examined on the South Fork Hoh River--main river channel, river off-channel areas, terrace tributaries, and valley wall tributaries. Species compositions, densities, and total fish biomasses are distinctly different for each habitat examined. Habitat formed by the main river channel and its tributaries is controlled by the valley terrace structure and the modifying effects of large woody debris. Without large wood, spawning and rearing habitat quality would be poorer, even in the large channel. Virtually all rearing of salmonid fish occurs in river off-channel areas and tributaries. The main channel is used mainly for spawning and migration. Fish densities and biomasses are highest in streams along the valley floor. Alteration of these areas will have greatest impact on fish production.

J. R. Sedell, U.S. Department of Agriculture, Forest Service, Forestry Sciences Laboratory, 3200 Jefferson Way, Corvallis, Oregon 97331; P. A. Bisson, Weyerhaeuser Company, 505 North Pearl Street, Centralia, Washington 98531; J. A. June, Department of Fisheries, University of Washington, Seattle, Washington 98195; and R. W. Speaker, Department of Fisheries and Wildlife, Oregon State University, Corvallis, Oregon 97331.

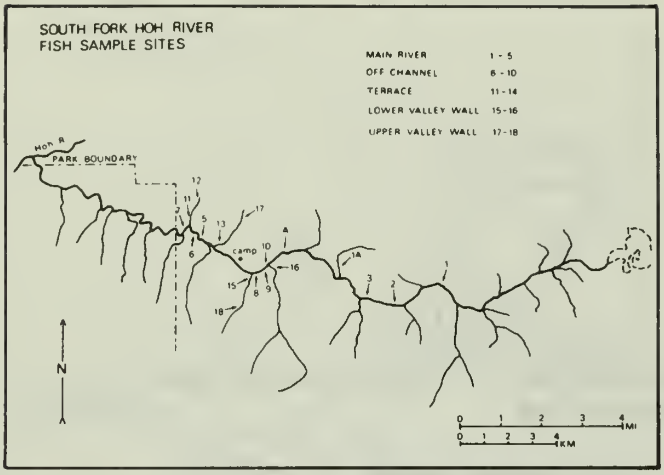


Figure 1.--Location of fish sample sites on the South Fork Hoh River and the tributaries.

INTRODUCTION

Stream ecosystems are adaptations to interacting geologic forces (hydrology and fluvial forms and processes) and biotic modifiers (riparian vegetation and large downed trees). Diversities of flow velocities, organic input quality and quantity, storage and processes of organic materials, and habitat types are all directly affected. The major interest in the South Fork Hoh River stems from the fact that the headwaters flow from a glacier, resulting in a channel that has many migrating point bars and a continual supply of glacial flow sediments in suspension. At present, stream ecologists have no benchmark descriptive data for naturally sediment-rich streams. We know very little about aquatic habitats and how they are formed in pristine sediment-rich river valley systems. For these reasons, a description of this river in the Olympic National Park provides a needed and significant baseline for stream ecologists and fisheries managers in the Pacific Northwest.

Our part of the South Fork Hoh River "pulse study" was to examine fish populations in relation to the four previously defined habitats (main river channel, river off-channel areas, terrace tributaries, and valley wall tributaries (see Swanson and Lienkaemper, and Ward and Cummins in this report)). Species compositions, densities, and total fish biomasses were defined for each habitat type. With each habitat type, we obtained a description of the pools, channel stability, and role of large woody debris in the formation and stability of the habitat.

MATERIALS AND METHODS

A beach seine was employed for sampling salmonid populations in the main stem South Fork Hoh River. A 600-volt backpack electric shocker was used to sample off-channel and tributary sites. A single pass method was used on 5 main stem sites and a two pass removal method on 13 off-channel and tributary areas (fig. 1). Fish collected from each site were anesthetized with MS 222 (tricaine methanesulfonate), identified to species, measured for fork length, and allowed to recover before release. Fish biomass estimates were calculated from length-weight relationships determined previously from other watersheds. Density, biomass, and species distribution were related to each habitat parameter and important relationships noted.

Each site was measured for length and width, and wetted surface areas were computed. Debris obstructions were counted; and their role in bank stability, fish cover, and flow deflection was noted. The stability of each site was determined using USDA Forest Service "Stream Reach Inventory and Channel Stability Evaluation," (Pfankuch 1975) and categorized as very stable, stable, or unstable. The quality of pools in each site was determined using a modified Duff and Cooper (1976) technique assessing pool volume and cover.

A survey of spring-summer chinook salmon spawning sites was conducted during September and October. Foot surveys were the primary method; helicopter surveys were utilized during peak spawning activity.

Gravel samples were taken at two sites on the main river and one tributary site. Likely spawning gravels were sampled with a McNeil cylinder and Koski Plunger. A total of 25 samples was analyzed volumetrically for percent material less than .85 mm.

HABITAT DESCRIPTIONS

Main River Channel

The main river was wide and shallow (table 1). Wet widths ranged from 8 to 10 meters in summer to 20 to 40 meters in winter. The main channel meandered within a wide channel of exposed gravel bars that averaged 100 m wide. The large cobble substrate was very unstable, gravel bars being formed and destroyed continuously. Some bank cutting was evident along the steep south valley side slope. The water was turbid due to suspended glacial material. Organic material transfer and storage was low. Edges of the main channel accumulated sediments, but riffle areas were relatively clean. The channel gradient was 2 to 3 percent and mainly riffles and deep runs with some pools associated with debris. Riparian vegetation did not significantly influence the course of the river; however, bank cutting caused inputs of large woody debris which would accumulate on bars and cutting edges to deflect the river flow (see Swanson and Lienkaemper in this report). Debris accumulations provided little fish cover in the main river, but diverted water through off-channel overflow areas.

Table 1--Physical characteristics of the major aquatic habitats in the South Fork of the Hoh River, autumn 1978

Habitat type	Physical characteristics			
	Stability	Debris	Pool	Riffle
Site number			Percent	Percent
Main river sites (1,2,3,4,5)	Poor stability, winter and spring floods cause cutting and deposition.	Debris collected in small jams at cutting areas on bends in river, stabilizes banks and deflects flow.	20	80
Off-channel sites (6,7,8,9,10)	Good stability except during extremely high main river flows.	Debris accumulations on main channel creates and maintains most off-channel area. Individual pieces offer fish cover.	70	30
Terrace tribs. sites (11,12, 13,14)	Very good stability low gradient, debris-protected banks.	Individual pieces reduce cutting of banks and offer fish cover.	80	20
Lower valley wall tribs. sites (15,16)	Very good stability high gradient, boulder- and debris-stabilized banks.	Individual pieces help stabilize banks and form some plunge pools.	40	60
Upper valley wall tribs. sites (17,18))	Excellent stability high gradient steep banks, boulder-formed plunge pool and falls.	Large individual pieces offer some bank stability and with boulders form plunge pools and fish cover.	90	10

Off-Channel Areas

Channels subsidary to the main river were located within the active exposed lower flood plain. Some were caused by debris accumulations on bars in the main channel, river flow was diverted, and a gravel berm was created downstream from the debris. Water percolated through the gravel berm and debris to create a side channel between the gravel berm and the bank opposite the main river flow channel. Other off-channel areas were intermittent overflow channels that received ground water from the main river and nearby terrace. Most were subject to direct flows during freshet periods; others became completely isolated during summer low flow periods. Flow velocities are lower than the main river, and water percolated through berm gravels carries reduced suspended sediment. Organic input from terrace vegetation and overflow accumulations from main river floods collected in off-channel pool bottoms. In the absence of heavy shading and the scouring effects of suspended glacial material, algal growth was promoted. High insect production occurred in these organically rich areas (see Ward and Cummins in this report). Woody debris and undercut bank vegetation provided cover for fish and created pool areas. Downstream tailouts offered good spawning locations.

Terrace Tributaries

Terrace tributaries result from spring networks on the flat valley flood plain and from tributaries draining the valley side slopes and continuing across the terraces to the main river. Many terrace tributaries paralleled the secondary river channels that cut through the lower terrace areas within the flood plain before emptying into the main river. These streams were very stable and had low gradients, slow velocities, and channel widths from 1 to 5 m. They were composed predominately of pools and short sections of riffle. Pools accumulated large amounts of riparian leaf litter from the dense forest canopy, thus producing abundant aquatic insects (see Ward and Cummins in this report). Pool substrate was primarily fine sediments, although riffles were relatively clean. Banks were stablilized by live vegetation and downed woody debris. Debris and undercut banks provided excellent fish cover.

Lower Valley Side Wall Tributaries

Side slope streams originated from runoff on the steep valley walls. The lower ends of these streams flowed on the upper terrace areas from the north valley walls and directly into the main Hoh River from the south valley walls. These streams were typified by high gradients with alternating sections of riffles and plunge pools over woody debris and boulder obstructions. The substrate ranged from fine materials deposited above some of the debris to large boulders and bedrock in the plunge pools. Lower valley side wall tributaries had clear water and high flow velocities. Organic material from the riparian vegetation was transported downstream or retained by the debris and boulders. The banks were steep but stable due to deeply embedded large boulders and debris. Productivity of algae and aquatic invertebrates was lower than other streams because the dense forest canopy limited light entry and scour forces of the rapidly moving water created considerable shear stress.

Upper Valley Side Wall Tributaries

Upper side slope streams had very steep gradients and high velocities. They flowed over a series of stair-step pools and cascades set up by boulders and large downed trees. The substrate was large cobbles, boulders, and bedrock, with some gravel accumulation at the tails of pools and behind embedded debris. The water ran clear and the high velocity transported downstream any organic material not retained by the boulders and debris. The steep banks with high boulder content and large downed trees maintained the stable riffle-cascade-pool nature of the channel. Low benthic algal production from reduced light penetration resulted in low densities of aquatic insects, except for some wood gougers.

THE ROLE OF LARGE ORGANIC DEBRIS IN THE MAINTENANCE OF FISH HABITATS

Large organic woody debris in streams of the spruce-hemlock forest have profound effects on channel form and fluvial processes, particularly in small sized streams. Woody debris (10-cm diameter) plays different roles in each of the habitat types described. We examined the extent to which debris intervened in the stream channel. We grouped debris interventions in the channel into three groups, depending on the extent of direct influence within the channel width. The groups were influences of one-third to two-thirds of the channel width and complete channel dams, bridges, or other direct interventions.

On large, main channels, the woody debris accumulated at the head of gravel bars and often regulated water movement into off-channel areas (see Swanson and Lienkaemper in this report). Even the largest trees seldom crossed the entire channel parallel with the flow or in accumulations below the curving bend of the river. We found large debris intervened up to one-third the channel width 10 times, two-thirds the channel width once, and crossed the main channel twice along 900 m of main river stem. Half of the debris interventions influencing up to one-third the channel were at the head of off-channel areas. The root wads of single trees in the main channel that were parallel to the flow sometimes deflected the flow toward other debris or boulders. These convergences of flow created pools, and the tailouts of these pools provided excellent spawning habitat for chinook salmon. The importance of a large downed tree to fish habitat in the stream channel cannot be minimized, even though it may intervene less than one-third of channel width. Their role as flow deflectors contributed to the diversity of flow velocities that helped maintain spawning areas free of the fine fluvial sediments which could smother incubating fish eggs.

Off-channel habitat responding to intervention by large woody debris were highly variable. Often the flood flows had resulted in accumulated debris along the edge of the main channel, deflecting the flow and producing large backwater pools or alcoves. These off-channel alcoves often were important juvenile coho and steelhead rearing areas. These kinds of habitat were created by 100 percent intervention of the debris. The secondary and tertiary channels frequently took the form of small off-channel streams. The woody debris intervening in these channels was derived primarily from sources upstream and was deposited through a major storm event. For every 100 m of off-channel area, there were 12 interventions of wood one-third of the channel water or less, two interventions influencing up to two-thirds of the channel, and four interventions which dammed or influenced the complete channel width. About 60 percent of these channels were high quality pools formed by debris and were primary rearing areas for large juvenile coho and steelhead.

Terrace tributaries had accumulated large wood from their surrounding forest. These were predominately pool environments except at their lower reaches where they merged with the main channel. For every 100 m of terrace tributaries channel, large woody debris less than one-third channel width category intervened nine times, four times for influences from one-third to two-thirds channel width, and three times the entire channel width was dammed or influenced directly. These pieces of wood were quite stable, and supported nurse trees and dense moss communities.

The valley wall tributaries had a stepped profile created by sediments stored behind large wood in the channel. Pools usually were created by debris and provided primary rearing areas for many of the river system's cutthroat trout. In general, for every 100 m of this stream type, we found 11 wood interventions influencing the channel width one third or less; 5 times the entire channel was dammed or directly influenced.

In general, the main channel and off channel areas utilized trees and large pieces of wood that originated upstream from where the accumulations were found. The forest along terrace tributaries and valley wall tributaries contributed the wood usually found in these streams. Debris was a major contributor to fish habitat for both spawning and rearing requirements of the different fish's life cycles. Although we tend to ignore debris influence on the physical channel of large rivers, its role in forming and maintaining anadromous fish habitats is very important regardless of size of streams. Without large trees being transported by the main channel, the very productive off-channel areas would maintain levels of invertebrate and fish densities and biomasses much lower than they now do.

Large trees or wood in streams do not have to dam a stream channel completely to have a major influence on fish habitat. The majority of debris intervening on channels influenced only one third or less of the channel width. This was enough to create diverse stream velocities, pocket pools, and cover, which resulted in stable and diverse fish habitat conditions.

LIFE HISTORIES OF SALMONID FISHES IN THE SOUTH FORK HOH RIVER

Mountain Whitefish - Prosopium williamsoni

Whitefish were taken only from the main river channel itself; no specimens were collected from off-channel or tributary areas. Within the main channel, whitefish probably frequented deeper runs and pools where they fed upon aquatic invertebrates. Car, Clemens, and Lindsey (1967) report that this species spawn in October and November, their eggs hatching around March. The mountain whitefish is not anadromous and apparently completes its entire life cycle within the main river channel.

Dolly Varden - Salvelinus malma

Most individuals of this species were collected from the main river channel, but a few juveniles were taken from off-channel areas. Larger adult fish have been known to feed extensively on small fish, including migrating smolts. Immature Dolly Varden feed mainly on aquatic invertebrates. This species is known to be anadromous in some cases, but we did not determine if the population in the South Fork Hoh was anadromous or resident. Dolly Varden are occasionally caught by anglers fishing the main river channel. With the exception of some off-channel rearing, this species also is confined to the main stem.

Coastal Cutthroat Trout - Salmo clarki

Cutthroat were captured in the tributaries, the majority of individuals being taken from the upper valley wall tributaries where they were collected from plunge pools and undercut banks and logs. All life history stages feed on aquatic and terrestrial invertebrates, although larger adult cutthroat will feed on small sculpins. Sea-run cutthroat populations occur in most coastal river systems of Washington, but scale analysis of samples collected from South Fork Hoh River specimens during this study indicated that the population was composed entirely of resident fish. This species spawns in the spring, probably in the valley wall tributaries. Emergence of young-of-the-year occurs in June and July. It is safe to conclude that cutthroat trout make up the great majority of the sport fishery in the valley wall tributary systems, and it is likely that more cutthroat are caught in the South Fork Hoh River drainage than any other sport fish.

Steelhead Trout - Salmo gairdneri

Juvenile steelhead were taken from the main channel, off-channel, terrace tributaries, and lower valley wall tributaries. No adult steelhead were captured, although they were known to be present in the main stem. Steelhead are anadromous rainbow trout; and two distinct runs are known to occur in the South Fork Hoh River--one run takes place in summer and a second run occurs in winter. Although the timing of the two runs is separate and individuals belonging to the runs are known to have certain genetic differences, spawning times show considerable overlap. Depending upon time of entry into fresh water, spawning can occur from December to May, although peak spawning activity probably takes place in February and March. Steelhead fry are usually out of the gravel by June, and most rearing occurs in off-channel and valley wall tributary areas. Size distribution of juveniles suggested that most steelhead spend 2 years in the South Fork habitat before smolting and migrating to sea. A notable sport fishery for adult steelhead exists on the main stem, and some legal-sized juveniles are probably caught in the tributaries along with cutthroat.

Coho Salmon - Oncorhynchus kisutch

Juvenile coho were found mainly in river off-channel and terrace tributary areas, where deep slow-moving water occurred. At the time of the study (late September), adult coho migration into the South Fork had not yet taken place; the bulk of the run was expected in November. Adult spawning probably occurs in both the main stem and valley wall tributaries; but juveniles were conspicuously absent from these areas, having moved to pools adjacent to the river and into the terrace tributaries for rearing. Young coho were heavily dependent upon terrestrial invertebrates for food, particularly during summer months. They usually spend over a year in fresh water before smolting in spring and returning as adults after 2 years at sea. The contribution of coho to the South Fork sport fishery probably is small.

Chinook Salmon - Oncorhynchus tshawytscha

No juvenile chinook were taken at any sample loction in the South Fork Hoh River; apparently this species does not rear there in early autumn. Like steelhead, there are two adult runs in the river--one in late spring and the other in autumn. We observed adults spawning in the main river channel and in the lower reaches of the larger tributaries. These were presumably spring-summer run fish. Approximately one-third of the total spring-summer chinook run entering the Hoh River drainage spawns in the South Fork. Of these, about two-thirds spawn in the main and secondary river channels and one-third spawn in the terrace tributaries and the lower valley wall tributaries (table 2). Juvenile emergence occurs in late winter; and young-of-the-year move downstream to rear in other parts of the system, principally in the estuary.

Table 2--Spring-summer chinook salmon spawning

Percent of total redd count	River channel and river off-channel	Terrace tributaries	Valley wall tributaries
170	65	22	13

FISH POPULATION DENSITY, BIOMASS, AND GROWTH

The largest density and biomass of salmonids occurred in the off-channel habitat (table 3). Steelhead young-of-the-year (fry) represented 79 percent of the total density (fig. 2A and 2B). Coho salmon fry made up 19 percent of the total density, but were larger than the steelhead fry (table 4) and accounted for 56 percent of the total biomass. Steelhead, although more abundant than coho, comprised only 39 percent of the biomass. Cutthroat trout and Dolly Varden contributed little to salmonid density and biomass. Sculpin density was one-fourth of the total salmonid density, but sculpin biomass was equal to that of the salmonids.

The terrace tributaries possessed the second highest density of salmonids, yet density was less than half of the off-channel areas. Coho were the most abundant, and made up 76 percent of the total density, followed by cutthroat trout, with 17 percent of the total density. Coho fry were smaller in the terrace tributaries (table 4) than in the off-channel areas but, because of their higher density, accounted for a biomass nearly equal to that of coho in off-channel areas. The coho biomass was 62 percent of the total salmonid biomass in the terrace tributaries. Cutthroat trout averaged 35 percent of the total salmonid biomass. Steelhead fry were both small and rare in the terrace tributaries. Sculpins in terrace tributaries were smaller than those of off-channel areas but were twice as abundant.

Upper valley side wall tributaries had a total salmonid density lower than both off-channel area and terrace tributaries; total salmonid biomass was lower than the off-channel areas but higher than the terrace tributaries. Cutthroat trout represented 97 percent of the density and 92 percent of the biomass of salmonids collected. Cutthroat biomass was relatively high, and the wide range of sizes represented in the population indicated that several year-classes were present. A single steelhead yearling was the only other salmonid captured in upper valley wall tributaries. Sculpins were present, but their density and biomass was less than a third of those found in the off-channel and terrace tributaries.

Lower valley side wall tributaries had lower total salmonid density and biomass than the off-channel, terraces and upper side wall tributaries. Steelhead trout fry dominated both density and biomass. The mean length of steelhead fry exceeded that found in the terrace and off-channel areas. Several coho salmon and cutthroat also were captured. Cutthroat trout made up only 13 percent of the total salmonid density but comprised 31 percent of the biomass due to two large yearlings in the sample. Sculpin density and biomass were lower than all the other habitat areas.

The main stem South Fork Hoh River had the lowest salmonid density and biomass of all habitats. A total of seven steelhead trout (three fry and three yearlings), one Dolly Varden, and one mountain whitefish were captured. No sculpins were collected. Total salmonid density was estimated to be less than .001 fish/m^2, and biomass was less than .01 g/m^2. Mature adult chinook salmon were observed migrating in the main stem to spawning sites in the off-channel areas and lower terrace tributaries, but none was collected in the seine samples. These low values probably reflect inefficient sampling techniques. While we believe the main river channel to possess fewer fish, the values in tables 3 and 4 and figure 2A should be considered tentative. Accurate main stem estimates will require a more effective large river sampling program.

Generally, the densities of fish in the South Fork Hoh River were lower than reports for other streams on the Olympic Peninsula outside of the Park. Coho density in off-channel and terrace tributaries were similar to values reported for some tributaries to the nearby Clearwater River (Edie 1975). Cutthroat trout density on the upper and lower valley wall tributaries were less than a third of that reported for lower gradient headwater streams in the Clearwater and Bogachiel Basins (Lestelle 1978, Martin et al. 1978).

Gravel samples taken in the main channel and lower valley wall tributaries (J. Cederholm, pers. comm.) were similar in percentage of fine sediment to pristine watershed in the Clearwater River. This is important, since the Clearwater is not a glacier-fed stream.

The importance of off-channel ponds in the successful rearing of coho salmon smolts in a river system has been documented by Peterson (1979). While our brief study did not include any ponds of the size and depth studied by Peterson, we feel that the numerous flood-influenced off-channel pools and alcoves along the river's border provided the bulk of the juvenile anadromous fish rearing areas.

MANAGEMENT IMPLICATIONS

Biological productivity of the South Fork Hoh River is largely dependent on stable terrace stream networks and valley wall tributaries. These productive zones can be protected from abuse by proper campground and trail placement. Major trails should avoid paralleling terrace tributaries; they would be better placed on lower valley walls. Avoiding terrace tributary areas for locating campgrounds also will help protect the streams. Existing road networks could be re-examined to determine if biologically diverse and productive areas have been cut off from the floor influence of the main channel and if fish passageways to and from off-channel rearing sites have been blocked.

Table 3--Density and biomass of fish species collected in stream habitats of the South Fork Hoh River, autumn 1978

	Coho		Steelhead		Cutthroat		Dolly Varden		Total salmonid		Sculpin		Total fish	
Habitat type	#/m2	g/m2	#/m2	g/m2	#/m2	g/m2	#/m2	g/m2	#/m2	g/m2	#/m2	g/m2	#/m2	g/m2
Main river	--	--	.003	.01	--	--	.001	.01	.004	.01	*	*	*	*
Off-channel	.070	.33	.286	.23	.001	.02	.003	.02	.364	.59	.087	.59	.451	1.18
Terrace tributaries	.118	.26	.010	.01	.026	.15	--	--	.154	.42	.156	.47	.310	.89
Lower valley wall tributaries	.003	.01	.044	.08	.007	.04	--	--	.053	.13	.029	.09	.082	.22
Upper valley wall tributaries	--	--	.002	.04	.065	.48	--	--	.067	.52	.042	.13	.109	.64

*Sculpins were not sampled in the main river; therefore, we omitted computation of total fish density and biomass.

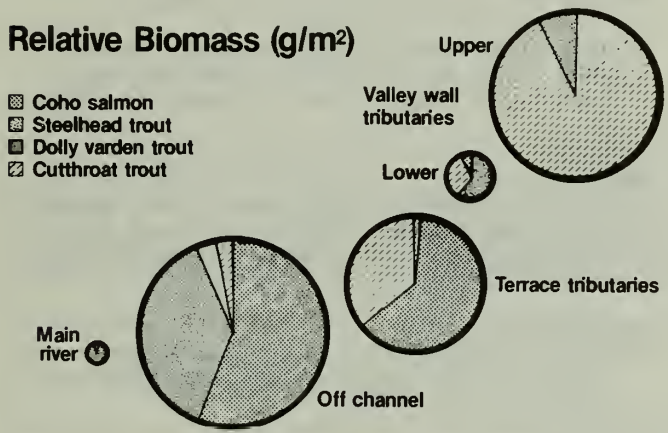


Figure 2A.--Average biomass of salmonid fishes in the South Fork Hoh River drainage system.

Figure 2B.--Average density of salmonid fishes in the South Fork Hoh River drainage system.

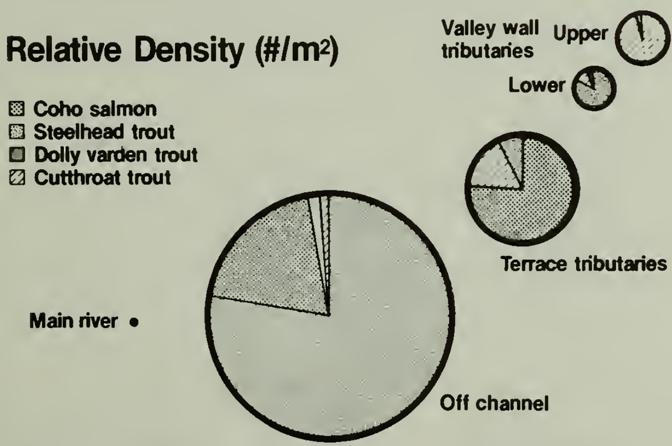


Table 4--Mean and range of length in millimeters of four species of fish collected in five aquatic habitats of the South Fork Hoh River, autumn 1978

	Species			
Habitat type	Coho	Steelhead	Cutthroat	Sculpin
Main river	--	125.0 (50-131)	--	--
Off-channel areas	73.6 (55-101)	42.0 (31-70)	113*	68.7 (24-117)
Terrace tributaries	57.3 (40-85)	36.3 (31-41)	77.0 (51-138)	57.0 (44-97)
Lower valley wall tributaries	68.5 (61-76)	51.3 (33-67)	74.0 (42-120)	55.0 (40-110)
Upper valley wall tributaries	--	131*	79.0 (38-170)	53.0 (41-95)

*Only one individual captured.

The Olympic National Park provides a full range of pristine river systems which can be used as a bench mark for thousands of square kilometers of adjacent altered river systems. There is a basic need in the State of Washington and throughout the Nation to improve both the systems we manage and the system we manage with. Aquatic biologists lack comprehensive knowledge of pristine systems with relatively unmanaged fish population. The information we collected is of the kind needed for understanding the functioning of aquatic ecosystems. Moreover, it allows us to begin comparing the condition of pristine systems with the condition of similar, but altered, basins to develop an understanding of the control mechanisms and stability features of aquatic systems. An understanding of pristine watersheds should lead to more meaningful interpretation of the processes and effects of both natural and artificial habitat alteration and will also help promote more effective habitat improvement programs.

ACKNOWLEDGMENTS

We are grateful to Phil Peterson, Steve White, Jeff Cedarholm, Bill Wood, Vickie Era, Brian Joannason, and Ray Palmason for technical assistance. Our paper also benefitted from discussions with Fred Swanson, U.S.D.A. Forestry Sciences Laboratory, Corvallis, Oregon, and Milt Ward, Ken Cummins, and Stan Gregory of Oregon State University.

LITERATURE CITED

Carl, G. C., W. A. Clemens, and C. C. Lindsey. 1967. The freshwater fishes of British Columbia. Br. Columbia Prov. Mus. Handb. No. 5. 192 p.

Duff, D. A., and J. L. Cooper. 1976. Techniques for conducting stream habitat survey on Natural Resource Land. U.S. Dept. Interior, BLM Tech. Note 283. 72 p.

Edie, B. G. 1975. A census of juvenile salmonids of the Clearwater River Basin, Jefferson County, Washington, in relation to logs. M.S. thesis, Univ. of Wash., Seattle. 86 p.

Lestelle, C. L. 1978. The effects of forest debris removal on a population of resident cutthroat trout in a small headwater stream. M.S. thesis, Univ. of Wash., Seattle. 85 p.

Martin, D. J., S. T. White, W. T. Foris, J. A. June, and E. O. Salo. 1978. Bear Creek streamside timber removal study; Progress Report 1978. Progress Rept., Fisheries Res. Inst., Univ. of Wash., Seattle. 61 p.

Peterson, P. 1979. The role of spring ponds in the winter ecology and natural production of coho salmon on the Olympic Peninsula, Wash. M.S. thesis, Univ. of Wash., Seattle.

Pfankuch, D. J. 1975. Stream reach inventory and channel stability evaluation. U.S.D.A For. Serv. Reg. 1, Missoula, Mont. 26 p.

Relationships Within the Valley Floor Ecosystems in Western Olympic National Park: A Summary

Jerry F. Franklin, Frederick J. Swanson, and James R. Sedell

ABSTRACT

The major findings of the South Fork Hoh River research team emphasize interrelationships among components of the Olympic valley-bottom ecosystems. Geomorphic structures provide the basic template for both terrestrial and aquatic communities. Vegetation has significant reciprocal impacts on geomorphic processes, however, and is a major element in formation of the most productive aquatic habitats. The South Fork pulse illustrates accomplishments possible with intense, short-term interdisciplinary research efforts and the valuable functions National Parks can perform as benchmark areas to compare with exploited land systems.

Other papers in this report consider geomorphology, forest communities, Roosevelt elk, and aquatic habitats and communities. There is some tendency to lose sight of the entire valley-bottom ecosystem in these more component-oriented presentations, however.

The objective in this paper is to racapitulate the major findings of the South Fork research pulse with an emphasis on interrelationships among various components and processes. We also suggest broader implications for Park management and point out how the Park is serving as a control or baseline site for interpreting man's impacts on adjacent managed landscapes and establishing guidelines for improved management. National Parks provide the rare opportunities to study natural, undisturbed, valley-bottom forests and river ecosystems.

Jerry F. Franklin and Frederick J. Swanson, U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station, Forestry Sciences Laboratory, 3200 Jefferson Way, Corvallis, Oregon 97331; and James R. Sedell, Weyerhaeuser Company, Forest Research Laboratory, 505 N. Pearl Street, Centralia, Washington 98531.

GEOMORPHIC RESULTS

Landforms can be viewed as the template on which the terrestrial and aquatic communities of the valley-bottom ecosystems develop. While geological processes determine the initial conditions, biological processes are significant modifiers. Vegetation-geomorphic interactions are particularly important in the cases of small streams and river bars and terraces which are entirely the interplay between vegetation and fluvial processes.

Woody debris creates some of the most conspicuous vegetation influences on geomorphic processes. Fluvial processes mobilize large amounts of woody debris, particularly by undercutting and uprooting trees on forested alluvial flats and higher terraces. Stabilized debris in the main river channel is important in setting up gravel bars, protecting pioneering vegetation from high flows and from buffeting by floated organic debris, and regulating flow into river side channels, thereby creating the especially productive off-channel aquatic habitat. Woody debris in off-channel and tributary habitats also provides physical stability (Swanson 1980), a diversity of biological habitats, and an ecosystem energy base both by retaining fine allochthonous material and directly through decomposition (Cummins 1980).

Four major categories of aquatic habitat are identifiable in river valleys: the main river channel with fast, turbid, silty water; river off-channel, such as side channels partially isolated from the main stream; terrace tributary, which is low gradient and generally carries clear, slow-moving water; and valley wall tributary, typically a high gradient stream with clear, fast water. Geomorphic, hydrologic, and vegetation factors combine to determine the basic types and arrangements of aquatic habitats.

AQUATIC RESULTS

Off-channel and terrace tributary habitats are of overwhelming importance for productivity of aquatic ecosystems of the South Fork and similar, broad, alluviated valleys in western Washington. These relatively protected sites have abundant, diverse food resources for both invertebrates and fish. Coho and cutthroat trout use these areas for rearing. Terrace tributaries provide important shelter when the main channel is in flood.

Glacial silt limits productivity of some parts of the main channel ecosystem, but not others. Primary production in fast water areas of the channel is severely limited by the scouring action of silt and fine sand being transported in suspension much of the year. Silt deposition in the few quiet water sites of the main channel prevents full utilization by invertebrates of these potentially very productive areas. Spawning is not greatly reduced by the fine sediment because hydraulic conditions prevent excessive accumulation in the major spawning sites where pools tail out into the heads of riffles.

Productivity of valley wall tributaries is limited by the extremes of high and low flows and the dense conifer overstory which reduces primary production by shading. Limited pool area and the difficulty of moving from pool to pool along these high gradient channels constrain use of valley wall tributaries by fish.

Large organic debris is an important factor in shaping microhabitats in each of these types of stream environments.

TERRESTRIAL RESULTS

The forest communities are strongly related to landform or geomorphic surface. *Alnus rubra* stands dominate youthful fluvial deposits and mature *Picea sitchensis*-*Tsuga heterophylla* forests occupy older, higher surfaces. In the study area, different *Picea*-*Tsuga* communities are formed on upper and lower terraces, although dominant trees on both terraces are approximately the same age and cannot be considered successionally related. The vegetation-landform model proposed for the main fork of the Hoh River (Fonda 1974) does not fit the South Fork, which probably reflects historical differences in timing and patterns of forest disturbances such as floods.

Mature valley-bottom *Picea sitchensis*-*Tsuga heterophylla* forests contrast with those found elsewhere in the coastal *P. sitchensis* zone of the Pacific Northwest (Franklin and Dyrness 1973). Stands, especially those on lower terraces, are open with relatively low density of above-ground biomass and numerous openings of up to a hectare or more. *Picea* is reproducing successfully, earning recognition as a climax tree species on these sites. While the relative success of *Picea* and *Tsuga* reproduction appear to have oscillated over the past century, there is no evidence that either is going to be replaced successionally. Grazing by Roosevelt elk is a factor that may favor survival of *Picea* reproduction over that of *Tsuga*, but grazing is almost certainly not the sole cause of variation in reproductive success. Wind and floods appear to be the major environmental factors disrupting these valley-bottom forests, while wildfire appears to be inconsequential.

Coarse woody debris is an extremely important structural feature of the terrace forests. Woody debris occupies much of the forest floor and contains large masses of carbon and nutrients. Reproduction of trees on older terrace surfaces is confined almost exclusively to rotten logs and associated stumps and root wads. Logs vary significantly in their value as nurseries depending upon log species, decay state, and terrace level. Forest renewal is dependent on seedbeds of coarse woody debris.

APPLICATIONS

The South Fork of the Hoh River appears to be the archetype of the western Olympic Mountain river valley ecosystem. Fluvial landforms and processes, mature *Picea*-*Tsuga* terrace forests, and valley-bottom aquatic habitats are well represented. The valley habitats have undergone minimal modification from adjacent mountain sideslopes and river tributaries in comparison with the other four major river valleys of the western Olympic Mountains. It therefore seems appropriate to manage and utilize the South Fork valley as a primary site for research on Olympic rainforests and associated streams.

Recognition that off-channel and terrace tributary habitats are aquatic hotspots and essential to anadromous fish in the Olympic river valleys has implications for managers inside and outside the Park. Park managers should locate trails, roads, and other developments so as to have minimum impact on these features. Resource managers outside the Park should appreciate the importance of providing off-channel and terrace tributary habitats with at least as much protection as the main channel. Rehabilitation of such habitats may be essential in areas where they have been destroyed by logging or road construction activities.

The significance of woody debris is further documented for both scientists and resource managers. Debris can now be seen to play important roles in larger streams and rivers, roles which must be accounted for by land managers in programs of riparian management and stream cleanup. The role of woody debris as critical seed bed in coastal forest types has implications on lands managed for timber production as well as on lands reserved from development.

CONCLUSIONS

The South Fork study demonstrates the use of a National Park and Biosphere Reserve as a benchmark site for scientific research and a control area for adjacent manipulated landscapes. The only remaining natural examples of river valleys in the coastal region are within Olympic National Park. The knowledge gained in the pulse study has extended our understanding of northwestern ecosystems to a distinctive variant (the rain forest) and a larger scale (river drainage).

Finally, the pulse in the South Fork of the Hoh River demonstrates the numbers and types of data that can be gathered by an interdisciplinary research team in a short time span. A successful project is based on substantial logistical planning and a balance between careful definition of objectives and ample opportunity to pursue promising leads and for serendipitous discoveries.

LITERATURE CITED

Cummins, Kenneth.
1980. The multiple linkages of forests to streams. *In* Richard Waring, ed. Proceedings, 20th Annual Biology Colloquium. Oregon State Univ. Press. Corvallis, OR. In Press.

Fonda, R. W.
1974. Forest succession in relation to river terrace development in Olympic National Park, Washington. Ecology 55(5):927-942, illus.

Franklin, Jerry F., and C. T. Dyrness.
1973. Natural vegetation of Oregon and Washington. USDA For. Serv. Gen. Tech. Rep. PNW-8, 417 p., illus. Pac. Northwest For. and Range Exp. Stn., Portland, OR.

Swanson, Frederick J.
1980. Erosion as an ecosystem process. *In* Richard Waring, ed. Proceedings, 20th Annual Biology Colloquium. Oregon State Univ. Press. Corvallis, OR. In Press.

Introduction and Dispersal of Mountain Goats in Olympic National Park

Bruce B. Moorhead and Victoria Stevens

ABSTRACT

Although native to the Cascade Range of central Washington, the mountain goat, Oreamnos americanus, was introduced to the Olympic Mountains of northwestern Washington by man prior to creation of Olympic National Park. There is no historical evidence of goats in the Olympic Mountains before release of 11 or 12 from Canada and Alaska between 1925 and 1929.

Dispersal of goats is traced in the last 50 years from release sites near the present north Park boundary. Moving east and south the population apparently reached the southern edge of the mountains (50 miles (80 km) distance) by about 1960. It is presently distributed throughout the Olympic Mountains in over 700 square miles (1 800 km^2). Ninety percent of the occupied habitat is in the Park.

Bruce B. Moorhead, Science and Technology Group, Olympic National Park; and Victoria Stevens, College of Forest Resources, University of Washington.

INTRODUCTION

Through its management policies, the National Park Service seeks to perpetuate and restore native ecosystems of plants and animals wherever possible. The presence of an introduced or exotic species in a National Park and its effect on the native ecosystem may require historical as well as scientific documentation prior to proposal of management plans (United States Department of the Interior 1978). This paper reviews the historical absence of mountain goats in the Olympic Mountains and their introduction by man prior to creation of Olympic National Park in 1938. It traces the dispersal of goats within the Park and their present distribution.

STUDY AREA

Olympic National Park is located on the Olympic Peninsula of Washington State, along the northwest coast of the conterminous United States. The Park is nearly 900,000 acres (365 000 ha) in size and occurs as two units: the interior Olympic Mountains, and a Pacific coastal area fronting the Pacific Ocean for over 50 miles (80 km). The climate is wet-maritime with a steep precipitational gradient resulting from the abrupt rise of the Olympic Mountains, 25 miles (40 km) inland and over 7,900 feet (2 400 m) in elevation, and the consequent interception of moist, westerly winds off the Pacific Ocean. Annual precipitation ranges from 80 to 200 inches (200 to 500 cm) along the western slopes and valleys to a "rain shadow" of about 20 inches (50 cm) on the northeast side of the mountains. With such abundant moisture and a cool climate, massive mixed-coniferous forests occur in over 50 plant communities between sea level and glaciated peaks.

The interior Olympic Mountains are deformed sedimentary rocks of Tertiary age, ringed on three sides by marine volcanic basalts of the Crescent Formation. A dome-like uplifting combined with glaciation and water erosion to shape the mountains in steep loosely arrayed peaks and ridges, from which 10 major watersheds radiate to the adjoining marine coasts. The Crescent Formation is exposed in high ridges and outcrops, which may descend 3,200 feet (1 000 m) or more and provide excellent cliff habitat for mountain goats.

METHODS

Historical data about goat releases were compiled from notes, correspondence, and newspaper clippings found in Olympic National Park and Olympic National Forest files. A major source was the Port Angeles Evening News (hereafter PAEN; the name changed to Daily News in 1972). Many long-time residents and mountaineers provided early goat observations. L. Lack of Port Angeles and C. Anderson, former Olympic National Forest biologist, kindly made available observations of goat distribution in the 1960's. More recently, goat sightings have been reported annually by Park Rangers, State wildlife agents, and backcountry visitors on provided forms. In 1972, the senior author initiated foot and aerial surveys to chart the distribution of the population. Between 1972 and 1976, 35 goats were color-marked on Mount Angeles, in the north central mountains, to provide some known reference about goat movements. Since 1977, an intensive mark-and-release project has been underway to examine goat population dynamics and their effect on the native ecosystem. The present paper, while benefiting from this work, is primarily historical and based on data available for the period 1925 to 1975.

RESULTS

Historical Occurrence of Mountain Goats in Washington

Mountain goats are mountain-antelope of Eurasian origin. Their ancestors apparently migrated to North America over a million years ago via the Bering Land Bridge connecting Siberia with Alaska. Dispersal south followed the nearly continuous chain of mountains across Western North America, and the expansion and retreat of continental glaciers (Cowan and McCrory 1970). In the last 10,000 years, as the climate warmed and continental glaciers withdrew northward, goat distribution has progressively been restricted to high mountain retreats in the Pacific Northwest, including Washington.

The fossil record of mountain goats is scant. Remains have been found in only eight widely dispersed localities in North America (Harrington 1971). In Washington, the only evidence is fossil horn fragments found at Washtucna Lake (Whitman County) in the eastern part of the State (Matthew 1902, Harrington 1971). The recent distribution of mountain goats in Washington, on the other hand, is well-documented by historical records and observations throughout the Cascade Range of central Washington, from the Canadian border south to Mount Adams (Johnson 1977). The initial record is probably by Lewis and Clark. In 1805 they reportedly saw hides and blankets woven from mountain goat hair by Indians along the Columbia River (Burroughs 1961).

In the isolated Olympic Mountains of northwestern Washington, however, no early faunal remains or ethnographic evidence of mountain goats have been reported (C. Gustafson, Department of Anthropology, Washington State University; and P. Amoss, Department of Anthropology, University of Washington, pers. comm.).

A composite list of early scientific collections of mammals on the Olympic Peninsula was assembled by Scheffer (1946). In 1897, a group of noted taxonomists, including C. Merriam, E. Preble, and V. Bailey, explored the Olympic Mountains. In 1898, a party from the Field Museum in Chicago explored the Olympic Mountains, collecting over 500 mammal specimens (Elliot 1899). Neither of these expeditions revealed any evidence of mountain goats. In a comprehensive account of Washington mammals, Dalquest (1948) makes no mention of goats in the Olympics. He limits their distribution to the Cascade Range, with one exceptional record from northeast Washington. Scheffer (1946)

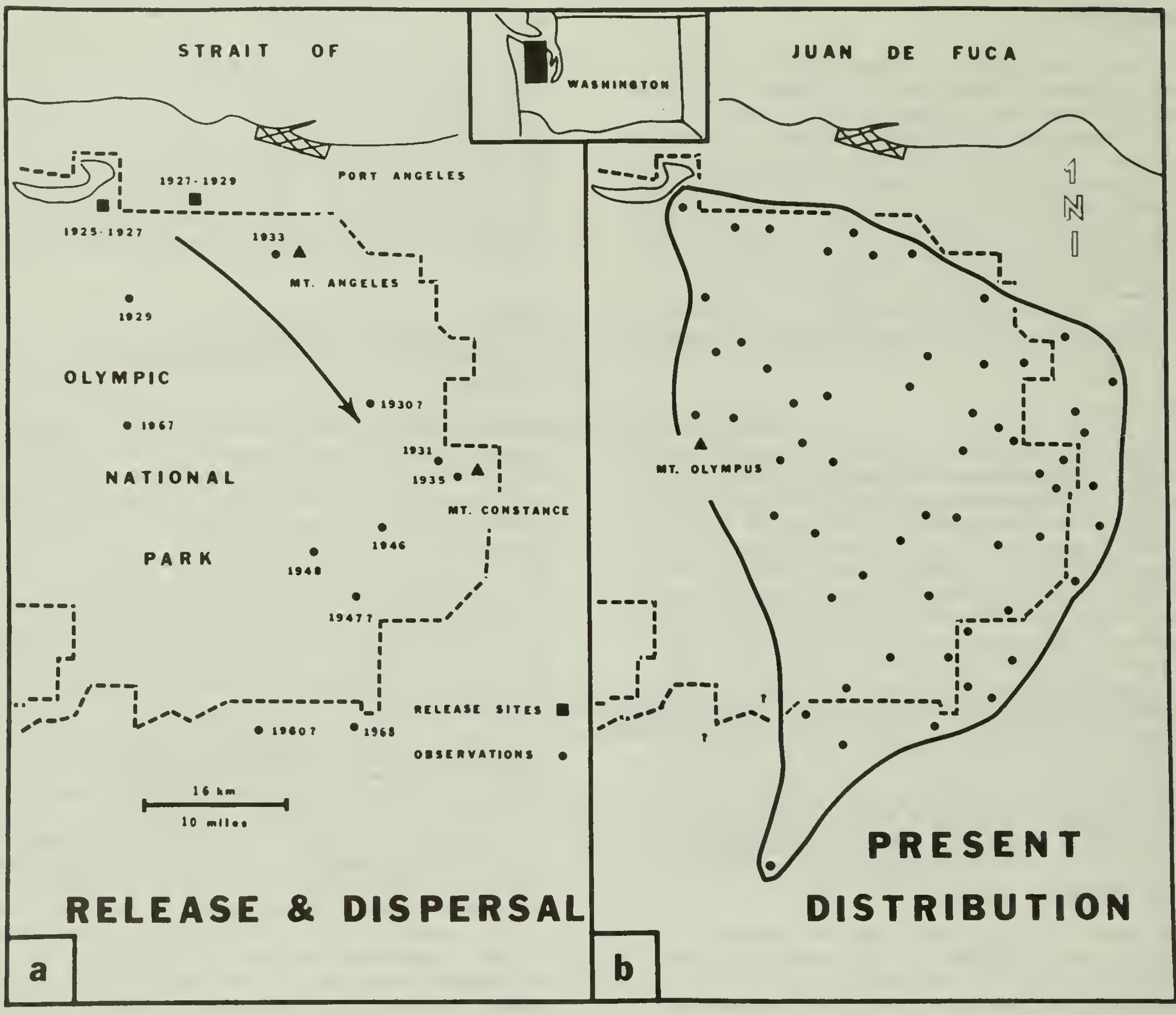


Figure 1.--Distribution of mountain goats in Olympic National Park, Washington: a) release and dispersal, b) present distribution.

states that goats were released in the Olympic Mountains from sources outside the State. Johnson and Johnson (1952) in their checklist of Olympic Peninsula mammals, treats them as an introduced species that is slowly increasing and spreading rather widely.

Goat Releases on the Olympic Peninsula

Late in the 19th Century, Roosevelt elk abundance declined on the Olympic Peninsula under pressures of settlement and market hunting. In 1909, to protect the interior mountains and elk, President Theodore Roosevelt proclaimed Mount Olympus a National Monument, under the administration of the U.S. Forest Service. By the 1920's, elk were apparently increasing under protection. County and Federal officials received requests from State Parks and even Alaska for elk. Local residents and officials considered the terrain south of Port Angeles to be ideal for mountain goats. Exchanges were conceived to send elk calves north and mountain goats south (PAEN January 2, 1925).

The first four goats were obtained from British Columbia. They were released January 1, 1925, along the northern edge of the Olympic Mountains near Lake Crescent (PAEN January 2, 1925; Webster 1925) (fig. 1a). The record of other releases is less clear (Webster 1932). In either 1927 or 1929, seven or eight goats from Alaska were released, all but two again near Lake Crescent. The latter were apparently released 8 miles (13 km) to the east, in the Elwha River valley near Baldy Ridge. A diary kept by one of the participants, Clallam County game warden Van Welch, is quoted later in a newspaper account (PAEN November 4, 1947). No other official records have been found. Welch indicated that all goat releases after 1925 occured in 1929.

Later accounts, however, report that after 1925, goats were released in 1927 or 1929. A letter dated May 7, 1938, from Alaska Game Commissioner F. Dufresne, recalls eight animals from Alaska being released in 1927, two from the Chugach Mountains near Anchorage and six from southeastern Alaska. Welch's diary says six goats were from Juneau and two from Cordova, Alaska, in 1929 (PAEN November 4, 1947). Correspondence signed by Park Superintendent P. Macy on October 6, 1947, also relates that one of the eight Alaskan animals died enroute.

Thus 11 or 12 mountain goats were released in the Olympic Mountains between 1925 and 1929. Seven or eitht were from Alaska, four from British Columbia. Early accounts refer to the animals released as "pairs," although no official records were kept of the number of males and females.

In exchange for these goats, eight young Roosevelt elk were shipped from Port Angeles in 1928 and established on Afognak Island as the only elk population in Alaska (Troyer 1960).

Goat Dispersal 1925-75

During the 1930's, groups of up to 12 goats were occasionally reported on the slopes of Mount Storm King above Lake Crescent (PAEN November 4, 1937). Observations during this period also indicate that goats were dispersing away from the release area. They were reported on Mount Appleton in 1929 (8 miles (13 km) south of Lake Crescent); on Mount Angeles in 1933 (16 miles (26 km) east); at the headwaters of the Dungeness River in 1931 (35 miles (56 km) east); and on Mount Constance in 1935 (37 miles (60 km) east) (fig. 1a).

Newspaper and Ranger reports suggest that mountain goats were established in small numbers by the early 1940's in the northern mountains and along the east Park boundary. By 1947 they were observed annually on Mount Anderson, 33 miles (53 km) south of Lake Crescent in the interior mountains. Observations by Olympic National Forest personnel indicate occasional sightings of goats south of the Park boundary prior to 1960 and annually thereafter (C. Anderson, B. Beckstead, pers. comm.). Although scant in supportive detail, these records suggest a dispersal east and south from Lake Crescent of up to 1 to 2 miles (2 to 3 km) per year, reaching the east Park boundary within 10 years and the south boundary in about 30 years.

During the 1960's and 1970's, goat observations were obtained from all sectors of the Olympic Mountains, although mainly the eastern half of the Park and lands adjoining in Olympic National Forest (fig. 1b). No goats were reported in the central Bailey Range or around Mount Olympus until the late 1960's. This high, central massif has the heaviest annual snowfall (150 to 200 inches (380 to 500 cm)), which may have slowed dispersal into the area. Few people (including scientists) visited the Bailey Range until the 1970's, which could also account for fewer reports. The most distant record of goat dispersal was an animal sighted in 1973 near Grisdale, Washington, 10 miles (16 km) below the south Park boundary and about 50 miles (80 km) south from Lake Crescent.

CONCLUSIONS

Scheffer (1946) and Dalquest (1948) discuss the isolation of the Olympic Mountains from the Cascade Range of central Washington, and the effect of intervening Puget Sound lowlands on the migration of certain mammals to this northwestern corner of the State. The Olympic marmot (Marmota olympus) is apparently a preglacial alpine mammal. Other alpine mammals found in the Cascade Range but not in the Olympics include the bighorn sheep (Ovis canadensis californiana), the pika (Ochotona princeps), and the golden-mantled ground squirrel (Citellus lateralis). Several authors have indicated that lowlands and broad valleys were barriers to mountain goat dispersal elsewhere (Klein 1965, Cowan and McCrory 1970, Harrington 1971). It seems reasonable to conclude that lowland and water barriers separating the Olympic Mountains from the Cascades were broad enough to prevent mountain goats and certain other mammals from natively migrating to the Olympics. In any case, there is neither historic nor prehistoric evidence to suggest that goats were ever native to the Olympic Peninsula.

Introduction of mountain goats by man in this century has successfully established a population on the Olympic Peninsula. Their dispersal has coincided with rock outcrops of the Crescent Formation, which surrounds the inner Olympic Mountains on three sides and, in general, has less snow than the interior mountains. Goats are now found in over 700 square miles (1 800 km^2). An estimated 90 percent of the habitat occupied is in Olympic National Park.

LITERATURE CITED

Burroughs, R.
1961. The natural history of the Lewis and Clark Expedition. Mich. State Univ. Press, Lansing.

Cowan, I. McT., and W. McCrory.
1970. Variation in the mountain goat (Oreamnos americanus) Blainville. Jour. Mamm. 51(1): 60-73.

Dalquest, W.
1948. Mammals of Washington. Vol. 2, Mus. Nat. Hist., Univ. Kansas Pubs., Lawrence.

Elliott, D.
1899. Catalogue of mammals from the Olympic Mountains, Washington. Field Mus. Chicago, Pub. 32, Zool. Ser., 1:241-276.

Harrington, C.
1971. A pleistocene mountain goat from British Columbia and comments on the dispersal history of Oreamnos. Can. Jour. Earth Sci. 8(9): 1081-1093.

Johnson, M. L., and S. Johnson.
1952. Check list of mammals of the Olympic Peninsula. The Murrelet 33(3):32-37.

Johnson, R.
1977. Status and management of mountain goat in Washington, p. 41-46. In Proc., First Int. Mountain Goat Symp. W. Samuel and W. Macgregor, Eds. Fish and Wildl. Br. Prov. Brit. Columbia.

Klein, D.
1965. Post-glacial distribution patterns of mammals in the southern coastal regions of Alaska. Arctic 18(1):7-20.

Matthew, W.
1902. List of the pleistocene fauna from Hay Springs. Nebr. Bull. Amer. Mus. Hist. 16: 317-322.

Scheffer, V.
1946. Mammals of the Olympic Peninsula, Washington. U.S. Fish and Wildl. Serv., unpub. manuscript, Olympic Nat. Park Library, Port Angeles.

Troyer, W.
1960. The Roosevelt elk on Afognak Island, Alaska. Jour. Wildl. Manage. 24(1):15.

U.S. Department of the Interior.
1978. National Park Service. Management Policies, Chapter IV (Natural Resource Management).

Webster, E.
1925. Status of mountain goats introduced into the Olympic Mountains, Washington. The Murrelet 6:10.

Webster, E.
1932. Status of mountain goats introduced into the Olympic Mountains, Washington. The Murrelet 13:25.

Factors Reflecting Mountain Goat Condition and Habitat Quality: A Comparison of Sub-Populations in Olympic National Park

Victoria Stevens

ABSTRACT

An introduced population of mountain goats in Olympic National Park has provided the opportunity to study sub-populations of different densities and conditions. During the summer of 1979, nine sub-populations were sampled for reproductive rate, standard morphological measurements, blood values, fecal nitrogen, and foraging behavior. Sub-population differences in hematocrit, hemoglobin, and girth correlated with differences in reproductive rate. An increase in feeding throughout the summer unexpectedly related to a decrease in forage quality monitored by fecal nitrogen.

Victoria Stevens, Cooperative Park Studies Unit, College of Forest Resources, University of Washington, Seattle, Washington 98195.

INTRODUCTION

The population dynamics of an introduced ungulate on an island have been documented on several occasions (Scheffer 1957, Woodgerd 1964, Klein 1968). In the absence of predation, populations tend to follow a pattern of exponential growth until a resource becomes limiting, after which they may crash to a few individuals. National Parks are often relicts of natural vegetation in a sea of disturbed habitat. The mountainous regions of Olympic National Park in particular share with islands the attribute of isolation. However, the island is large enough for within-island dispersal to enter into the dynamics of an introduced species. Dispersal provides an outlet which may delay the effects of over-population.

The deliberate introduction of mountain goats onto the Olympic Peninsula more than 50 years ago has resulted in a population that now provides an opportunity to observe sub-populations at different chronological stages of development. A change in the density of a population and the impact of density on the habitat are the major results of longer establishment. Although the population was not studied in earnest until 1977, 52 years after the first introduction, it may be possible to reconstruct the pattern of growth and dispersal and predict the future size of the population by examining in detail differences in the sub-populations as they exist today. Visual differences between effects of goat density on habitats in different areas have been noted by laymen as well as scientists in the Park. More precise methods, however, for distinguishing relative impact on the habitats and the resultant change in the condition of individuals in the resident sub-populations are desirable. This approach seems promising in that both demographic and morphologic variations have been demonstrated between conspecific ungulate populations in different physiological condition (Nievergelt 1966, Geist 1971). The physiological condition of a sub-population is the average physical condition of the individuals making up the population; and although related to habitat quality, it may be studied directly in terms of physiological characteristics of the individuals.

An initial step in setting up a historical continuum of sub-populations is the determination of appropriate attributes to measure both condition of sub-populations and quality of habitats. This paper is the result of attempts during one summer to determine accurate indices.

METHODS

In each of four areas, data relating to animal condition and habitat quality were compared to the reproductive rate. Overall reproductive rate or fecundity was used as the indicator of relative sub-population condition (Klein 1970, Franzmann and LeResche 1978). Against this were compared standard morphological measurements and blood values for direct measures of goat condition. Fecal nitrogen and foraging behavior were tested as indices of comparative habitat quality.

Reproductive Rate

Reproductive rate was measured as the number of kids per 100 adult females 2 years or older. Two year olds were included as the lowest reproductive age parkwide since this age class demonstrated its ability to reproduce under favorable conditions in some sub-populations. Increased productivity may occur by three mechanisms: reduction in age of puberty (Caughley 1970, Markgren 1974), increases in litter size (Zuckerman 1953, Coop 1966, Markgren 1974, Caughley 1976) and an increase in ovulation rate (Allen and Lamming 1961, Coop 1966, Markgren 1974). An increase in reproductive rate may be related to nutrition (forage quality and availability) in all cases.

Standard Morphological Measurements

Some morphological measurements vary considerably with age while others remain stable throughout the adult life of the animal. Those that change with overall growth may indicate the relative condition of the sub-populations when statistical means are compared.

We baited goats with salt and captured them with a manually operated, rope leg snare. Their eyes were covered to reduce stress while we took measurements of total length, right horn length, right hind foot, girth, and weight. Unfortunately, weight had to be eliminated because of between population discrepancies in field technique. Horn growth positively relates to nutritional status in at least two bovids, Dall sheep (Bunnell 1978) and mountain goats (Foster 1978). Klein (1964) demonstrated differences in skeletal growth of deer depending on range differences.

Blood Values

While the goat was restrained, 30 mls of blood were taken from the jugular vein with a 19 gauge butterfly needle. The sample was divided among three vacutainer tubes, one containing the anti-coagulant EDTA (ethylene diamine tetra-acetic acid), and stored in snow until taken to a hospital laboratory in Port Angeles. The time between blood drawing and analysis was 12 to 24 hours. Parameters examined were red blood cell counts (RBC), hemoglobin (Hgb), hematocrit (Hmct), mean cell volume (MCV), white blood cell counts (WBC), calcium, and phosphorous.

The use of blood values to assess the condition of populations of wild mammals has increased in recent years (Lee et al. 1977, LeResche et al. 1974, Warren and Kirkpatrick 1978). Considerable work has been done relating specific parameters to condition and to external effects such as drugs and stress (Blankenship and Varner 1977, Franzmann and LeResche 1978, Karns and Crichton 1978, Scanlon 1979). Franzmann and LeResche (1978) noted a significant difference in some blood values between moose populations of different physiological condition measured by reproductive rate. They found that anemia (indicated by low hematocrit) was one of the best indicators of condition in moose and not significantly influenced by stress. Hematocrit is the number of red cells per volume multiplied by the mean cell volume. It can also be measured by packed cell volume. Other indicators of good condition in moose are Hgb, calcium, and phosphorous (Franzmann and LeResche 1978).

Fecal Nitrogen .

Between one and seven fresh fecal samples were collected during each visit to a sample area. These were predominately from adult females and were frozen until the end of the season when they were dried and ground. Nitrogen was determined by Kjeldahl analysis with a lithium sulfate digest (Parkinson and Allen 1975). Fecal nitrogen offers an index of forage protein content. Price (1977) found fecal nitrogen positively correlated to protein intake in the hartebeest. Although this correlation is not linear due to an increase in metabolic fecal nitrogen (MFN) with increased dry matter ingested (Gallup and Briggs 1948, Lancaster 1949, Hutchinson 1958) and an apparent increased true nitrogen digestibility with increased nitrogen intake (Hutchinson 1958), diets can be ranked using a fecal nitrogen index especially if dry matter intake can be assumed to be similar between diets.

Foraging Behavior

Foraging behavior was observed in each area to test the hypothesis that the amount of food ingested increases with an increase in forage quality; i.e., an increase in nitrogen and a decrease in fiber content. It was hoped this would provide an indirect means of evaluating range conditions either between seasons or between ranges.

The hypothesis is well supported in the literature. Ungulate feeding strategies are dominated by limitations of rumen size and rate of passage. Rate of passage and nutritive quality (protein content) increase with decreased fiber content (Balch and Campling 1965, McDonald et al. 1973, Milton 1979). Therefore, to keep the rumen full, more forage is likely to be ingested during early summer when the quality is highest.

In 1978 more than 5,000 systematic observations of goat activity were made in one area in the Park. These showed that goats steadily increased the amount of time per day spent foraging from early June through early September (Stevens 1979). Foraging was defined for the purposes of the 1978 observations, as either searching or feeding. The increase in absolute foraging time coincided with a decrease in forage quality as measured by plant phenology and as reflected in fecal nitrogen levels from the area. In the 1979 field season, we hoped to explain this contradiction with the above hypothesis by separating foraging time into actual feeding time and searching time. Perhaps as the resource becomes more patchy towards the end of summer, the goats spend more time searching for each bite but are actually spending less time feeding on the lower quality forage (fig. 1).

Foraging adult females were timed with a wrist watch and a stop watch. The stop watch was running only when the goat was taking a bite and chewing; it stopped when she was searching. The observation was terminated by any interruption in the foraging activity, when the goat went out of sight, or after 1 hour when a new subject was located and observed. The stop watch lapsed time divided by the wrist watch lapsed time and multiplied by 100 indicates the percentage of total foraging time spent actually feeding.

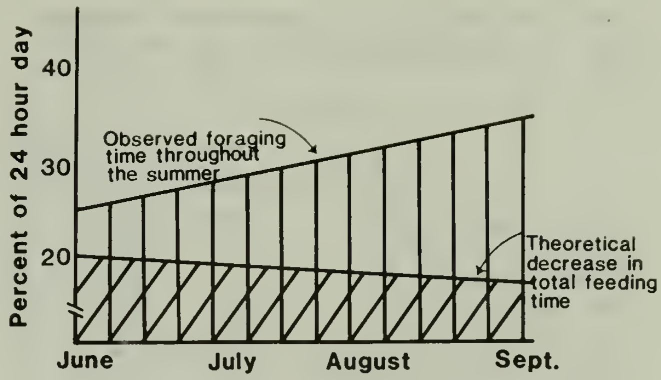


Figure 1.--A hypothetical explanation for the increase in foraging time documented during the summer of 1978 (perpendicular lines). As the forage quality declined, the amount of searching time increased relative to the amount of feeding time (diagonal lines). Theoretical search time is the difference between total feeding time and the theoretical feeding time.

RESULTS

Direct Measures of Goat Condition

Reproductive rate was used as an indicator of relative condition (table 1). The best correlation with reproductive rate among the parameters measured is with hematocrit (fig. 2). In addition, hemoglobin and girth positively correlate with reproductive rate when the statistical means for adult females in each sub-population are compared. Other measures show no correlation (tables 2 and 3). The small size of the sample in many of the smaller, more remote areas hinders statistical treatment of differences between populations. Since the largest difference occurs between Klahhane Ridge (the densest sub-population) and any other area, we have lumped all the values except those from Klahhane Ridge, including those from areas not specifically mentioned, in tables 2 and 3.

T-tests were used to compare means from Klahhane Ridge and means from the rest of the sub-populations. None of the morphological measurements was significantly different although girth had a tendency to be higher in sub-populations off Klahhane Ridge ($p < .18$). RBC, Hgb, and Hmct were significantly higher in the sub-populations with higher reproductive rates ($p < .001$).

Table 1--A comparison of reproductive rates between sub-populations in Olympic National Park, 1979

Area	Reproductive Rate[1]
Klahhane Ridge	59
Appleton Pass	60
Sawtooth Ridge	67
Royal Basin	75

[1]Kids per 100 adult females 2 years old and older.

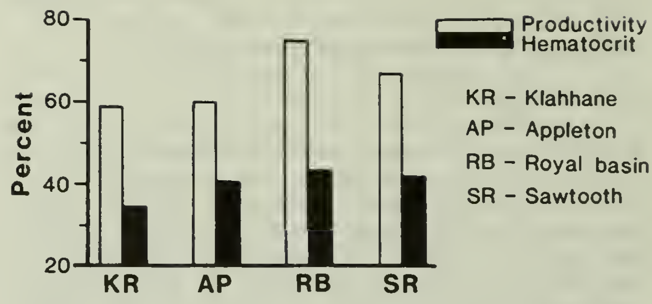


Figure 2.--A comparison of reproductive rate and hematocrit for each of four sub-populations in Olympic National Park in 1979.

Table 2--Mean blood values for adult females in four sub-populations of Olympic National Park, 1979

Group	N	Hematocrit	Hemoglobin	Total protein	Calcium	Phosphorus
			- - - - - gms/dl	- - - - -	- - - - mg/dl	- - - -
Population mean:						
(male and female)	60/59	37.68	13.06	6.6	10.2	5.5
female mean	41/41	38.63	13.09	6.5	10.0	5.3
Klahhane Ridge	17/17	34.53	12.21	6.6	10.0	5.1
Appleton Pass	4/1	40.75	13.9	7.1	10.6	7.2
Sawtooth Ridge	6/5	41.83	13.87	6.5	10.0	6.4
Royal Basin	8/8	43.50	14.25	6.6	9.2	5.1
Mean of all areas except Klahhane	24/23	41.54	13.73	6.5	10.0	5.4

Table 3--Morphological means for adult females (4 years or older), 1979[1]

Group	Total length	Hind foot	Girth	Horn length
	- - - - - -	- - - - - - cm	- - - - - -	- - - - - -
Klahhane Ridge	143.7 (7)	34.24 (7)	99.7 (7)	22.2 (7)
Appleton Pass	145.3 (3)	36.00 (2)	102.67 (3)	22.5 (1)
Royal Basin	148.5 (4)	34.50 (4)	106.25 (4)	20.75 (4)
Mean of all areas except Klahhane	143.8 (11)	34.40 (11)	103.09 (11)	21.33 (11)

[1]Number of individuals measured appears in parentheses.

Indirect Measures of Habitat Quality

Fecal nitrogen was used as a measure of forage quality because of the correlation between fecal nitrogen values and plant phenology noted during 1977 and 1978 in the Olympic Mountains (Driver et al. 1978). These values reflect the quality of the vegetation if it is assumed that the phenology of the plants dictate relative quality. When the plants are growing most actively, the nutrient quality of the vegetation is highest (Braun 1972). Fecal nitrogen values from Klahhane Ridge in the 1979 samples followed the expected curve, being highest in mid-June (fig. 3).

If forage quality can be measured between months on Klahhane Ridge using fecal nitrogen, it should be possible to measure differences in quality between areas, with the same general climatic regime, at similar time periods during the year (assuming similar dry matter intake). Figure 3 shows the values of fecal nitrogen for the four major sub-populations throughout the summer. The most complete data came from Klahhane Ridge which has been shown to have the lowest reproductive rate. The other three sub-populations also show decreasing forage quality throughout the summer, but the comparison with Klahhane Ridge is not clear. In two of the three areas, the early summer value is higher than Klahhane and the late summer value is lower indicating a more extreme change throughout the summer. If this is a reflection of the true forage quality, the higher reproductive rates in these areas indicate the higher relative importance of the early summer to the overall condition of the goats. A closer look at specific plants and parts of plants utilized between areas throughout the summer would be helpful.

Unexpectedly, the proportion of time spent feeding decreased with declining forage quality. Figure 4 shows how foraging behavior varied with fecal nitrogen (forage quality) on Klahhane Ridge. On Klahhane Ridge, where once again we have the most complete information, the amount of time spent feeding; i.e., the quantity of forage ingested (assuming a constant bite volume) decreases with increased forage quality. Ungulate feeding theory predicts a decrease in forage consumption with a decrease in quality because of the limitations of the digestive system.

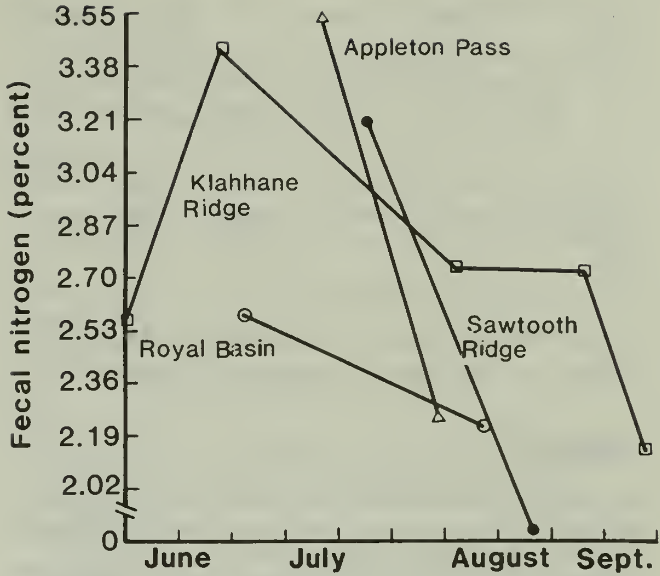


Figure 3.--A comparison of fecal nitrogen values from four sub-populations in Olympic National Park during the summer of 1979: Klahhane Ridge □, Royal Basin ○, Appleton Pass △, and Sawtooth Ridge ●.

Figure 4.--The relationship of the percent of foraging time actually spent feeding as fecal nitrogen (protein content of the forage) increases as demonstrated by mountain goats on Klahhane Ridge in 1979.

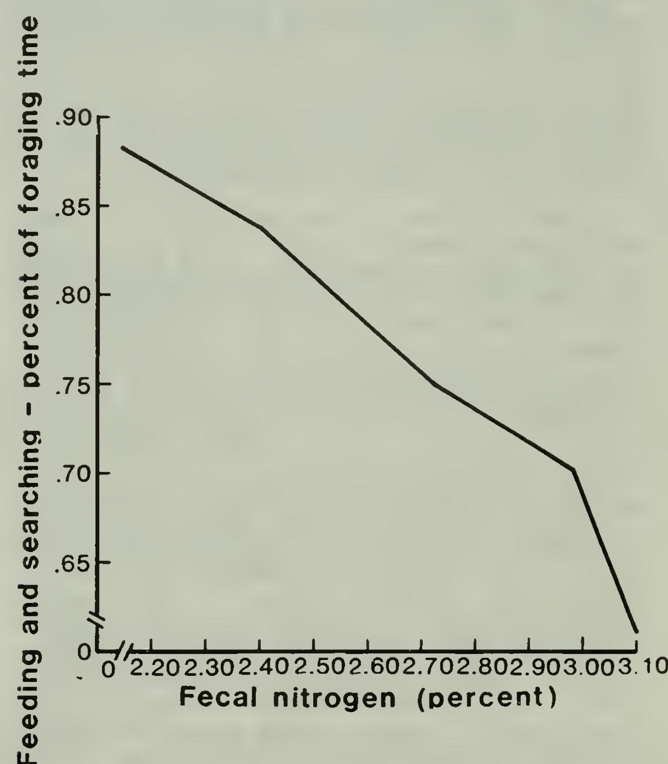


Table 4--Reproductive rates since 1976 on Klahhane Ridge

Year	Reproductive rate[1]
1976	78
1977	98
1978	25
1979	59
1980	72

[1]Kids per 100 females 2 years and older.

DISCUSSION

The measures which showed significant differences between sub-populations were blood values, parameters which reflect changes in condition most rapidly. Of all the morphological measurements taken, girth, while not showing statistical significance, showed the greatest difference between the populations of different reproductive rates. Skeletal measurements reflect the cumulative conditions of an individual throughout its life, whereas girth includes fat and muscle tissue--parameters more responsive to changes in immediate condition. This indicates that conditions on Klahhane Ridge have changed only recently relative to the other areas on the Olympic Peninsula, a conclusion supported by changes in reproductive rate on Klahhane Ridge over the last 5 years (table 4). Overall fecundity has gone from a high of 98 percent to 25 percent and has been recovering for the last 2 years (Stevens 1979, Stevens unpublished data). This rapid change in reproductive rate is consistent with the pattern observed in other introduced ungulate populations when a resource becomes limiting.

The inconclusiveness of the use of fecal nitrogen or foraging behavior as variables in quality comparisons may be a consequence of the small number of sample points which in turn reflects the difficulty in acquiring data in the more remote goat ranges in Olympic National Park. The unexpected trend in the foraging behavior with respect to forage quality points out either a major fault in the reasoning of ecologists studying ungulate feeding or an omission of some critical measurement between populations. The latter is strongly suspected since current theory has been supported repeatedly. The missing information may be the difference in the volume of bites throughout the summer. Bite volume was assumed to be constant; but as forage quality decreases, it may be advantageous for goats to be more selective and take only those parts of the plant having the highest nutritive value, thereby decreasing the size of bites. Smaller bite volume would necessitate more time feeding to ingest a given amount and would have been interpreted by us to mean higher overall forage quality.

The increased selectivity of the goats also would result in an artificially high fecal nitrogen level in relation to overall forage quality. This suggests a mechanism for testing the changes in forage selectivity by goats throughout the summer by comparing direct measures of nitrogen in plant samples to fecal nitrogen at several intervals during the summer. Further studies including the collection and analysis of plants for nitrogen content are necessary to evaluate the usefulness of foraging behavior as an index to relative forage quality, and therefore to the projected condition of the sub-population.

Selected blood values appear to be useful means for the evaluation of sub-population condition. It would be helpful, however, to have an index such as foraging behavior or fecal nitrogen to indicate possible trends in population condition. Measures which do not involve handling large ungulates are often more efficient and less costly as management tools.

ACKNOWLEDGMENTS

Appreciation is expressed to Lee Anne Ayres, Peter Wimberger, Marie Morin, and Angela Alston for invaluable assistance in the field. This research was funded by Olympic National Park and through the University of Washington Cooperative Parks Study Unit, contract no. CX-9000-7-0065.

LITERATURE CITED

Allen, D. M., and G. E. Lamming.
1961. Nutrition and reproduction in the ewe. J. of Ag. Sci. 56:69-79.

Balch, C. C., and R. C. Campling.
1965. Rate of passage of digesta through the ruminant digestive tract. In Physiology of digestion in the ruminant. R. H. Dougherty, ed. Butterworths, Washington, D.C. p. 108-123.

Blankenship, L. H., and L. W. Varner.
1977. Factors affecting hematological values of white-tailed deer in South Texas. Proc. Annual Conf. S. E. Assoc. Fish and Wildl. Agencies. 31:107-115.

Braun, H. M. H.
1972. Primary production in the Serengeti: purpose, methods and some results of research. Annales de l'Universite d'Abidjan, Section Biologique. 6:171-188.

Bunnell, F. L.
1978. Horn growth and population quality in Dall sheep. J. Wildl. Manage. 42:764-775.

Caughley, G.
1970. Liberation, dispersal and distribution of Himilayan Thar (Hemitragus jemlahicus) in New Zealand. New Zealand J. of Sci. 13:220-239.

Caughley, G.
1976. Wildlife management and the dynamics of ungulate populations. In Advances in Applied Biology. T. H. Coaker, ed. Academic Press, New York.

Coop, L. E.
1966. Effect of flushing on reproductive performance of ewes. J. of Ag. Sci. 67:305-323.

Driver, C. H., V. Stevens, and D. Pike.
1978. Olympic Mountain goat--annual report. Univ. of Washington, Cooperative Parks Study Unit. Contract no. CX-9000-7-0065.

Foster, B. R.
1978. Horn growth and quality management for mountain goats. Proc. of the Northern Wild Sheep and Goat Conf. Penticton. p. 200-226.

Franzmann, A. W., and R. E. LeResche.
1978. Alaskan moose blood studies with emphasis on condition evaluation. J. Wildl. Manage. 42:334-351.

Gallup, W., and H. M. Briggs.
1948. The apparent digestibility of prairie hay of variable protein content, with some observations of fecal nitrogen excretion by steers in relation to their dry matter intake. J. of An. Sci. 7:110-116.

Geist, V.
1971. Mountain sheep: a study in behavior and evolution. The Univ. of Chicago Press, 383 p.

Hutchinson, K. J.
1958. Factors governing fecal nitrogen wastage in sheep. Aus. J. of Agric. Res. 9:508-520.

Karns, P. D., and V. F. J. Crichton.
1978. Effects of handling and physical restraint on blood parameters in woodland caribou. J. Wildl. Manage. 42:904-908.

Klein, D. R.
1964. Range related differences in growth of deer reflected in skeletal ratios. J. Mammal. 45:226-235.

Klein, D. R.
1968. The introduction, increase and crash of reindeer on St. Matthew Island. J. Wildl. Manage. 32:350-367.

Klein, D. R.
1970. Food selection by North American deer and their response to over-utilization of preferred plant species. In Animal populations in relation to their food sources. A. Watson, ed. Brit. Ecol. Soc. Symp. 10:25-46.

Lancaster, R. J.
1949. Estimation of digestibility of grazed pasture from faeces nitrogen. Nature 163:330-331.

Lee, J., K. Ronald, and N. A. Oritsland.
1977. Some blood values of wild polar bears. J. Wildl. Manage. 41: 520-526.

LeResche, R. E., U. S. Seal, P. D. Karns, and A. W. Franzmann.
1974. A review of blood chemistry of moose and other cervidae with emphasis on nutritional assessment. Naturaliste Can. 101:263-290.

Markgren, G.
1974. Factors affecting the reproduction of moose (Alces alces) in three different Swedish areas. Int. Congr. of Game Biol. 11:679-690.

McDonald, P., R. A. Edwards, and J. F. D. Greenhalgh.
1973. Animal nutrition. Oliver and Boyd, Edinburgh.

Milton, K.
1979. Factors influencing leaf choice by howler monkeys: a test of some hypotheses of food selection by generalist herbivores. Am. Nat. 114:362-378.

Nievergelt, B.
1966. Der alpensteinbock (Capra ibex L.) in seinem Lebenstraum. Mammalia depicta. Verlag Paul Parey, Hamburg und Berlin. 85 p.

Parkinson, J. A., and S. E. Allen.
1975. A wet oxidation procedure suitable for the determination of nitrogen and mineral nutrients in biological material. Commun. Soil Sci. and Plant Anal. 6:1-11.

Price, M. R. S.
1977. The estimation of food intake, and its seasonal variation, in the Hartebeest. E. Afr. Wildl. J. 15:107-124.

Scanlon, P. F.
1979. Constraints in evaluating data from blood of wild animals immobilized by drugs. Presented at the 14th International Wildl. Congr., Dublin, Ireland. October.

Scheffer, V. B.
1957. The rise and fall of a reindeer herd. Sci. Mon. 73:356-362.

Stevens, V.
1979. Mountain goat habitat utilization in Olympic National Park. M. S. Thesis, Univ. of Washington, Seattle.

Warren, R. J., and R. L. Kirkpatrick.
1978. Indices of nutritional status in cottontail rabbits fed controlled diets. J. Wildl. Manage. 42:154-158.

Woodgerd, W.
1964. Population dynamics of bighorn sheep on Wildhorse Island. J. Wildl. Manage. 28:381-390.

Zuckerman, S.
1953. Breeding seasons of mammals in captivity. Proc. of the Zoolog. Soc. of London. 122:827-950.

Mother-Infant Interactions Among Free-Ranging, Non-Native, Mountain Goats (*Oreamnos americanus*) in Olympic National Park

Michael Hutchins and Craig Hansen

ABSTRACT

Preliminary results are presented on nursing behavior, weaning, and retention of older offspring. Nursing behavior was investigated on the assumption that a conflict of interest exists between mothers and offspring over the disposition of maternal resources during weaning. A relationship was found between the behavior of kids during nursing attempts and the behavior used by mothers to terminate attempts. Results suggest a progressive decrease in the overall rate of successful nursing attempts and mean duration of suckling bouts over time, especially between the 1st and 2d month following parturition. Several cases were identified in which females retained older offspring and continued to allow close physical contact, including nursing. Theoretical implications of these results are discussed.

Michael Hutchins and Craig Hansen, Department of Psychology, University of Washington.

INTRODUCTION

Studies of mother-offspring relationships among free-living animals have been accumulating steadily; however, many species still lack detailed investigation. Research of this kind is of great interest to behavioral ecologists who strive to understand the evolution of parental care and the role parent-offspring relationships play in the development of social behavior. In addition, there has been an increased appreciation of the potential for applying such information to the management of wild and captive animal populations (Geist 1971a, Cowan 1974, Lent 1974). Here we present data on mother-offspring relationships among a free-ranging, non-native population of mountain goats (Oreamnos americanus) in Olympic National Park, Washington. This preliminary analysis is based on data collected during a comprehensive, on-going study of mountain goat social biology and is far from complete in either its scope or conclusions. Three topics are discussed: nursing behavior, weaning, and the retention of older offspring.

The mountain goat is a large herbivore that typically inhabits rock outcrops and alpine meadows lying at or above timberline (Walker 1975, Rideout 1975). The mating system is polygynous; adult males and females live apart for most of the year, associating consistently only during the rut which occurs in late November and early December (DeBock 1970, Geist 1965). Gestation lasts about 178 days, and kids are born in late May or early June (Rideout 1974). Adult females typically isolate themselves at the time of birth, but on summer range they congregate with juveniles of both sexes and kids in loosely organized bands where a variety of social interactions has been observed (Brandborg 1955, Holroyd 1967, DeBock 1970). The natural distribution of O. americanus is restricted to the mountains of western North America (Cowan and McCrory 1970). Because of the relative inaccessibility and rugged nature of its habitat, it remains one of the least studied of the continent's big game animals.

STUDY AREA AND POPULATION

Olympic National Park is a 3 600-km^2 island of wilderness occupying a majority of the Olympic Peninsula in northwestern Washington State. The Olympic Mountains are uniquely isolated, being surrounded on three sides by salt water and by lowlands on the fourth. The mountains, which form the core of the Park, are dominated by 2 428-m-high Mount Olympus and represent a complex concentration of peaks, ridges, and valleys.

The region's climate is maritime and influenced heavily by the easterly flow of weather off the Pacific Ocean. Summers tend to be relatively cool and dry, and winters are relatively mild and wet. Precipitation patterns are influenced by topography; northern and eastern portions of the Park receive considerably less rainfall than do coastal areas. At high elevations, winter precipitation is usually in the form of snow.

Research efforts were concentrated on Klahhane Ridge which is located in the northeastern portion of the Park. This 1 829-m-high ridge is bounded by 1 950-m Mt. Angeles on the west and by 1 889-m Rocky Peak on the east. The area is geologically complex, being composed primarily of pillow basalt and volcanic breccia (Tabor 1975). It has been described as "excellent" mountain goat habitat, with rugged, steep terrain above timberline and sufficient vegetation for forage (Olmstead 1976). The ridgetop is narrow with the major vegetational habitats being distributed on north- and south-facing slopes. Vegetation of the area is dominated by stands of Krummholz and meadows composed of hardy alpine perennials.

No natural mineral licks occur within the study area, but the remains of a large artificial lick still exist. Park Service officials discontinued the practice of provisioning salt several years ago; but goats still use the area extensively in the late spring and early summer, apparently seeking minerals that have leached in the soil.

Several potential predators and competitors of goats occur in the Olympic Mountains. Although no conclusive evidence of predation has been discovered in the study area, possible predators include: the cougar (Felis concolor), bobcat (Lynx rufus), coyote (Canis latrans), black bear (Ursus americanus), and golden eagle (Aquila chrysaetos). Potential competitors include the abundant Columbian black-tailed deer (Odocoileus hemionus), Olympic marmot (Marmota olympus), mountain beaver (Aplodontia rufa), and snowshoe hare (Lepus americanus).

Mountain goats are not indigenous to the Olympic Mountains. The present inhabitants of the Park are descended from 11 or 12 individuals, which were released between 1925 and 1929 (see Moorhead and Stevens in this report). The animals were obtained from the Canadian Rocky Mountains near Banff, Alberta, and from two separate locations in Alaska. The absence of native mountain goats in the Olympic Mountains appears to be due to geographic isolation. The species is native to the Cascade Range, less than 160 km to the east. The Olympic Peninsula currently supports a population estimated to be close to 700 (Driver et al. 1979), and Klahhane Ridge has the highest concentration in the region. As many as 165 animals use the 13-km^2 summer range.

METHODS

Behavioral data were collected during 30-minute sample periods using a continuous sampling technique (Altmann 1974). Observations focused on identifiable mother-offspring pairs. Focal pairs were chosen at random, with the exception of females associating with yearlings or 2-year-olds, which were selected for their particular interest to the study.

To facilitate data collection, a behavioral inventory (ethogram) was formulated and a two- or three-letter phonic code was devised to represent each behavioral category (Appendix I). Time of occurrence (within each minute) and the type of behavior exhibited were recorded for each behavior of interest occurring during the sample period. Identity

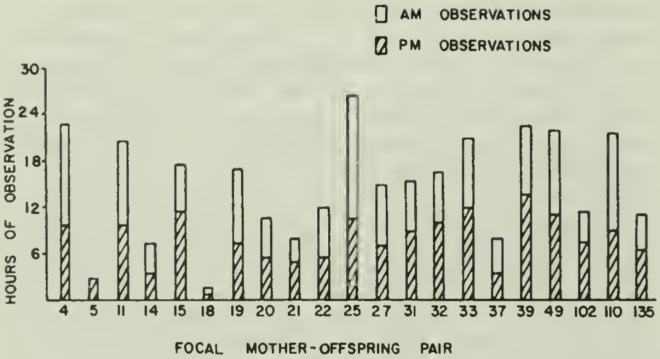


Figure 1.--Distribution of observation time by timeblock for each designated focal pair in 1979.

of the actor and recipient were recorded for each social behavior to preserve the directionality of the interaction. Uncoded behaviors of interest or behaviors occurring outside the sample period were recorded in the form of qualitative or "ad libitum" (Altmann 1974) notes.

Several rules were formulated to disperse samples as evenly as possible between subject pairs and to provide some measure of randomization. While in the field, observers made daily trips through the study area in an effort to locate focal pairs. If two or more pairs were encountered simultaneously, selection for observation was based on the number of previous samples collected within the timeblock (AM: 0000h to 1200h or PM: 1200h to 2400h). The pair having the fewest samples in that timeblock was consistently given preference, although a maximum of two samples/timeblock per day (one hour) was allowed on any one pair in 1978, and a maximum of four samples/timeblock per day on any one pair in 1979.

To minimize potential influence of observers on behavior, observations were conducted from a minimum distance of 10 m, except when special circumstances necessitated closer approach. This was sometimes necessary when animals moved through terrain that made following or observing difficult. Every effort was made not to disturb the animals, but no special attempts at concealment were deemed necessary since the animals were accustomed to people and relatively tolerant of their presence.

Over 100 animals have been captured and marked for individual identification. Capture was accomplished with the use of hand-held rope foot-snares placed in the vicinity of the salt lick. Animals were marked with Y-Tex Cattle ear tags. Tags were inserted into the pinnae with a specially designed applicator. The 8.4-cm-long plastic tags are seen easily from great distances, as they are bright yellow in coloration and have 2.54-cm-high black numerals on both sides. Females were tagged in the left ear and males in the right ear. Estimates of the age of adult females were obtained by counting the number of annual growth rings on the surface of the horns (Brandborg 1955).

RESULTS

This preliminary analysis is based on 54.5 hours of quantitative data collected on 9 mother-kid and 7 mother-yearling pairs from June 27 to August 23, 1978, and on 312 hours collected on 17 mother-kid, 2 mother-yearling, and 2 mother-2-year-old pairs from June 12 to August 24, 1979. The distribution of observation time for each focal pair during 1979 is presented by timeblock in figure 1 and indicates that observations were distributed relatively evenly between timeblocks, and between most focal pairs.

Nursing Behavior

The following analysis is based on a total of 461 nursing attempts recorded during continuous sampling in 1979, and is restricted to observations of mother-kid pairs. Offspring attempted to nurse when the mother stopped her forward progress during travel or foraging, when she arose from a reclining position, when she was preoccupied with another activity (e.g., agonistic interactions with other conspecifics, licking salt, or urination), and upon reunion of the pair after a brief separation. In some instances, offspring appeared to stimulate their reclining mothers to stand so that they could nurse. They accomplished this by various methods, usually by climbing on or over the mother, or by nuzzling the udder region. Nursing was not observed while the mother was lying down.

When offspring approached the udder during a nursing attempt; they did so in a variety of orientations with respect to the mother's body. We recognized four basic modes of approach: Side (S), Front (FR), Rear (R), and Run Around (RA) (Appendix I). A typical S approach is depicted in figure 2. In the overwhelming majority of cases, offspring approached the udder in a short, rapid run, although running approaches were never used during R-oriented attempts. During 1979, a majority of attempts (81.4 percent) were initiated from the mother's side. R attempts comprised 10.3 percent of the total; RA and FR approaches accounted for 6.5 and 1.9 percent. Besides being the most frequently utilized of modes, S approaches also had the highest success rate; 44 percent were successful (3 seconds or longer) compared with 27 percent of RA approaches, 22 percent of FR approaches, and 21 percent of R approaches.

While nursing, kids frequently exhibited "bunting" behavior--a vigorous butting of the mother's udder. An average of 4.7 bunts was delivered to the udder during each successful attempt.

All nursing attempts recorded during continuous sampling were terminated by mothers and not by kids. Four primary modes of termination were observed: Step-Over (SO), Walk-Away (WA), Rear Leg Stamp (RLS), and Jump-Away (JA). All other forms of termination were subsumed under an "other" category (Appendix I) and described in qualitative notes. The most common method utilized by females during 1979 was SO, which accounted for 63.7 percent of all terminations. Next most frequent was WA (27.6 percent), followed by RLS (4.3 percent) and JA (2.0 percent). The use of aggression to terminate nursing was very infrequent, representing only 1.5 percent of the total. This usually consisted of a low intensity horn present, horn swipe, or butt (Appendix I). Only four cases of maternal aggression involved any physical contact with the offspring. Only a single ad libitum observation was made in which an offspring appeared to terminate a bout on its own initiative, this occurred after a 23-second nursing bout.

In 1979 we found an apparent relationship between the approach mode used by kids and the termination mode used by mothers (fig. 3). When kids approached the udder from the side, either directly or in a RA, females terminated most frequently with a SO or WA. This was also true of FR approaches. R approaches were terminated most frequently with a WA or RLS. RLS was never used to terminate a FR or RA approach, and was used very infrequently during S approaches. JA was associated only with R and S approaches; maternal aggression was seen only during S approaches.

Retention of Older Offspring

During 1978 and 1979, we documented 22 separate cases in which identifiable females consistently associated with yearlings or 2-year-olds (table 1).

The mean estimated age of females associating with yearlings (N=22) was 5.7 years; that for females associating with 2-year-olds (N=2) was 6.0 years. Ages ranged from 3 to 10 years. Among yearlings, 9 of 25 (37.5 percent) were males, 8 of 24 (33.3 percent) were females, and 7 (29.2 percent) were not sexed. Among 2-year-olds, one was male and one was female.

We are convinced that these relationships represent cases of offspring retention in females that either lost their young of the year or did not conceive. For 4 of the 20 cases (20 percent) in 1978, direct evidence was available from tagging. Animals 51, 52, 53, and 54 were born in the spring of 1977 and tagged in August of that year while still associating with their mothers. During 1978, all continued to associate with their mothers through late August when observations were terminated.

The conclusion is also supported by a closer examination of behavior. While adult females generally tended to be antagonistic toward other conspecifics, all instances of retention were characterized by relatively frequent "friendly" contact, including nursing. During 1978, 10 attempts to nurse by five different yearlings were recorded during continuous sampling and an additional 11 attempts were observed during ad libitum observations. Including ad libitum observations, nursing was seen among 10 of 20 identifiable mother-yearling pairs. All attempts were directed toward the female with which that yearling had shown consistent association.

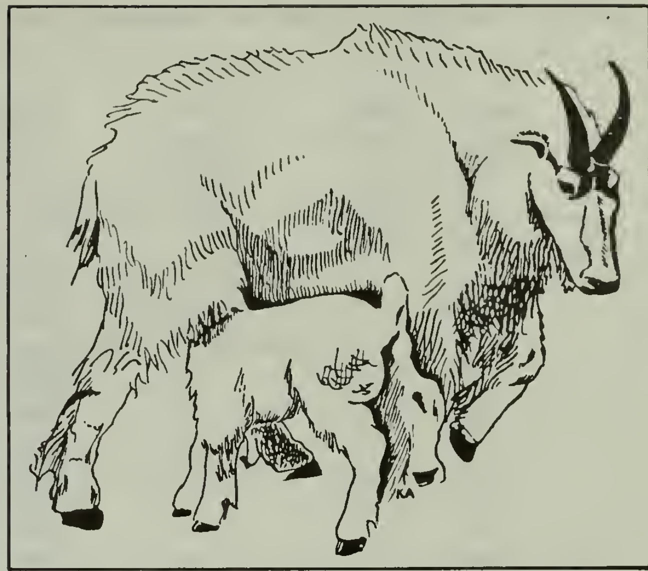


Figure 2.--Typical side-oriented nursing attempt.

Figure 3.--Approach mode of kid by termination mode of the mother.

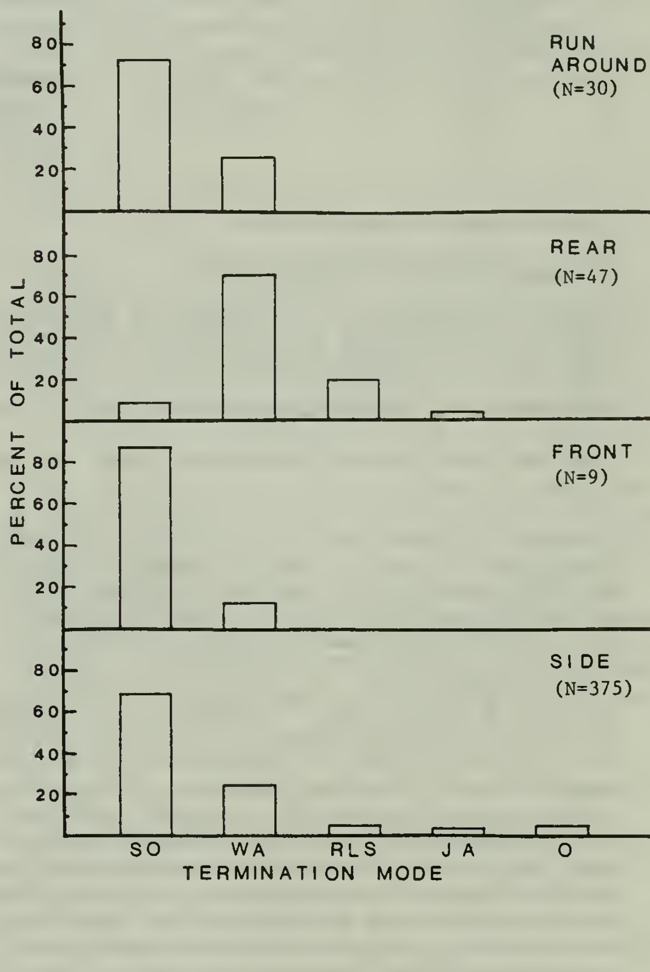


Table 1--Instances of offspring retention during 1978 and 1979

Year	Female tag number	Focal subject	Estimated age at time of retention	Offspring retained as	Offspring produced by year			Retained offspring number (sex)[1]	Date offspring tagged
					1977	1978	1979		
1978[2]	7	*	4	Yearling	1	0	0	44(M)	6-78
	13		4	Yearling	1	0	1	52(F)	8-77
	[3]17		7	Yearling	2	0	1	128(F), UM(?)	7-78
	18		5	Yearling	1	0	0	UM(F)	
	[3]19		7	Yearling	2	0	0	UM(?), UM(M)	
	21	*	7	Yearling	1	0	[4]1	107(M)	6-78
	23	*	7	Yearling	1	0	1	108(M)	6-78
	27		5	Yearling	1	0	0	78(M)	7-79
	28		4	Yearling	1	0	1	UM(?)	
	29	*	10	Yearling	1	0	1	115(F)	6-78
	32		3	Yearling	1	0	1	UM(?)	8-77
	33	*	7	Yearling	1	0	1	51(M)	8-77
	35		5	Yearling	1	0	1	UM(?)	
	36		4	Yearling	1	0	1	54(F)	6-78
	37	*	6	Yearling	1	0	1	43(F)	6-78
	38		6	Yearling	1	0	1	UM(?)	
	39		4-5	Yearling	1	[5]0	1	UM(M)	
	106	*	9	Yearling	1	0	0	117(M)	6-78
	109 (1-side)		5	Yearling	1	0	1	UM(?)	
	Green tag		?	Yearling	1	0	?	53(M)	8-77
1979	5	*	8	Yearling	1	1	0	UM(F)	
	14	*	5	Yearling	1	1	0	UM(F)	
	18	*	6	2-year-old	1	0	0	UM(F)	
	27	*	6	2-year-old	1	0	0	78(M)	6-79

[1]UM indicates an unmarked animal.

[2]Includes only identifiable females.

[3]Early in 1978, both 17 and 19 associated with two yearlings that were presumably their twins from the preceding year. 128 continued the association with 17 throughout the summer, while the unmarked yearling did not. Similarly, only one of 19's yearlings was seen with her in August.

[4]Kid born to 21 in 1979 disappeared in late July and was presumed dead.

[5]Kid born to 39 in 1978 disappeared in early June and was presumed dead.

Although the sample is admittedly small, the overall rate of successful nursing attempts/hr observed was higher in kids than retained yearlings (0.42 vs. 0.09/hr). The mean duration of a successful bout, however, was slightly higher for retained yearlings than for kids (6.5 vs. 5.8 s). Only 2 (18.2 percent) of all the 11 bouts by yearlings recorded ad libitum were "successful," one lasting for 3 seconds and the other for 4 seconds. Kids had a much higher rate of attempt/hour of observation (5.9 times) than did yearlings. During 1979, no instances of nursing were observed in the two mother-yearling pairs; but this may be a result of small sample size; both pairs disappeared early in the field season. One unsuccessful nursing attempt was observed between female 18 and her unmarked female 2-year-old; however, this relationship deteriorated after the 2-year-old was radio-collared. Radio-collars may interfere with the ability of mothers to recognize their offspring. We have observed radio-collared kids threatened by their own mothers for up to 3 days after their release. Tagging, however, appears to have no discernable affect on mother-kid relationships. We did observe six instances of nursing between female 27 and her retained 2-year-old male; two of these occurred during 24 hours of continuous sampling; the other four instances were recorded ad libitum. Two of the attempts were successful, one lasting 40 seconds and the other 12 seconds.

A variety of other social interactions occurred between females and retained offspring. Many resembled those observed between mothers and kids. For example, females allowed retained offspring to maintain a close relationship while using the salt lick. This often involved close physical contact, such as leaning against one another, or licking salt face to face in the same location. Instances of close physical contact at the lick were recorded for all females having retained offspring in 1979, and for five of seven focal mother-yearling pairs in 1978. No other individuals--regardless of age class--were tolerated in this manner. This observation is particularly significant since the incidence of overt aggression in the vicinity of this clumped, defensible resource was comparatively high.

Retained offspring continued to bed in close association with their mothers and to exhibit a strong following response. In two instances during 1979, retained offspring produced loud "bleating" vocalizations when separated from their mothers. The behavior closely resembled that exhibited by mother-kid pairs. For example, on June 23, female 18 and her retained 2-year-old female became visually separated from each other in fog. The 2-year-old vocalized three times in 4 minutes and appeared to be searching for her mother. Female 18 responded to her offspring's vocalizations by vocalizing herself; both were vocalizing just prior to their reunion and both ceased calling upon being reunited.

Eight instances of allogrooming (Appendix I) were recorded between three of nine mother-yearling pairs during continuous sampling in 1978; and although no instances were observed among mother-2-year-old pairs in 1979, the two mother-yearling pairs exhibited 17 instances during 10 hours of observation. Twenty-one of 25 total grooming bouts (84 percent) observed between mother-yearling pairs involved offspring grooming their mothers. In 1979, the unmarked female yearling of female 14 groomed her mother extensively. Nearly all of the 15 instances recorded (92 percent) were directed toward the mother's right eye which was seriously injured. No instances of allogrooming were observed between individuals who were not mother and offspring.

Females were never observed to actively defend older offspring from the threats of other conspecifics, but offspring occasionally moved into close contact with their mothers when approached by a dominant individual. During 1979, at least eight instances were observed in which retained yearlings or 2-year-olds moved into physical contact with their mothers following the approach or threat by another conspecific. This also was true for kids; mothers tended to defend their own personal space, and when their kids remained within this "sphere of influence," they were protected by her antagonism toward intruders. When they ventured away, however, they could be threatened without maternal retaliation.

Weaning

During 1979, females regularly terminated their offsprings' attempts to nurse 2 weeks after birth. Since systematic data were not collected until June 12, there was no way of determining the exact age at which mothers began to reject attempts on a regular basis; nor is it known if there is any individual variation in this regard. Assuming that most births occurred during the last week of May or 1st week of June, qualitative observations of nursing behavior suggested that terminations began very early, perhaps during the 1st week of life. Some females rejected nursing attempts as early as May 27 (M. Morin, pers. comm.).

Table 2--Nursing data by month for mother-kid pairs during 1979

	June	July	August
N of mother-kid pairs	17	17	[1]16
Hours of observation	70.5	112	103.5
Total nursing attempts observed	183	150	128
N of "successful" attempts ($\geq$ 3 s)	59	38	37
Rate of "successful" attempt/ hour of observation	.84	.34	.36
Mean duration of "successful" attempts	14.0	9.7	8.3
Standard deviation	9.4	4.1	3.4
Range	40	15	13

[1]Kid of female 21 lost or deceased in late July.

Although detailed statistical analyses have not been undertaken, the results suggest a trend toward lower nursing durations from June to August (table 2). In the 17 mother-kid pairs observed in 1979, the rate of successful attempts/hour of observation and the mean duration of successful attempts were comparatively higher in June than either July or August and the maximum duration recorded during June was more than two times longer than in July or August.

DISCUSSION

Nursing Behavior

Maternal-offspring interactions involved in nursing attempts and terminations can be viewed as an indicator of weaning. Trivers (1974) proposed the concept of "parent-offspring conflict" as an explanation for the weaning phenomenon based on modern evolutionary theory. The theory predicts a conflict of interest between mother and offspring over the disposition of maternal resources (in this case milk), with the offspring wanting more than the mother has selected to give. Viewed from this perspective, interactions between mothers and offspring take on new meaning. In an attempt to exploit maternal resources as best they can, offspring are expected to employ behavioral "strategies," while mothers are expected to display appropriate "counter-strategies" that prevent over-exploitation. When we use the term "strategy," we do not imply that animals make conscious decisions. We simply refer to behavioral traits which have been favored by natural selection over other alternatives.

Looking at mother-offspring interactions from that viewpoint, offspring should employ behavior that results in more nursing time. Alternatively, mothers should limit unrestricted access to the udder but, at the same time, minimize risk of injury to offspring. Energy expended on behavior associated with nursing reduces the amount available for other activities, such as those involved in maintenance or reproduction. The results seem consistent with this interpretation.

Methods of termination employed by females seem to be situation-appropriate. When offspring approach the udder from the S or FR, they position themselves below the mother's abdomen and directly anterior to her rear legs. In such a position they impede her ability to move forward. To terminate an attempt, some forward movement appears necessary to dislodge the kid from the nipple. SO's may reduce the possibility that a female steps on and injures her offspring when it is positioned beneath her body and, at the same time, allow her to move forward and terminate the attempt.

When her kid is positioned beneath her body, a female may also employ WA; however, as Brandborg (1955) and Chadwick (1975) have noted, those terminations often result in the kid being "bowled over." This may explain why WA is seen so infrequently when compared with the SO, even though it involves less movement and is therefore likely to be less energetically expensive. Forcibly knocking a kid from the udder may increase the risk of injury, particularly when nursing occurs on cliff ledges, steep scree slopes, or other precarious locations. That might also explain why WA was the most common method of termination in response to R approaches. Because the kid is behind its mother, it cannot impede her forward progress and also is in no risk of being stepped on or falling if she does move. The few SO's that occurred during R approaches happened in those rare instances when the kid was able to position itself beneath its mother.

RLS was seen most frequently during R approaches, which suggested that it was relatively ineffective once the kid had ahold of a nipple. It may be effective against R approaches because kids appeared to experience some difficulty in grasping a nipple from that orientation. DeBock (1970) thought that R-oriented attempts may be difficult because of the forward positioning of the teats and relatively small size of the mountain goat udder.

The infrequent expression of aggression during nursing terminations also suggested that risk of injury to offspring was a major determinant of maternal behavior. Aggression was used only to terminate side-oriented attempts, the most successful mode for offspring. Females apparently employ aggression only when probability of successful exploitation is high. Additionally, the fact that JA or running away from offspring occurred so infrequently may be due to the higher energetic cost as compared to other methods of termination. Both involve a good deal more movement than other methods.

Offspring also appeared to exhibit behavior which can be interpreted as advantageous. In approaching the udder from the S or FR, offspring position themselves so that it is difficult for mothers to terminate nursing attempts. Additionally, the S approach is the most direct route to the udder.

Although RA and S approaches involved the same basic orientation during nursing, S approaches were considerably more successful. This difference may be due to a higher probability of early maternal detection. In RA and FR attempts, kids passed within their mother's primary visual field before making contact with the udder. The R approach does not share this disadvantage and the S approach is probably less subject to early detection than the RA or FR modes. That may explain why R attempts were never preceded by a running approach; kids may not have to move in rapidly since the probability of early detection is low.

R-oriented attempts were rare, which attests to the difficulty in nursing from this position. Anatomical positioning of the udder and teats, and ease of termination by the mother may render it relatively disadvantageous. It is the only method of approach in which the apparently energetically inexpensive RLS seems to be a highly effective form of termination.

The RA approach may have an additional advantage that could account for its higher rate of success when compared with the R or FR modes. This mode appeared situation-specific, being exhibited when the mother was moving, either in foraging or travel. Among others, Geist (1971b) viewed RA as a behavioral strategy used by young ungulates to restrict their mother's movement so that they can nurse. Nursing attempts directed at the mother when she is moving are unlikely to be successful, since it makes grasping the nipple a difficult task.

Bunting behavior is a universal behavioral pattern in young ungulates (Lent 1974) and can also be viewed as a strategy. Vigorous stimulation of the udder may result in the release of more milk and/or stimulate further milk production.

The situations in which kids try to suckle also appear to be advantageous. Chadwick (1975) noted that kids "exploited minor events" to gain access to the udder. In the present study, attempts tended to be made when mothers stopped forward movement, stood up from a reclining position, were preoccupied with other activities, and upon reunion of the pair. Kids may increase the probability of gaining access to a teat by attempting to nurse when mothers are preoccupied with some other activity. For example, an increase in attempts to nurse while the mother was urinating was noted toward the end of the summer when the rate of success was comparatively low. It is possible that an element of surprise may be important, and that the probability of early detection is lower when the mother is engaged in some other activity. Once the kid begins nursing, it can be very difficult to dislodge. We noticed kids continuing to hold onto the nipple after mothers had stepped over them and were walking forward in an attempt to pull them off. Older, presumably stronger kids sometimes were dragged a considerable distance before letting go. Kids at times appear to stimulate their mothers to rise so that they can nurse which supports the notion that offspring are not passive by-standers in the weaning process. Similar behavior has been noted in other ungulates, such as domestic sheep (Ewbank 1967).

Retention of Older Offspring

Little is known about the breakdown of social bonds between mother and offspring in ungulates (Lent 1974). Brandborg (1955) and Hanson (1950) believed that mountain goat young remained with their mothers until April or May of the year following parturition and that they are driven off by the female just prior to the birth of a new offspring. Holroyd (1967) states that yearlings may rejoin their mothers after parturition has taken place, but that they are kept at a distance and "treated no differently from any other intruder if the welfare of the newborn kid is threatened in any way." Chadwick (1975) noted that dissociation of females and kids occurred in April. He believed the break-up to be primarily passive, although some low intensity maternal aggression appeared to be involved. As maternal interest waned, young began to follow other females and sub-adults. He felt that the only permanent relationship among goats was the association of females and offspring from birth to 10 to 11 months. He does describe two separate instances, however, in which females "adopted" yearlings and "treated them like kids in most respects" (p. 146). Those yearlings were allowed to travel and bed in close association with their female companions. DeBock (1970) stated that the bond between mountain goat mothers and their offspring was broken at the birth of a new infant; however, he did observe three instances of nursing by yearlings which led him to suggest that barren females may occasionally allow them to remain in close proximity. Unfortunately, DeBock and Chadwick did not have marked animals, and their conclusions concerning length or permanency of association were therefore limited to speculation.

We suggest that the retention of older offspring in ungulates may represent an evolved reproductive strategy (Hutchins 1980). Associations between yearlings and barren females have been reported in a wide variety of species and may be much more common than now realized (Lent 1974, Hutchins 1980). Chadwick's (1975) suggestion that close relationships between females and yearlings represent cases of adoption is probably incorrect, since this implies that the pair is genetically unrelated.

Several studies have shown a strong correlation between habitat quality, population density, physical condition of females, and reproductive success in ungulates (Geist 1971b, Sinclair 1977, Wilson and Hirst 1977). When habitat quality becomes poor, or competition intense such that reproduction is curtailed, then females may be able to increase their previous offspring's probability of survival and/or competitive ability by continuing their association. For example, retained offspring appear to share in their mother's higher dominance status while utilizing limited resources, such as the salt lick. Such an advantage may extend into the winter, when deep snow covers vegetational habitats, and there is competition for patchily distributed forage. Petocz (1973) has noted an increase in aggression among mountain goats under conditions of deep snow, and competition for forage has been noted in other ungulates with similar winter range conditions (Denniston 1956). Older offspring are also allowed to nurse occasionally, thus possibly having access to an energetically rich food supplement that is not available to unattached members of the same age class (see discussion of weaning, this paper). If mothers were not lactating, they appeared to incur little cost in continuing the association and may have received some benefit. We have noted offspring grooming serious injuries sustained by the mother. This may help to promote healing and therefore decrease the chances of infection as, for example, in rodents (Li et al. 1980). Females may also gain some competitive advantage. For example, female 27 and her retained male 2-year-old (78) were observed to approach the salt lick in tandem, simultaneously threatening and displacing other conspecifics.

The hypothesis that retention is likely to be associated with adverse environmental conditions and reduced reproductive success is indirectly supported through data on the Klahhane Ridge females (Driver, Stevens, and Pike 1979). In 1977, the estimated ratio of kids to adult females was 97:100, but in 1978 this figure dropped dramatically to 28:100. Low reproductive success was associated with a high incidence of retention in 1978. It is evident from table 1 that all known cases of retention took place during years in which females did not reproduce. Additional evidence indicating an environmental or density dependent influence on reproduction in 1978 comes from data on the timing of birth and incidence of dispersal. Kids were born 2 weeks later on the average in 1978 than in 1977 or 1979. Additionally, the incidence of dispersal was considerably higher in 1978 than in 1977 or 1979, it is estimated that 17 percent of the tagged population left Klahhane Ridge during 1978 (Driver et al. 1979). It has been suggested that a comparatively low snowpack during the preceding 2 years may have had a negative effect on forage quality and that this combined with the high population density acted together to reduce reproductive capability.

Weaning

In comparison with studies conducted on parturition and bond formation, few exist on the process of "weaning" in ungulates (Lent 1974); and in many cases, the term has been used rather loosely. Lent (1974) has noted that most authors do not make a strong distinction between an offspring's transition from milk to forage and the breakdown of social bonds between mother and offspring. The two processes are not always synonomous (Lent 1974). Here we restrict our discussion to the former, which we refer to as "nutritional weaning" to avoid confusion.

Our findings concerning nutritional weaning are in general agreement with other reports. Brandborg (1955) observed kids foraging and ruminating when less than a week old; at 6 weeks, they were feeding regularly on vegetation. Chadwick (1975) found that females rejected nursing attempts in the 2d week after birth. He felt that kids were weaned between 3 and 4 weeks of age, basing his conclusion on the observation that suckling durations had "stabilized at less than 15 seconds" and nursing attempts were "sporadic and usually rejected." He did not provide quantitative data on rejection frequency. Furthermore, he observed nursing until mid-November and kids attempted to nurse as late as January. DeBock (1970) thought that weaning occurred at 4 months of age and noted that the mean duration of nursing bouts stabilized at 15 seconds once the young were 6 weeks old. He also found a progressive decrease in the frequency and duration of bouts over time. His results are questionable, however, since he did not have marked animals and did not collect data systematically. Ad libitum observations do not control for observer bias or for differences among particular mother-infant pairs.

Our results suggest that a progressive decrease in nursing occurs over time, but we still hesitate to classify kids as weaned even by the end of August. Of course, the problem of whether an offspring is weaned or not is chiefly one of semantics. Nutritional weaning could be considered to be complete when (1) an offspring has shifted its nutritional dependence from mother's milk to forage, or (2) the offspring fails to receive any nourishment--no matter how seemingly trivial--in the form of mother's milk. If the former definition is employed, then we might follow the reasoning of Chadwick (1975) and consider kids weaned at 4 weeks when there is a dramatic drop in the frequency and duration of successful nursing attempts. If, however, the latter definition is employed, the possibility exists that complete weaning may not occur for up to 2 years. Unfortunately, we were unable to determine if females with retained older offspring were lactating. If those females were tolerating older offspring because they lost young-of-the-year, then they may have been physiologically capable of producing milk. Alternatively, nursing by yearlings may simply represent a form of non-nutritive "comfort suckling" as seen in many young mammals, as for rats (Kenny et al. 1979) or ponies (Tyler 1972). Considering the enormous energetic costs involved in lactation (Hanwell et al. 1977), we would predict nursing by yearlings and 2-year-olds to be non-nutritive and that prolonged suckling may function only in the maintenance of social bonds.

The meaning of the phrase "nutritional dependence" has important implications for a definition of nutritional weaning. While even 1- to 2-week-old kids do not appear to be completely dependent on mother's milk as a source of nutrition, it is undoubtedly important, particularly when forage quality is poor. Milk is considerably higher in energetic value than forage, and even small amounts may provide some nutritional advantage. Brandborg (1955) has noted that young-of-the-year are the age class most susceptible to mortality and suggests that failure to over-winter is the primary cause of death. This would suggest that a kid's physical condition just prior to the onset of inclement weather may affect its ability to survive. Among bighorn sheep (Ovis canadensis), larger lambs are more likely to survive the rigors of winter than are smaller lambs (Geist 1971b). Viewed from this perspective, a few extra suckling bouts may make the difference between survival and death.

The point to be made here is that the process of nutritional weaning needs to be considered on the level of the individual mother-infant pair. Considerations of weaning on a populational level do not take into account variations in the ability of mothers to produce milk or in the need of particular offspring for this resource. Efforts to define weaning as a populational characteristic are gross generalizations and provide only superficial insight into an issue of immense complexity.

ACKNOWLEDGMENTS

Funding for this research was provided by grants from the Theodore Roosevelt Memorial Fund of the American Museum of Natural History and Sigma Xi, the Scientific Research Society of North America. We would like to extend our appreciation to the staff of Olympic National Park, especially Mr. Bruce Moorhead, Research Biologist, and Mr. Roger Contor, Superintendent, for their interest and assistance. Thanks are also due to Mr. Raymond Rasker and Ms. Margaret Davis who served as field assistants during 1979, and to Mr. Kim Agrimson for figure 2. Much of the data were collected in collaboration with Ms. Victoria Stevens who has been studying the population biology of the Olympic goats since 1977; her friendship and assistance are greatly appreciated.

LITERATURE CITED

Altmann, J.
1974. Observational study of behaviour. Behav. 49:227-267.

Brandborg, S. M.
1955. Life history and management of the mountain goat in Idaho. Idaho Dept. Fish Game Wildl. Bull. 2:1-142.

Chadwick, D. H.
1975. Mountain goat ecology-logging relationships in the Bunker Creek Drainage of Western Montana. Unpubl. M.S. thesis, Univ. Mont., Missoula.

Cowan, I. McT.
1974. Management implications of behaviour in the large herbivorous mammals. p. 921-934. In V. Geist and F. Walther, eds. The behavior of ungulates and its relation to management. Vol. II, IUCN, Morges, Switzerland.

Cowan, I. McT., and W. McCrory.
1970. Variation in the mountain goat Oreamnos americanus (Blainville). J. Mammal. 51(1):60-73.

DeBock, E.
1970. On the behavior of the mountain goat in Kootenay National Park, British Columbia. M.S. thesis, Univ. Alberta, Edmonton, Canada.

Denniston, R. H.
1956. Ecology, behavior and population dynamics of the Wyoming or Rocky Mountain moose, Alces alces shirasi. Zoologica 41:105-118.

Driver, C. H., V. Stevens, and D. K. Pike.
1979. Terrestrial baseline surveys, non-native mountain goats of the Olympic National Park. Annual Report, 1978. Univ. Wash., Coll. For. Resour., Seattle.

Ewbank, R.
1967. Nursing and suckling behaviour amongst Clun Forest ewes and lambs. Anim. Behav., 15:251-258.

Geist, V.
1965. On the rutting behavior of the mountain goat. J. Mammal. 45:551-568.

Geist, V.
1971a. A behavioral approach to the management of wild ungulates. p. 413-424. In E. Duffey and A. S. Watts, eds. The scientific management of animal and plant communities for conservation. Blackwell Publ., Oxford.

Geist, V.
1971b. Mountain sheep, a study in behavior and evolution. Univ. Chicago Press. 383 p.

Hanson, W. O.
1950. The mountain goat in South Dakota. Ph. D. diss. Univ. Mich., Ann Arbor.

Hanwell, A., and M. Peaker.
1977. Physiological effects of lactation on the mother. Symp. Zool. Soc. Lond. 41:297-312.

Holroyd, J. C.
1967. Observations of Rocky Mountain goats on Mt. Wardle, Kootenay National Park, British Columbia. Can. Field Nat. 81(1):1-22.

Hutchins, M.
1980. Offspring retention in ungulates; a reproductive strategy? Unpublished paper presented to the 1980 Annual Meeting of the Animal Behavior Society, Fort Collins, Colo.

Kenny, J. T., M. L. Stoloff, J. P. Bruno, and E. M. Blass.
1979. Ontogeny of preference for nutritive vs. non-nutritive suckling in albino rats. J. Comp. Physiol. Psychol. 93(4):752-759.

Lent, P. C.
1974. Mother-infant relationships in ungulates. p. 14-55. In V. Geist and F. Walther, eds. The behaviour of ungulates and its relation to management, Vol. I, IUEN, Morges, Switzerland.

Li, A. K. C., M. J. Koroly, M. E. Schattenkerk, R. A. Malt, and M. Young.
1980. Nerve growth factor: acceleration of the rate of wound healing in mice. Proc. Natl. Acad. Sci., USA. 77(7): 4379-4381.

Olmstead, I.
1976. Alpine and subalpine vegetation under the influence of non-native mountain goats, Olympic National Park. p. 1143-1148. In Proceedings of the first conference on scientific research in the national parks, Vol. II, U.S. Department of the Interior.

Petocz, R. G.
1973. The effect of snow cover on the social behavior of bighorn rams and mountain goats. Can. J. Zool. 51:987-993.

Rideout, C. B.
1974. A radio-telemetry study of the ecology and behavior of the mountain goat in western Montana. Ph. D. thesis, Univ. Kans., Lawrence.

Rideout, C. B., and R. S. Hoffman.
1975. Oreamnos americanus. Mamm. Species. 63:1-6.

Sinclair, A. R. E.
1977. The African buffalo, a study of resource limitation of populations. Univ. Chicago Press.

Tabor, R.
1975. Guide to the geology of the Olympic National Park. Univ. Wash. Press, Seattle.

Trivers, R. L.
1974. Parent-offspring conflict. Amer. Zool. 14:249-264.

Tyler, S. J.
1972. The behavior and social organizations of the New Forest Ponies. Anim. Behav. Monogr. 5(2):85-196.

Walker, E. P.
1975. Mammals of the world, Vol. II. John Hopkins Univ. Press. London, England.

Wilson, D. E., and S. M. Hirst.
1977. Ecology and factors limiting roan and sable antelope populations in South Africa. Wildl. Monogr. 54:1-111.

Behavior	Code	Description
Mother-offspring behaviors:		
Nursing	N	A nursing attempt was defined as an approach and attempt to suckle from the mother by her offspring. Attempts were usually preceded by a short, rapid rush by the offspring toward the udder. When this event was followed by contact with the udder, it was classified as an attempt. An attempt was considered "successful" only if the offspring remained in contact with the udder for 23 seconds.
Approach modes	S	The kid approaches the udder from the mother's side and on the same side on which it had been positioned just before the event occurred.
	FR	The offspring approaches the udder from between the mother's front legs.
	R	The offspring approaches the udder from between the mother's rear legs.
	RA	The offspring approaches the udder from the mother's side, but before doing so, runs directly in front of her and makes udder contact from the opposite side from which it began the approach.
Termination modes	SO	The mother terminates a nursing attempt by lifting her rear leg up over the offspring and walking forward.
	WA	The mother terminates a nursing attempt by walking forward, without lifting the rear leg.
	RLS	The mother terminates a nursing attempt with a quick kicking motion of the rear leg.
	JA	The mother terminates a nursing attempt by leaping away from the offspring.
	O	Any other termination. Descriptions were recorded in the form of qualitative notes.
Allogrooming	GR	The licking of some portion of the body of another individual.
Agonistic Behavior:		
Horn present	HP	The subject pulls in its chin and lowers the head, tilting the horn tips slightly forward while pointing them in the direction of another individual (Geist 1965, DeBock 1970).
Horn swipe, without contact	HSW	The subject tucks in the chin, lowering the horn tips as in the HP, then proceeds to sweep them upwards in a half arc in the direction of another individual without making any physical contact (Geist 1965, DeBock 1970).
Horn swipe, with contact	HSC	Same as the preceding category, except that the animal performing the behavior strikes some portion of another individual's body with the horns.
Butt	BT	The subject makes physical contact with another individual by striking it with the anterior portion of the head and horns, without, however, making the upward sweeping motion as is characteristic of the horn swipe.
Avoidance	AV	Any avoidance behavior associated with the approach or threat behavior of another individual. This may include crouching and/or leaning in the opposite direction of a threatening individual or, more commonly, actual movement away from the antagonist upon being approached or threatened.

Home Range and Habitat Use by Non-Migratory Roosevelt Elk, Olympic National Park

Kurt J. Jenkins and Edward E. Starkey

ABSTRACT

Radiotelemetry was used to describe the home ranges, habitat use and social behavior of Roosevelt elk (Cervus elaphus roosevelti) in the Hoh Valley of Olympic National Park. Cow elk were found to be nonmigratory and home ranges were influenced primarily by topographic features. Flood plain areas were selected during most seasons, but use of south-facing valley slopes increased during winter. Cow elk formed relatively stable associations of adult females and their offspring. Olympic National Park provided a unique opportunity to study native ungulates in undisturbed habitat, and additional research is recommended.

Kurt J. Jenkins and Edward E. Starkey, Cooperative Park Studies Unit, School of Forestry, Oregon State University, Corvallis, Oregon 97331.

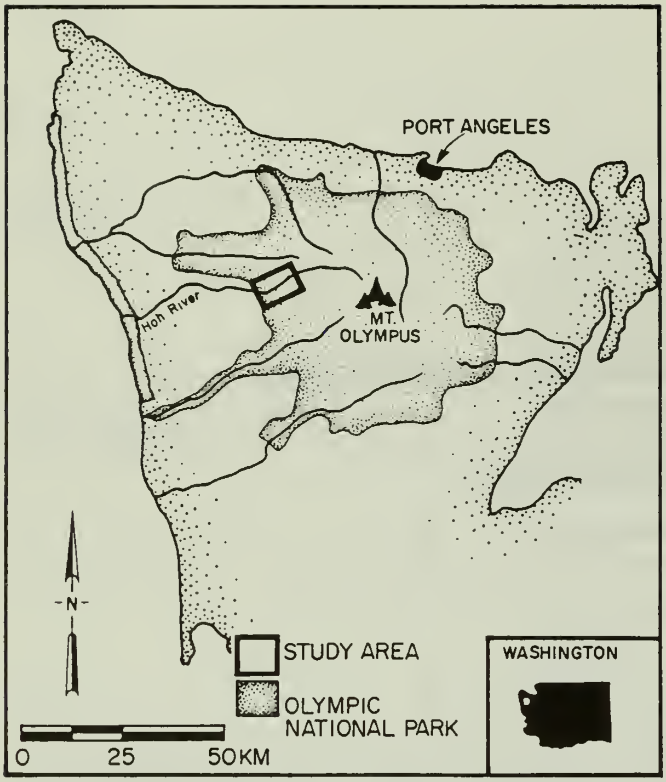


Figure 1.--Geographical location of Olympic National Park and the Hoh valley study area.

INTRODUCTION

This research is part of a long-term investigation of the behavior and ecology of Roosevelt elk (Cervus elaphus roosevelti Merriam) in Olympic National Park. The objective of this first phase of the research was to describe the distribution and movement of cow elk in a representative watershed near the boundary of the Park. A primary purpose was to determine the extent to which elk within Olympic National Park made use of non-Park land. That information was needed to assess effects of hunting and forest management outside the Park on Park elk. A second goal was to provide baseline information so that changes in the distribution and behavior of elk within the Park can be identified.

THE STUDY AREA

Olympic National Park occupies the central mountainous portion of the Olympic Peninsula in northwest Washington (fig. 1). The study area is located in the valley of the main fork of the Hoh River and extends from Canyon Creek, 3 km west of the National Park boundary, upriver approximately 15 km. A single paved road extends the length of the study area along the north side of the Hoh River. The area west of the National Park boundary is managed for timber production by the Washington Department of Natural Resources.

Climate in the Hoh Valley is maritime, with mild, wet winters and cool, dry summers. Average annual precipitation is 345 cm. Areas below 600 m receive mostly rain during winter, although approximately 25 cm of snow falls in valley bottoms each winter.

The Hoh valley has the broad U-shaped configuration characteristic of glaciated watersheds. Elevations range from 150 m on the valley floor to 910 m on adjacent ridgetops. The valley floor is 1.0 - 2.0 km wide and consists of gravel bars, at least four river terraces, and various glacial deposits. The vegetation has been described by Fonda (1974) and represents a sequence of primary succession from bare gravel adjacent to the river, to mature Sitka spruce-western hemlock forests on older terraces (fig. 2). Gravel bars, periodically flooded by the Hoh River, support pioneer communities of young red alder (Alnus rubra) and willow (Salix spp.). The youngest river terrace is an alluvial deposit 80-100-years-old and supports a mature red alder community. The next oldest terraces, 400 to 700 years of age, also are alluvial deposits and support seral Sitka spruce-black cottonwood (Populus trichocarpa) and mature Sitka spruce-western hemlock communities, respectively. The oldest most extensive terrace is a pleistocene glacial deposit, and it too supports the climax Sitka spruce-western hemlock forest. The valley bench, also a pleistocene deposit, supports an additional climax forest characterized by a dense canopy of western hemlock.

The spruce-hemlock forest of the Hoh valley, commonly referred to as rain forest (Kirk 1966) or moist coniferous temperate forest (Fonda 1974), is a variation of the Picea sitchensis vegetation zone, which occurs in coastal areas of Oregon and Washington. Massive Sitka spruce and western hemlock are common, and variable canopy coverage results in a complex mosaic of understory vegetation. Small forest clearings are numerous and are dominated by salmonberry (Rubus spectabilis), vine maple, and grasses. The shrub layers of denser forest stands are dominated by huckleberry (Vaccinium parvifolium, V. alaskense), vine maple, and sword fern (Polysticum munitum). Overall, heterogeneity is an important characteristic of the spruce-hemlock climax forest.

Two additional plant communities on the valley floor appear to be edaphically controlled. Bigleaf maple communities occur on shallow, rocky soils of alluvial fans formed by tributaries of the Hoh River or of colluvial deposits at the base of the valley wall. Vine maple communities occur on alluvial outwashes as well as in areas that are seasonally flooded by winter rains.

METHODS AND MATERIALS

Nine adult cow elk were immobilized and radio-collared. They were immobilized by injecting liquid or powdered succinylcholine chloride into the hips of the animals, using a powder charged Capchur™ rifle. Transmission frequencies of radio-collars were approximately 164 MHz. The collars were distributed evenly among three cow groups within the Park.

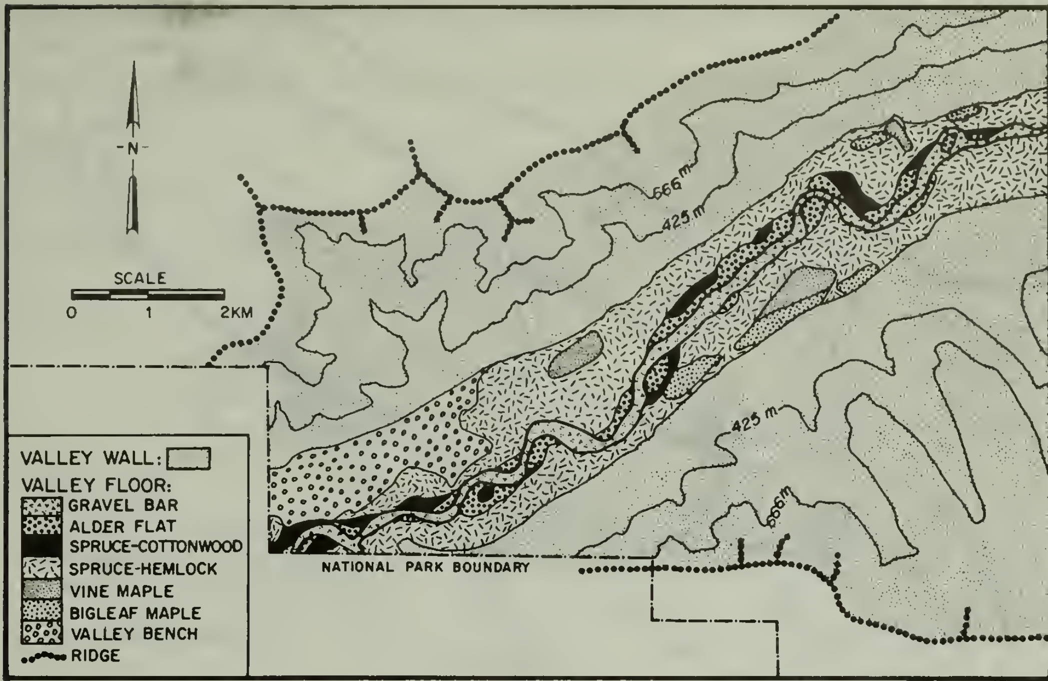


Figure 2.--Habitat units within the Hoh valley study area.

Collared elk were located during March 1978, from 1 June to 15 September 1978, and from 1 January to 20 March 1979, by triangulating from the ground using an AVM LA-12 receiver and hand held yagi antenna and by direct observation. The location of a collared elk was established by determining the direction of the strongest radio-signal from three receiving stations and by plotting azimuths on an orthographically corrected aerial photograph (scale - 1:24,000). To minimize error, triangulation stations were located on open gravel bars where reflection of radio-signals was minimal. If three bearings intersected, a circle was inscribed within the resulting triangle. The center of the circle was used as the estimated elk location and assigned coordinate values. If bearings did not intersect or if the accuracy of the location was doubtful, telemetry equipment was used to locate the elk visually or aurally. Each elk was located one to three times daily usually at different times each day.

Home range was defined as "the area over which an animal normally travels in pursuit of its routine activities" (Jewell 1966). Therefore, infrequent journeys by elk beyond their normal range were excluded from analyses. An elliptical home range model (Koepple et al. 1975) was used to delineate annual, home ranges of collared elk. Home ranges lacked definite boundaries by that method and were expressed as elliptical areas that included 95 percent of an animal's activity.

Daily movements were estimated each season by measuring the line distance between an elk's location one morning and its first location the following morning. Undoubtedly, the actual distance moved each day was greater than the distance calculated. However, the index was useful in examining seasonal changes in daily movements.

Habitat was examined by comparing availability within the composite home range of all radio-collared elk to utilization (Neu et al. 1974). Availability was defined as the percent of area within composite home ranges covered by each habitat unit and utilization as the percent of radio locations within each habitat unit. Elk selected a zone or habitat unit if utilization was significantly greater ($p<0.05$) than availability or avoided it if utilization was significantly less than availability ($p<0.05$). Use of habitat units was described during summer (10 June to 31 August 1978), winter (1 January to 28 February 1979) and early spring (1 March to 20 March 1978, and 1979). Early spring was delimited because there was a noticeable shift in habitat use at the beginning of March.

Interactions between elk groups were described by examining spatial overlap of home ranges and association of collared elk within each group. Association referred to the percent of time a collared elk was located in the presence of each other collared elk. Coefficients of association were calculated according to the procedure described by Cole (1949) and applied to elk by Knight (1970) and Schoen (1977). Values range linearly from 0.0 to 1.0, indicating no association to perfect association, respectively. Inferences concerning stability of elk groups were drawn by comparing association of elk between groups.

RESULTS AND DISCUSSION

Approximately 180 elk inhabited the study area. These were distributed among three groups of about 60 indivuduals each.

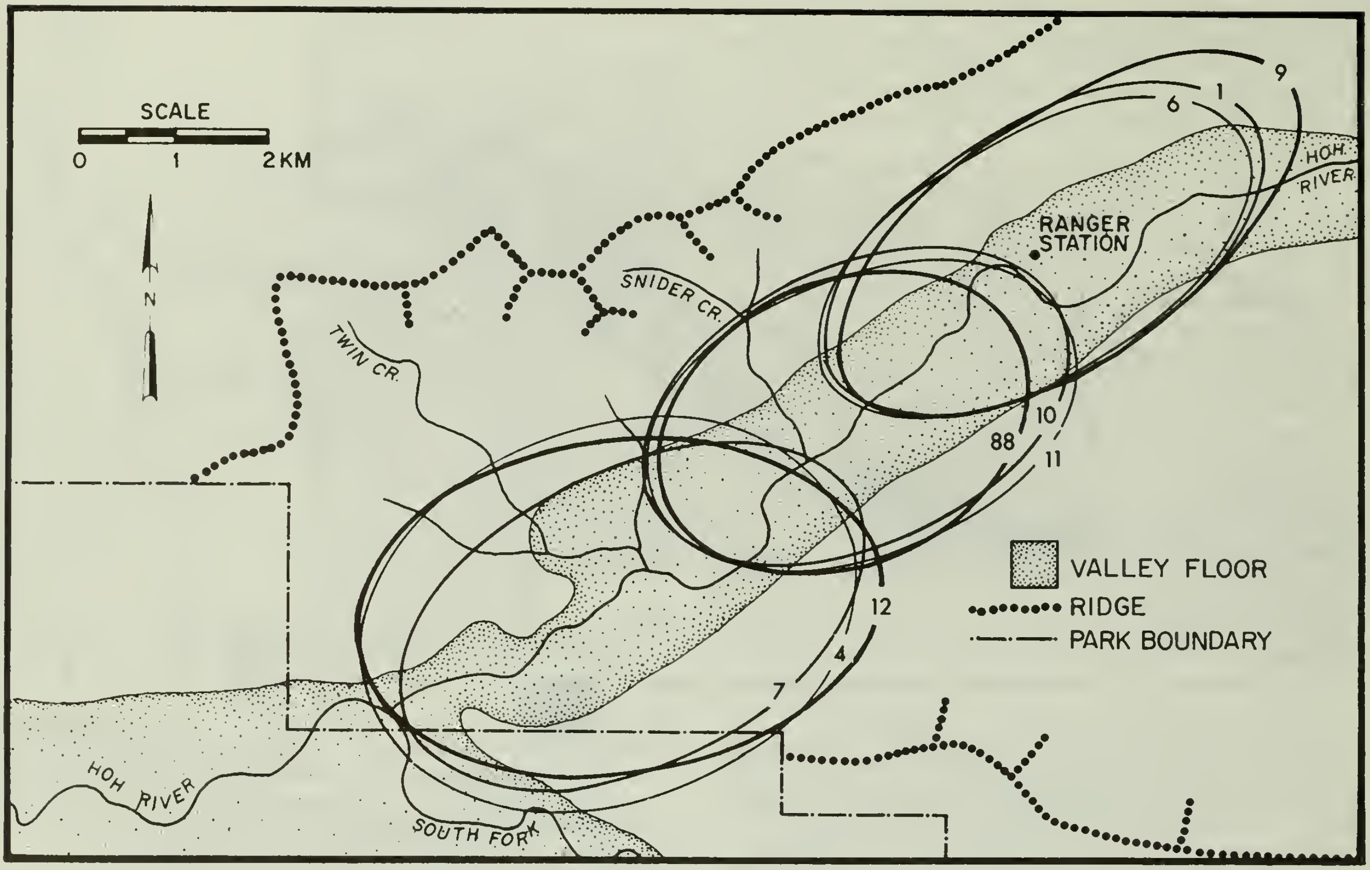


Figure 3.--Home ranges of cow elk in three home range groups in the Hoh valley.

Home Range and Movements

Radio-collared elk were non-migratory. None dispersed from the lowlands to summer range at higher elevations; nor was there an observable seasonal movement of elk across the National Park boundary. No collared elk observed in Olympic National Park was ever located more than 2.0 km outside of the Park. Additionally, no elk from more than 5.0 km within the Park was ever observed on State-owned land adjacent to the Park.

Skinner (1933) nd Schwartz (1939) suggested that a migratory portion of the population remained in the upper Hoh River watershed unless deep snow caused them to move down river. Under such conditions, migratory elk may cross the National Park boundary. It is unlikely, however, that cutover areas outside the Park would be available to elk during severe winters because of snow accumulation. Elk would probably occupy densely timbered hillsides within the Park, as observed by Newman (1956). Therefore, it seems doubtful that either resident or migratory elk in the Hoh valley make use of non-Park land during winter. Information on migratory elk in the Hoh valley still is lacking.

Seasonal movement of elk up and down valley was minimal. Two elk, however, traveled independently to the Bogachiel valley to the north on 14 August 1978 and 17 August 1978. Each traveled 4.8 km from its last confirmed location in the Hoh valley and was absent from its home range for 12 to 18 days before returning. Although the cause was unknown, the movements may have been associated with reproductive behavior since they occurrred near the onset of the rut. Lieb (1973) reported that cow elk in Prairie Creek Redwoods State Park occasionally left their group and wandered prior to the onset of the rut. Hormonal changes during estrus probably contribute to the restlessness of cow elk (Lieb 1973). Movement of cow elk between watersheds indicated that intermingling of populations from adjacent drainages may occur; however, interchanges of non-migratory elk between watersheds probably is uncommon. Only two elk moved extensively during this study, and both returned to their normal range.

A total of 2,565 locations of the radio-equipped elk was obtained. Annual home range areas, during the entire study period, average 1 112 ha. Orientation and size of home ranges within the Park were influenced by the valley floor (fig. 3). The major axis of each ellipse was alined closely to the flood plain of the valley. Additionally, width of home range was related significantly to the breadth of the valley floor measured through the geometric center of the home range ($r^2 = 0.57$, $p<0.05$). Home ranges were broadest near Twin Creek where the valley floor was most extensive. In southwest Oregon, home ranges of Roosevelt elk also were influenced by topographic features. Home range diameters averaged 1.3 mi in steep

Table 1--Percent availability and use of vegetation types in the Hoh valley, Olympic National Park

Location	Vegetation type	Availability (percent of composite home range)	Utilization (percent of radio-relocations)		
			Summer	Winter	Early spring
Valley floor	Gravel/willow	0.06	0.04(o)[1]	0.02(-)	0.01(-)
	Red alder	.05	.09(+)	.10(+)	.25(+)
	Spruce-cottonwood	.02	.02(o)	.03(o)	.13(+)
	Spruce-hemlock	.35	.53(+)	.44(+)	.47(+)
	Bigleaf maple	.04	.13(+)	.10(+)	.05(o)
Valley wall[2]					
South exposure	Western hemlock	.23	.10(-)	.20(o)	.07(-)
North exposure	Western hemlock	.25	.09(-)	.11(-)	.02(-)
Total		1.00	1.00	1.00	1.00
No. of radio-locations(n)			683	759	541

[1]Symbols indicate significant habitat selection (+), avoidance (-), and neutrality (o) based on family confidence intervals using Bonferroni Z-statistics (Neu et al., 1974).

[2]Represents only the lower one-third of the valley wall (150-225 m of elevation) because upper two-thirds were not within composite home ranges.

canyons; whereas in valley floor plains, they averaged 3.0 mi (Harper 1971).

Daily movements of cow elk were greater during summer than winter ($p<0.05$). Elk traveled an average minimum distance of 843 m between successive mornings in summer and 688 m in winter. This reduction of activity in winter may conserve energy at a time when weather is typically severe and forage does not satisfy maintenance requirements. The metabolic rates of black-tailed deer (Odocoileus hemionus columbianus), mule deer (O. h. hemionus), and white-tailed deer (O. virginianus) fluctuate annually with fasting heat production highest during summer and lowest during winter (Regelin 1979, Silver et al. 1969, Thompson et al. 1973). It seems likely that metabolic rates of elk are reduced similarly during winter, resulting in decreased movement and home range size.

Daily movements of cow elk with calves were least in June, traveling an average minimum distance of 541 m/day in June; whereas those without calves, traveled an average of 1 040 m. Movement of cows with calves was restricted in June because frequent nursing required that cows stay close to the less mobile calves.

Darling (1937) emphasized the importance of tradition as a determinant of movement and home range use of red deer (C. e. elaphus). Similarly, a high level of traditionality appeared to be associated with home range use by elk in the Hoh valley. Several heavily used foraging areas and travel corridors existed within home ranges and were used in a sequential, and often predictable pattern. Generally, elk remained in a favored foraging area for 1 to 3 days. Although elk often moved through their home ranges in a predictable manner, an overall circuit of travel did not exist.

Patterns of Habitat Use

Elk selected valley floor zones during all seasons and generally avoided valley walls (table 1). The valley floor was probably the most important habitat because the assemblage of plant communities provided the best dispersion of forage and cover. Clearings on the forest floor were used heavily by feeding elk, generally sustained the highest browsing intensity, and probably provided more abundant and diverse forage than valley walls.

Although the valley floor was important in all seasons, elk used lower parts of the valley wall under certain conditions. Use of the lower north valley wall (south-facing) increased during winter 1978 (table 1) and was frequented by elk during clear, cold periods and when snow cover existed. South facing slopes intercept more solar radiation, which results in warmer temperatures and lower snow depths than on the valley floor. The relatively dense canopy on valley walls may intercept more snow and contribute to reduced snow depths (Jones 1974). At night, significantly more

Entire Study

ELK NO.	1	6	9	10	11	88	4	7	12	3	8
1	1.00										
6	0.94	1.00									
9	0.76	0.71	1.00								
10	0.00	0.00	0.00	1.00							
11	0.01	0.01	0.00	0.75	1.00						
88	0.02	0.02	0.01	0.88	0.88	1.00					
4				0.01	0.01	0.01	1.00				
7				0.01	0.01		0.49	1.00			
12				0.01	0.01	0.01	0.88		1.00		
3							0.01	0.01	0.00	1.00	
8							0.05	0.01	0.00	0.13	1.00

June Only

ELK NO.	1	6	9	10	11	4	7	3	8
1	1.00								
6	0.94	1.00							
9	0.85	0.92	1.00						
10	0.00	0.00	0.00	1.00					
11	0.00	0.00	0.00	0.26	1.00				
4				0.00	0.00	1.00			
7				0.00	0.00	0.11	1.00		
3						0.00	0.00	1.00	
8						0.00	0.06	0.00	1.00

Figure 4.--Coefficients of association for pairs of radio-collared elk in the Hoh valley. Shaded cells represent pairs of elk within a home range group and non-shaded cells represent pairs from adjacent groups.

downward infrared energy is radiated from a relatively dense canopy than from either less dense canopies or the clear sky (Moen 1973). Temperature inversions probably are common, and together with the above factors, may create more moderate thermal conditions on the valley wall than on the valley floor during winter.

Elk on the valley floor selected spruce-hemlock and red alder habitat units during all three seasons. Gravel bars were generally avoided; their use was greatest during summer, especially during hot midday periods in July. Breezes may have provided relief from insects and summer heat. Big leaf maple habitats were selected during summer and winter, and used in proportion to availability in spring. Spruce-cottonwood habitats were used in proportion to availability except in the spring, when they were selected.

The shift in utilization to red alder and spruce-cottonwood habitats during early spring probably was a response to abundant new growth of grass. Grass is an important springtime dietary component for elk (Schwartz and Mitchell 1945). Frequently, elk traveled from these communities to adjacent spruce-hemlock stands to bed during the midday period.

Social Group Interactions

The individual home ranges of three collared elk in each of the three groups coincided closely (fig. 3). Although home ranges of elk from adjacent groups overlapped, no permanent interchange of collared elk occurred between groups. Elk from adjacent groups were observed together in only eight cases. Association lasted for 3 days or less ($\bar{x}$ = 1.4 days), and the original groups of collared elk were preserved after temporary associations. Coefficients of association for pairs of elk within a group ($\bar{x}$ = 0.71, range = 0.13 to 0.94) were greater than those between groups ($\bar{x}$ = 0.01, range = 0.00 to 0.05) (fig. 4). The lack of perfect association between elk in a group indicted that subgroups were periodically absent from the main group. Duration of those periods average 5.4 days (n = 42) but was highly variable (S.D. = 6.2 days). The coefficients of association between elk No. 7 and No. 8, which were known to have calves, were lowest in June (fig. 4). This may indicate subgrouping was more common during calving.

Previous studies suggested that stability of elk groups was variable. Darling (1937) believed that groups of red deer consisted of a dominant female, her mature daughters, and their offspring. The matriarchal concept has been accepted widely (Altmann 1952, McCullough 1969, Franklin et al. 1975). It implied that home range was passed on through generations, a trait known as home range conservation (Murie 1951), and that elk groups were stable, comprised of a constant membership. In contrast, Knight (1970) found that the mean coefficient of association between female Rocky Mountain elk (C. e. nelsoni) never exceeded 0.47, and felt that elk groups should be considered aggregations rather than social groups. Schoen (1977) reported a mean coefficient of association of 0.20 for 39 female Rocky Mountain elk in western Washington, which also indicated low group stability. Marcum (1975), Mackie (1970), and Shoesmith (1979) reported that Rocky Mountain elk groups changed composition frequently; however, the effect of seasonal migration and hunting on the constancy of those groups is unknown.

Harper (1971) found that Roosevelt elk herds on managed forest lands in southwest Oregon continuously changed composition and that marked members of adjacent groups interchanged freely. In contrast, non-migratory and unhunted elk in the unmanaged Prairie Creek Redwoods State Park formed more stable associations of adult females and their immature offspring (Franklin et al. 1975). In that population, small fluctuations in group size occurred as subgroups entered and left the herd; however, absent individuals always returned. Franklin and Lieb (1979) hypothesized that variations in group stability of non-migratory elk in Prairie Creek Redwoods State Park and in southwest Oregon may be caused by differences in habitat. They suggestd that the continual alteration of vegetation due to logging in southwest Oregon created changing habitat conditions which affected the development and maintenance of social organization. They concluded that relatively stable social organizations may be expected in elk populations that inhabit stable, unmanaged environments which permit long-term bonding among individuals.

SUMMARY AND CONCLUSIONS

Home ranges of elk were influenced primarily by topographic features of the Hoh valley. Major axes of each home range were alined to the flood plain of the valley, and widths of home ranges were related to the breadth of the valley floor. Additionally, radio-locations of the collared elk were concentrated on the valley flood plain. It seems likely that the distribution of elk in the unmanaged forest setting is governed largely by the location of suitable foraging areas. Numerous forest clearings on the flood plain provide environmental heterogeneity and abundant forage for elk. Thus, the extent of valley floor may be an important determinant of elk density in unmanaged fluvial forests on the Olympic Peninsula.

Current logging practices are sometimes suggested to be beneficial to elk because the removal of the overstory trees creates new foraging areas for elk. We found, however, that use of densely timbered, southfacing walls increased in winter, especially during cold periods with snow cover. Closed canopy forests on south-facing slopes may be extremely important habitat during periodically severe winters, both because they provide a more moderate thermal environment and because lower snow depths may result in greater availability of forage (Jones 1974). Although the relative value of mature forests and clearings as foraging areas on elk winter range remains poorly understood, managers should be aware of the importance of mature forest under certain winter conditions.

Seasonal differences in phenology and thermal regimes appear to have influenced distribution of elk in the Hoh valley. Additionally, dietary preferences probably influenced selection of habitat units on the valley floor.

During summer and winter, relatively more use occurred on the older river terraces and valley walls. During early spring, use shifted to riparian alder-flat and spruce-cottonwood habitats. This appeared to be in response to new growth of grasses. Late winter is a crucial period for cow elk nutritionally. Protein and energy reserves are low after winter, and demands of rapid fetal growth are high (Moen 1973). Thus red alder and spruce-cottonwood communities should be considered critical elk range in the fluvial rain forest valleys.

Cow elk formed relatively stable associations of adult females and their offspring and conformed to the model of group behavior of Franklin and Lieb (1979). There was no permanent interchange of collared elk between groups, and elk within groups were more highly associated than reported elsewhere. These findings support the hypothesis that more stable elk groups may form where habitat is constant and not disturbed by logging. Additional comparative research on the behavior of elk groups in managed and unmanaged forest settings is needed to further test the hypothesis.

Apparently, non-migratory cow elk in Olympic National Park are influenced little by forest and wildlife management practices that occur outside the Park. Park elk within 5.0 km of the Park boundary made use of non-Park land and thus, may be hunted and influenced by habitat changes which occur there. Beyond a 5.0-km strip, elk were isolated from events outside the Park. Therefore, management practices outside the Park do not affect the majority of cow elk within the Park and may not be used to manage them. Information on migratory and male segments of the Hoh valley population is needed before the overall influence of external factors on elk in Olympic National Park can be described completely.

Results of this study also indicate that because the majority of elk in the Hoh valley are not influenced by events outside the Park, the behavior and ecology of elk within the Park are the most accurate reflection of the primeval condition of elk on the Olympic Peninsula. These elk provide a unique opportunity to research natural regulation of herbivore populations and the influence of elk on forest communities. Additionally, comparative research on elk within and outside of Olympic National Park is important to determine the influence of forest management on elk movement, productivity, and social organization.

LITERATURE CITED

Altmann, M.
1952. Social behavior of elk (Cervus canadensis nelsoni) in the Jackson Hole area of Wyoming. Behavior 4:116-143.

Cole, L. C.
1949. The measurement of interspecific association. Ecology 30(4):411-424.

Darling, F. F.
1937. A herd of red deer. Oxford University Press, London. 215 p.

Fonda, R. W.
1974. Forest succession in relation to river terrace development in Olympic National Park, Washington. Ecology 55:927-942.

Franklin, W. L., A. S. Mossman, and M. Dole.
1975. Social organization and home range of Roosevelt elk. J. Mammal. 56;102-118.

Franklin, W. L., and J. W. Lieb.
1979. The social organization of a sedentary population of North American elk: a model for understanding other populations. p. 185-198. In M. S. Boyce and L. D. Hayden-Wing, eds. North American elk: ecology, behavior and management. Univ. of Wyo., Laramie. 294 p.

Harper, J. A.
1971. Ecology of Roosevelt elk. Oreg. State Game Comm., Portland, OR. P-R Proj. W-59-R. 44 p.

Jewell, P. A.
1966. The concept of home range in mammals. Symp. Zool. Soc. Lond. 18:85-109.

Jones, G. W.
1974. Influence of forest development on black-tailed deer range on Vancouver Island. p. 139-148. In H. C. Black, ed., Wildlife and forest management in the Pacific Northwest. Oregon State University, Corvallis. 231 p.

Kirk, R.
1966. The Olympic rain forest. Univ. Wash. Press, Seattle. 86 p.

Knight, R. R.
1970. The Sun River elk herd. Wildl. Monogr. 23:1-65.

Koepple, J. W., N. A. Slade, and R. S. Hoffman.
1975. A bivariate home range model with possible application to ethological data analysis. J. Mammal. 56:81-90.

Lieb, J. W.
1973. Social behavior in Roosevelt elk cow groups. M.S. thesis. Humboldt State Univ., Arcata. 82 p.

Mackie, R. J.
1970. Range ecology and relations of mule deer, elk, and cattle in the Missouri River Breaks, Montana. Wildl. Monogr. 20:1-79.

Marcum, C. L.
1975. Summer-fall habitat selection and use by a western Montana elk herd. Ph.D. thesis. Univ. Mont., Missoula. 294 p.

McCullough, D. R.
1969. The tule elk: its history, behavior and ecology. Univ. Calif. Publ. Zool. 88:1-209.

Moen, A. N.
1973. Wildlife ecology. W. H. Freeman and Co., San Francisco, Calif. 458 p.

Murie, O. J.
1951. The Elk of North America. The Stackpole Co., Harrisburg, Pa., and Wildlife Management Institute, Washington, D.C. 386 p.

Neu, G. W., C. R. Byers, and J. M. Peek.
1974. A technique for analysis of utilization-availability data. J. Wildl. Manage. 38(3): 541-545.

Newman, C. C.
1956, Biologist's annual report--Elk. Unpublished manuscript. Olympic National Park, Port Angeles, Washington.

Regelin, W. L.
1979. Nutritional interactions of black-tailed deer with their habitat in southeast Alaska. p. 60-68. In O. C. Wallmo and J. W. Schoen, eds. Sitka black-tailed deer: proceedings of a conference in Juneau, Alaska. USDA Forest Service, Series No. R10-48. Juneau, Alaska. 231 p.

Schoen, J. W.
1977. The ecological distribution and biology of wapiti (*Cervus elaphus nelsoni*) in the Cedar River watershed, Washington. Ph.D. thesis. Univ. Wash., Seattle. 408 p.

Schwartz, J. E.
1939. The Olympic elk study. Unpublished manuscript. U.S. Forest Service, Olympia, WA.

Schwartz, J. E., and G. E. Mitchell.
1945. The Roosevelt elk on the Olympic Peninsula, Washington. J. Wildl. Manage. 9:295-319.

Shoesmith, M. W.
1979. Seasonal movements and social behavior of elk on Mirror Plateau, Yellowstone National Park. p. 166-176. In M. S. Boyce and L. D. Hayden-Wing, eds., North American elk: ecology, behavior, and management. Univ. of Wyo., Laramie. 294 p.

Silver, H., N. F. Colovos, J. B. Holter, and H. H. Haynes.
1969. Fasting metabolism of white-tailed deer. J. Wildl. Manage. 33:490-498.

Skinner, M. P.
1933. Report on elk conditions in Olympic Mountains to Boone and Crockett Club. Unpublished manuscript. Olympic National Park, Port Angeles, Washington.

Thompson, C. G., J. B. Holter, H. H. Haynes, H. Silver, and W. E. Urban, Jr.
1973. Nutrition of white tailed deer I. Energy requirements of fawns. J. Wildl. Manage. 37:301-311.

Pollutant Monitoring in the Olympic National Park Biosphere Reserve

Kenneth W. Brown and G. Bruce Wiersma

ABSTRACT

Scientific interest in global contamination has been instrumental in the establishment of 33 Biosphere Reserve sites throught the United States. These sites, including many pristine areas that are and have been protected from industrial development, serve as areas in which present and future environmental pollution can be assessed.

The Olympic National Park Biosphere Reserve was selected by the National Park Service as the second U.S. site, following Great Smoky Mountains National Park, for pollutant monitoring studies. These studies, conducted by the U.S. Environmental Protection Agency, were designed to identify levels of trace elements and organic contaminants in both the physical and biological media. Based on the Great Smoky Mountains experience, 10 remote sites within the Park were selected for intensive sampling. Sampling areas were located in the Hoh, Quinault, and Dosewallips River drainages; at Anderson and Grand Pass; and near the northern most edge of Blue Glacier. Their proximity to vehicle-traveled roads varied from 5 to 12 miles. An additional sampling area was located close to Ozette Lake near the Pacific Ocean.

The media sampled included air, water, soils, litter, and several different plant species. These samples were processed and analyzed for selected organic and 26 different heavy metal contaminants such as lead, cadmium, nickel, and zinc. Additional analyses included airborne particulate characterization, such as size determinations and the identification of chemical constituents.

The data obtained identify then current baseline contaminant concentrations and will assist in resource management and environmental quality programs.

Kenneth W. Brown and G. Bruce Wiersma, Exposure Assessment Research Division, Environmental Monitoring Systems Laboratory, U.S. Environmental Protection Agency, Las Vegas, Nevada 89114.

INTRODUCTION

In August 1979, a study was initiated to identify pollutant concentrations in specific biological and physical media in Olympic National Park for the development of a pollutant monitoring system. This study, similar to that conducted in Great Smoky Mountains National Park as described by Wiersma et al. (1979), was a cooperative effort between the U.S. Environmental Protection Agency's Environmental Monitoring Systems Laboratory at Las Vegas (EMSL-LV) and the National Park Service (NPS).

Olympic National Park, a public reserve of approximately 360 000 ha (889,000 acres), is one of the 33 designated biosphre reserves in the United States. The origination of the Biosphere Reserve System and the subsequent selection of Olympic National Park and other specific Biosphere Reserve sites were initiated in part because of a concern for United States and global contamination from human industrial activities.

The concept and criteria used to establish this reserve system have been described previously by many researchers including Franklin (1977) and Wiersma and Brown (1979). Basically, the Biosphere Reserve sites are physically and biologically undisturbed and protected natural background areas where life processes occur with minimal human interference. They are of value to concerned environmentalists and scientists because they:

1. provide permanent and undisturbed areas where long-term background or baseline studies can be conducted on environmental and biological features;
2. are natural sources of genetic pools of animal and plant species;
3. provide areas for assessing, identifying, and recording the physical and biological state of the environment;
4. provide endemic habitat to obtain data from local environmental studies instrumental to the formation of management plans and policies for the Reserve;
5. provide areas for long-term biological research; and
6. serve as sites for measuring and assessing the concentration and impact of human made pollutants on biological systems.

Use of Biosphere Reserves as pollutant monitoring sites originated with the Man and Biosphere program (MAB) at the 16th General Conference of the United Nations Educational, Scientific and Cultural Organization (UNESCO) and with a 1970 ad hoc task force concerned with the Global Network for Environmental Monitoring (GNEM). The recommendations, criteria, and coordination of these groups of concerned scientists have been described previously (Wiersma and Brown 1979).

The experimental design, methods, and approach used for collecting data to develop a pollutant monitoring system for Olympic National Park followed the basic principle of the monitoring systems design described by Schuck and Morgan (1975) and Morgan et al. (1979). The approach used addresses both the multimedia concept (sampling and analysis of pertinent biological and physical media) and the systems concept (identification of the interaction and/or kinetics between media). The methods for assessing and addressing the systems concept using kinetic modeling have been described by O'Brien (1979) and Barry (1979). Wiersma (1979) applied this method to the analysis of a monitoring project conducted by the Environmental Protection Agency, Environmental Monitoring Systems Laboratory, Las Vegas, and National Park Service in Great Smoky Mountains National Park.

This report describes and identifies the sampling locations, media collected, and equipment used in Olympic National Park. Objectives were to determine pollutant levels, assess variability between collected media, determine biological accumulators of selected contaminants, and evaluate sampling equiment. Media sampled included air, litter, water, vegetation, and soil.

SAMPLING METHODS

To sample adequately this biologically diverse National Park, seven multimedia and eight single media locations were selected. All the sites were chosen to obtain data representative of a particular set of relatable biological and/or physical parameters. For example, multimedia sampling locations were selected in areas impacted and influenced by ocean environments. In addition, high and low altitude sampling locations, representative of indigenous forest communities and influenced by both regional and local meteorological conditions, were selected. Single media sampling locations were established to provide pollutant data on the major incoming and outgoing routes of exposure. These included high altitude air sampling sites and water sampling locations in the Park's major drainage systems.

The major route of exposure for this Park is considered to be the air pathway. As such, emphasis was placed upon the methods and means to collect and measure airborne contaminants. This is especially important in Olympic National Park, in that, even though the predominant air masses originate to the north and northwest, local topography influences the air flow to a great extent. According to B. Moorhead (Research Biologist, Olympic National Park, Port Angeles, Washington, personal communication, 1979), the air flow is affected by the conical shape of the local terrain. This phenomenon can create problems in assessing contaminant impact from large incoming air masses versus that from possible transport and redeposition by local meteorological conditions.

The techniques and procedures for sampling air in Biosphere Reserves have been described previously by Brown et al. (1979). Equipment used in the Olympic National Park study included a pump and air sampling devices. The pump, a Dupont P400A air pump, is capable of a maximum flow of 4000 cm^3/min. The power sources are Gates[1] sealed acid batteries connected in parallel that are capable of operating the pump for 10 continuous days.

---

[1]Registered trademark.

The air sampling devices used to collect samples at each air sampling site consisted of combinations of both plastic Millipore aerosol monitors and stainless steel holders. Both types were loaded with 47-mm-diameter Millipore filter membranes with a 0.45-µm pore size.

Collection of four air samples per site was due in part to the three different analytical procedures used to identify trace-element contamination: X-ray fluorescence, atomic absorption spectrometry, and scanning electron microscopy (SEM). The fourth sample was archived in case of loss or for further analytical requirements. Prior to use, all stainless steel holders and filter membranes were cleaned and packed in a clean laboratory facility. The clean laboratory techniques (C. Davidson, Carnegie-Mellon Univ., Pittsburg, Pa., personal communication, 1979) were necessitated because of the low flow rates which varied between 900 and 1 000 cm^3/min per sample and the expected low elemental concentrations at each of these sampling sites (fig. 1).

Contamination of air samples was minimized after collection by wrapping each filter in aluminum foil and placing each in a plastic bag. The samples were then transported to the appropriate laboratory for analysis.

Dry fall deposition of airborne particulates was collected and examined on Teflon plates at 10 of the sampling locations. The simultaneous measurements of airborne concentrations and Teflon plate concentrations allow calculations of deposition velocities for a number of contaminants. Clean laboratory procedures also were used for the deposition plate components.

Water samples were collected by two different methods. At each sampling site, a 250-ml grab sample was collected from a nearby stream. The sample was placed in a precleaned (acid-washed) polyethylene bottle and fixed with 1 ml of ultrex nitric acid. At four sites, a gravity flow resin column was used. This column, packed with selected resin filters for entrapping selected organic compounds, was placed in the river or stream to be sampled. Natural water flow forced water through the column. The resins selected for this water sampling device are described by Wiersma et al. (1979).

Vegetation, soil, and litter were collected at seven locations (fig. 1). The design and number of samples collected were based upon previously defined factors and limitations as described by Wiersma et al. (1979) and Wiersma and Brown (1979). At each collection location, five different plant species were taken from 10 different subsites. Thus, a total of 50 plant samples, representing 10 replications of 5 different species, was collected for analysis. In addition, one soil sample (0-5 cm in depth) and one litter sample was collected from each of the subsites, making a total of 10 samples each per sampling location. The 50 plant, 10 soil, and 10 litter samples were placed in clean polyethylene bags and sealed. All were analyzed for trace elements. One soil and one litter sample collected from one of the subsites were placed in clean 1-liter Teflon bottles for organic analysis.

Figure 1.--Sampling locations in the Olympic National Park.

Rain gauges were installed at the seven plant- and soil-collection locations to collect and measure any precipitation. No precipitation fell at these sites during the collection period.

SAMPLING LOCATIONS

Single Media Air Sampling Sites

Three different sites were selected for high altitude air sampling. As shown in figure 1, the sites are fairly evenly distributed in the higher elevations of the Park. The first site was located on the ridge above Moose Lake, with access via the ridge line or by the Grand Pass Trail from Hurricane Ridge. The second site was located about 900 m south of the Glacier Meadows Ranger Station near the eastern edge of the Blue Glacier moraine. The third site was located about 1 800 m west of Anderson Pass and 400 m south of the Anderson Pass Trail.

The following criteria were used for site selection: the site should be

1. free of local contamination and at least 5 km from the nearest road used by automobiles and other vehicles;
2. located at as high an elevation as possible, and
3. located in a clearing in which the diameter is at least five times the height of the surrounding forest.

The sampling heads at these three sites were supported by aluminum stands. The heads were 1.5 m from the ground. The pumps, battery, and flow meters were placed on the ground during operation.

Single Media Water Sampling Sites

Four different major drainage systems were chosen for the resin filter collectors. Grab samples, as previously described for elemental analysis, also were collected. The drainage systems selected for sampling, as shown in figure 1, included the Elwha, Hoh, Quinault, and Dosewallips. These four drainage systems drain slightly more than 50 percent of the Park's watersheds. Length of sampling varied from 5 to 8 days.

In addition to water samples, surface snow samples were collected from the Blue Glacier for trace element analysis. Location of this collection site, as shown in figure 1, was the eastern edge of the glacier near its midpoint.

Multimedia Sampling Sites

At these sites (fig. 1), air, water, vegetation, soil, and litter were collected. Air monitoring equipment and techniques used for sampling air in these locations were identical to those used for the single media air sampling sites. The only difference was that the filter holders were placed under a canopy and supported by young saplings. The number of samples and the techniques used for sampling vegetation, soils, and litter were described previously. In addition, deposition plates were placed near the air sampling equipment and grab samples of water were collected from each location.

Low Altitude Hoh

On the north side of the Hoh River approximately 1 800 m west of the Olympus shelter, the site is dominated by Sitka spruce, Picea sitchensis, and western hemlock, Tsuga heterophylla. As described by Franklin and Dyrness (1973), the distinctive characteristics of this forest are (1) an abundance of Acer macrophyllum and A. circinatum; (2) conspicuous coverage of epiphytic plants, with one of the most abundant being Selaginella oregana, a club moss; (3) abundant nurse logs; and (4) relatively great densities of Roosevelt elk (elk are both seasonal and resident).

The major herbaceous species are Oxalis oregana, Polystichum munitum, Tiarella unifoliata, Carex deweyana, Trisetum cernuum, Maianthemum dilatatum, Rubus pedatus, Montia sibirica, Athyrium filix-femina, and Gymnocarpium dryopteris; Polystichum and Oxalis are clearly the most important. A heavy moss layer is typical including Eurhynchium oreganum, Hypnum circinale, Rhytidiadelphus loreus, Leucolepis menziesii, Plagiomnium insigne, and Hylocomium splendens as more common species. The heavy epiphyte coverage includes the cryptogams Isothecium stoloniferum, Porella navicularis, Rhytidiadelphus loreus, Radula bolanderi, Frullania nisquallensis, Scapania bolanderi, and Ptilidium californicum, and the vascular plants Polypodium vulgare and Selaginella oregana. This vegetation type occurring on the second terrace stage is further characterized by areas of shallow stony soil.

Plant species collected included:

1.	Acer circinatum	vine maple
2.	Tiarella trifoliata	foam flower
3.	Oxalis oregana	wood sorrel
4.	Polystichum munitum	sword fern
5.	Rhytidiadelphus loreus	moss

High Altitude Hoh

Located about 2 000 m north of the Glacier meadows shelter just west of the Hoh trail, this sampling area is dominated by mountain hemlock, Tsuga mertensiana with areas of silver fir Abies amabilis. This vegetative type usually dominates the higher forested zones along the western slopes of the Olympic National Park.

Chamaecyparis nootkatensis is a major associate, with Pseudotsuga menziesii, Abies lasiocarpa, and Pinus monticola as minor associates. Of the wide variety of understory species, many belong to the Ericaceae, Rosaceae, and Compositae families.

Soils are podzolic; however, the degree of podzolization varies depending on location.

Species collected included:

1.	Vaccinium ovalifolium	oval-leaf huckleberry
2.	Vaccinium membranaceum	thin-leaved huckleberry
3.	Vaccinium alaskaense	Alaska huckleberry
4.	Rubus pedatus	blackberry
5.	Streptopus streptopoides	twisted-stalk

Ocean Site (Ozette)

This sampling site was located about 5 000 m southwest of the Ozette trailhead to Sand Point. Described by Franklin and Dyrness (1973), this vegetation type is a western hemlock-Sitka spruce/Gaultheria shallon, salal, association, commonly found along the coastline and including a dense shrub layer of salal. This species commonly contributes over 40 percent of the species compositon. Other common species include Oxalis oregana and Thuja plicata.

Species collected included:

1. Moss species (genus and species unidentified)
2. Fern species (genus and species unidentified)

3.	Lysichitum-americanum	skunk cabbage
4.	Vaccinium ovatum	evergreen huckleberry
5.	Gaultheria shallon	salal

Low Altitude Quinault

About 2 000 m northeast of the Enchanted Valley trailhead in the east fork of the Quinault River, this sampling area was a forest type dominated by Pseudotsuga menziesii and western hemlock, a type that has a rich abundance of understory species including grasses, ferns and a wide variety of mosses. Located on a second-stage terrace, the soils were well drained and well developed.

Table 1--Analytical methods utilized for the analysis of the Olympic National Park samples

Sample type	Analytical method	Analysis
Water	Gas chromatograph-mass spectrometry (GC-MS)	Purgeable organics Non purgeable Organics
Water	Inductively coupled plasma emission (ICPES) Spark source mass spectrometry (SSMS)	Multi-element
Air	X-ray fluorescence Scanning electron microscope (SEM) Atomic absorption spectrometry	Multi-element Particular sizing and composition Multi-element
Vegetation (includes litter)	Plasma emission spectroscopy Gas chromatograph-mass spectrometry	Multi-element Organic
Soils	Atomic absorption spectrometry	Multi-element

Species collected included:

1.	*Maianthemum dilatatum*	beadruby
2.	*Pteridium aquilinum*	bracken
3.	*Cornus canadensis*	bunchberry dogwood
4.	*Clintonia uniflora*	queens cup
5.	*Vaccinium parvifolium*	huckleberry

High Altitude Quinault

Located 50 m north of the Enchanted Valley Trail, approximately 1 800 m northeast of the Chalet shelter, this area was in a vegetative zone characterized and dominated by western hemlock *Tsuga heterophylla*. Associated species include *Pseudotsuga menziesii* and *Thuja plicata*. Trees such as *Alnus rubra*, *Acer macrophyllum* and *Castanopsis chrysophylla* are widespread.

Soils are moderately deep and of medium acidity. Organic matter is high in some areas.

Species collected included:

1.	*Vaccinium alaskaense*	Alaska huckleberry
2.	*Tiarella trifoliata*	foam flower
3.	*Rubus spectabilis*	blackberry
4.	*Lobarium oreganum*	lichen
5.	Moss species	moss

Low Altitude Dosewallips

This sampling area was located about 2 500 m west of the Dosewallips trailhead on the west fork of the Dosewallips River. It was dominated by western hemlock and *Pseudotsuga menziesii* the subdominant species, and the general aspect was similar to that found at the high Quinault sampling site.

Species collected included:

1.	Moss species	moss
2.	*Polystichum* species	fern
3.	*Berberis nervosa*	Oregon grape
4.	*Gaultheria shallon*	salal
5.	*Rhododendron* species	rhododendron

High Altitude Dosewallips

The location of this sample area is about 2 500 m northeast of the Anderson Pass shelter on the west fork of the Dosewallips River. The dominant species and the vegetative aspect were similar to that found at the high altitude Hoh sampling site.

Species collected included:

1.	Moss species	moss
2.	*Abies amabilis*	silver fir
3.	*Ribes* species	gooseberry
4.	*Vaccinium ovalifolium*	oval-leaf huckleberry
5.	*Vaccinium membranaceum*	thin-leaved huckleberry

ANALYTICAL TECHNIQUES

All samples were prepared for analysis at the U.S. Environmental Protection Agency's Environmental Monitoring Systems Laboratory at Las Vegas. Detailed procedures and techniques concerning the analytical methods used for each sample type have been described (Wiersma et al. 1979) and (Wiersma and Brown 1979). Table 1 shows the analytical methods presently being utilized for analysis of the Olympic National Park samples.

All the samples have been prepared and presently are being analyzed for selected contaminants. (See Wiersma and Brown 1979).

CONCLUSIONS

The collection and assessment of biological and physical media from selected areas of the Olympic National Park will be used to develop a multimedia pollutant monitoring system. The techniques used, associated with long-term monitoring data, will serve to identify baseline levels, identify pollutant concentrations, determine trends, and define the physical and biological responses to synthetic contaminants.

LITERATURE CITED

Ad Hoc Task Force on GNEM.
1970. A global network for environmental monitoring. A report to the Executive Committee, U.S. National Committee for the Intern. Biolog. Progr.

Barry, P. S.
1979. An introduction to the exposure commitment concept with reference to environmental mercury. MARC Rep. 12. Monit. and Assess. Res. Cent. Chelsea Coll., Univ. London.

Brown, K. W., G. B. Wiersma, and C. W. Frank.
1979. A battery-operated air sampler for remote areas. EPA-600/4-79-071. U.S. Environ. Prot. Agency, Las Vegas, Nevada.

Franklin, Jerry F.
1977. The Biosphere Reserve program in the United States. Science 195:262-267.

Franklin, Jerry F., and C. T. Dyrness.
1973. Natural vegetation of Oregon and Washington. USDA For. Serv. Gen. Tech. Rep. PNW-8. 417 p.

Morgan, G. B., G. B. Wiersma, and D. S. Barth.
1979. Monitoring on Biosphere Reserves for regional background levels of pollutants. In Proc. of the United States-Union of Soviet Socialist Republics, Symp. on Bios. Res., Moscow, USSR, May 1976. USDA For. Serv. Gen. Tech. Rep. PNW-82, p. 90-104. Pac. Northwest For. and Range Exp. Stn., Portland, Oreg.

O'Brien, B. J.
1979. The exposure commitment method with application to exposure of man to lead pollution. MARC Rep. 13. Monit. and Assess. Res. Cent. Chelsea Coll., Univ. London.

Schuck, E. A., and G. B. Morgan.
1975. Design of pollutant oriented integrated monitoring systems.. Intern. Conf. on Environ. Sensing and Assessment. Pap. No. 20-6.

Wiersma, G. B.
1979. Kinetic and exposure commitment analyses of lead behavior in a Biosphere Reserve. MARC Rep. 15. Monit. and Assess. Res. Cent. Chelsea Coll., Univ. London.

Wiersma, G. B., and K. W. Brown.
1979. Recommended pollutant monitoring system for Biosphere Reserves. Proc. Second Conf. on Sci. Res. in the National Parks. San Francisco. Nov. 26-30.

Wiersma, G. B., K. W. Brown, R. Herrmann, C. Taylor, and J. Pope.
1979. Great Smoky Mountains preliminary study for Biosphere Reserve pollutant monitoring. EPA-600/4-79-072. U.S. Environ. Protec. Agency, Las Vegas, Nevada.

Research/Management Prescribed Burning at Lava Beds National Monument

Robert E. Martin, Craig M. Olson, and James Sleznick, Jr.

ABSTRACT

Prescribed burning at Lava Beds National Monument has been developed for research and management. Research objectives have been to develop burning techniques and prescriptions, evaluate effects, and develop cost data. Management objectives have been to restore the historic vegetation sequence, and reduce accumulated fuels. Twenty-seven prescribed burns have been conducted, ranging in size from 0.1 to 570 hectares (ha) for a total of 1 088 ha or 5.8 percent of the Monument area. Prescriptions and techniques have been developed for burning all vegetation types on the Monument, primarily shrub-grass and pine-shrub types.

Robert E. Martin and Craig M. Olson, research foresters, U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station, Silviculture Laboratory, Bend, Oregon; and James Sleznick, Jr., superintendent, Lava Beds National Monument, Tulelake, California.

INTRODUCTION

Lava Beds National Monument has received extensive attention since 1973 concerning prescribed burning and fire effects on flora and fauna. In this paper, we summarize the prescribed burning portion of the program. Prescriptions, techniques, area descriptions, general effects, and costs of prescribed burning in comparison to wildfires are used to illustrate both the research and management aspects of the program. Specific effects are covered in other papers.

The Monument lies in extreme northern California about 80 km southeast of Klamath Falls, Oregon. A modified maritime climate prevails with the Cascade Range to the west providing a distinct influence on the climate. Summers are dry, with only 9 cm of the annual 33.7 cm precipitation falling in May through August. Elevation ranges from about 1 230 m (4,030 ft) in the big sagebrush, Artemisia tridentata,-grass types at the north end of the Monument to 1 600 m (5,250 ft) in the ponderosa pine, Pinus ponderosa,-antelope bitterbrush, Purshia tridentata, types in the south end of the Monument. The north slopes of buttes, which rise to 1 670 m (5,480 ft), often are covered by a ponderosa pine-greenleaf manzanita, Arctostaphylos patula, -snowbrush ceanothus, Ceanothus velutinus, community.

Fires, started by Indians or lightning, were frequent in most parts of the Monument area before the advent of successful fire control. Prehistoric fires occurred every 5 to 15 years, as determined from examination of 76 fire-scarred cross-sections of downed logs. Since 1933, the Monument has experienced an average of about 40 lightning fires per million acres per year (Martin et al. 1977). Until 1950, much of the northern two-thirds of the Monument with flashy shrub-grass fuels, burned every 5 years.

Fire control, in connection with a catastrophic western pine beetle, Dendroctonus brevicomis, outbreak in the late 1920's and heavy grazing around the turn of the century has done much to modify the vegetation and allow heavy fuel accumulation. Heavy grazing and fire exclusion contributed to decline of native bunchgrasses, enhanced invasion of cheatgrass, Bromus tectorum, and other exotic plants, and allowed increased numbers of big sagebrush, gray rabbitbrush, Chrysothamnus nauseosus, and western juniper, Juniperus occidentalis. At middle elevations, curlleaf mountainmahogany, Cercocarpus ledifolius, and bitterbrush have proliferated from fire exclusion following loss of pine. These stands are now old and decadent and form an explosive fuel complex as evidenced by the 1973 Lava Wildfire. At higher elevations, the pine-bitterbrush-manzanita complex, in some places being invaded by white fir, Abies concolor, can now be lost entirely in a wildfire. The 1977 Scarface-Mud Wildfire (36 000 ha) and 1978 Twins Wildfire (10 000 ha) burned nearby in types similar to Lava Beds fuel types. These fires attained large sizes even though suppression efforts were vigorous, the terrain is very accessible, and no extreme weather conditions prevailed. These fires indicate a potential for catastrophic fire in the Monument.

OBJECTIVES OF THE RESEARCH/MANAGEMENT PRESCRIBED BURNING PROGRAM

The research/management prescribed burning program has several objectives. These may conveniently be separated into two groups, though there is overlap between them.

Research

(1) Develop burning techniques and prescriptions to achieve objectives in fuel and vegetation management.
(2) Record effects of fire under differing conditions on flora, fauna, and fuels.
(3) Develop cost data.

Management

(1) Restore "historic" vegetation sequence.
(2) Reduce accumulated fuels.
(3) Train personnel in fire use.
(4) Develop fire management plans and programs.

The interdependency of the objectives may or may not be apparent. The prescription and technique development, however, has often been conducted on management-sized units. Thus, cost data can be obtained, along with flora and fuel changes. Monument personnel are trained on the burns in reducing fuels and the beginning steps of restoring the historic vegetation sequence that have been taken. The historic vegetation sequence is considered to be that which would have existed had we not interfered following the 1873 Modoc Indian War, which occurred on the northern end of the Monument. The supposed vegetation has been constructed from photographs, live and dead vegetation, historic accounts, and fire history. Since most burns have been planned in strategic locations, they fit into overall fire management planning. We have been able to move toward accomplishment of the multiple objectives by combining the efforts of two small staffs at the Bend Silviculture Laboratory and Lava Beds National Monument, with the assistance of personnel from the Doublehead Ranger District of the Modoc National Forest.

Our main discussions will center on prescriptions and techniques for the major vegetation complexes of the Monument, the costs for burning these areas, and how these fit into fire and vegetation management of the Monument. Effects of fire on flora and fauna are covered in several other papers in this report. Johnson and Smathers (1976) discussed historic vegetation on the Monument and the role of grazing, beetles, and fire control in changing it. Martin and Johnson (1979) discuss stages of the prescribed burn research program, including fire history, succession under varying fire regimes, and general management planning. Other papers relating to fire effects in the Lava Beds cover small mammals (Frenzel 1978, Frenzel et al. 1979), Columbia sharptail grouse, Pedioecetes phasianellus, (Starkey and Schnoes 1979), deer, Odocoileus hemionus, (Schnoes 1977), bobcats, Lynx rufus, (Zezulak 1978), vegetation (see Olson in this report), and bird nesting (see Tiagwad et al. in this report). We will only allude to results of these studies here as space will permit us to show only the relationship to prescription and technique development.

PRESCRIPTION RECOMMENDATIONS

The following prescription conditions are for the major vegetation types of Lava Beds National Monument and were developed from our experience at the Monument and elsewhere. When considering conditions for burning, never use all the "worst" or "best" conditions for a given burn. For example, don't pick the driest fuels, lowest humidities, and highest temperatures in a situation where heavy fuels exist in stands with low crowns. Prescription conditions, as given, represent a range of conditions we have found to be satisfactory. Modifications should be made to fit specific vegetation conditions or transitions from one type to another.

Prescribed burning began in 1974 with two 0.01-ha units burned in cheatgrass. From 1974 to 1979, 27 fires have been conducted, some as reburns to evaluate the effect of repeated fires (table 1). The largest unit of 570 ha (1,400 acres) was burned in the fall of 1979. Little burning was done in 1978 because resources were limited. The units, their size, burning conditions, and specific comments pertinent to each burn are given in table 1 for the information of those who might use fire in similar vegetation and fuel situations. These data contributed to the prescription ranges given below.

Cheatgrass

Burning has reduced cheatgrass seed density on soil surfaces, although apparently not enough to enable native bunchgrasses to become reestablished rapidly (Olson et al. 1981). Where some native bunchgrass, particularly bottlebrush squirreltail, Sitanion hystrix, is present, burning has appeared to increase both vigor and density of this species even though our early sampling techniques were not sensitive enough to record these changes.

The flammability and horizontal fuel conductivity of cheatgrass stands permit a relatively wide range in prescription conditions. Prescription development has the important objective of reduction of cheatgrass as an undesirable exotic invader.

Season: Anytime following cure in June until fall precipitation.
Wind: 0 to 15 km/hr.
Relative humidity: 20 to 45 percent.
Precipitation: Preferably at least 3 days following precipitation to permit duff drying and higher seed kill.
Temperature: 10° to 30°C.
Burning pattern: Backfire downwind line; strip headfire to develop burnout of 10 to 30 m, depending on wind, humidity, and fuel; headfire unit; center or ringfiring can be used under zero wind conditions.
Fireline: Excellent fuel for use of wetline (Martin et al. 1977); where duff exists, extra caution in use of wetline is necessary.

Shrub-Grass

Dominant shrubs in these situations are primarily sagebrush, gray rabbitbrush, or bitterbrush. Grasses may be quite varied but are generally a mix of bunchgrasses interspersed with cheatgrass. Burns in these types are generally conducted to reduce shrub and increase native bunchgrass cover. In our burning, we have sought to achieve a mosaic of burned and unburned areas within the burn units. If the original burn does not achieve a satisfactorily high burn percent, additional ignition can be used to increase burn percent in the days following the main burn.

Season: Early summer through late fall will be satisfactory; if bunchgrass recovery is a major consideration, late fall has been most productive (see Olson et al. in this report).
Wind: 3 to 16 km/hr most desirable; lower winds will reduce probability of spread if fuels are discontinuous; gusts to 25 km/hr or higher are no problem if fire is not near fireline.
Relative humidity: Line burnout 20 to 40 percent; general burn 15 to 40 percent; in early season burns when grasses are not cured, humidity should be 30 percent or less.
Precipitation: Not critical; could be only 1 or 2 days before fire.
Temperature: 10° to 30°C.
Burning pattern: Back out downwind lines,[1] then strip headfire[2] 30 to 80 m, depending on wind fuels; then headfire.[3]
Fireline:[4] Wetline[5] or handline.[6]

Ponderosa Pine

Most ponderosa pine types have bitterbrush as an understory. Small areas of pine within the Monument may have big sagebrush, greenleaf manzanita, or snowbrush ceanothus as the dominant shrub. Prescriptions would not be much different for the other shrubs, although slightly drier conditions may be appropriate.

---

[1]Set a fire that burns into the wind from the downwind side of the fireline.

[2]A fire lighted at a designated distance upwind from the burned strip resulting from the back out fire.

[3]A fire burning with the wind.

[4]An established or natural break in the fuel, generally down to mineral soil.

[5]Two wet strips, usually made by a pumper unit, with a dry area between.

[6]A fuel break dug with hand tools.

Terminology has been taken from Glossary Terms for Fire Management Planning, USDA For. Serv., January 1979; and Planning for Prescribed Burning in the Inland Northwest, by Martin and Dell, USDA For. Serv. Gen. Tech. Rep. PNW-76; 1978.

Table 1--Summary table of prescribed burns conducted at Lava Beds National Monument, 1974 to 1979

Prescribed burn	Date burned	Vegetative types	Size	Temperature		Humidity
			ha	°C	°F	Percent
Cheatgrass	6/--/74	Cheatgrass	0.1			
West Wildlife Overlook 1	6/25/75	Sagebrush-grass	7.3	14-18	58-64	33-52
West Wildlife Overlook 2	6/24/76	Cheatgrass	2.0	20-21	69-70	34-35
Gillem Cheatgrass	6/26/75	Cheatgrass	0.8	17	63	42
Lava Overlook 1	6/26/75	Sagebrush-bunchgrass	0.15	21	69	30
Lava Overlook 2	8/22/75	Sagebrush-bunchgrass	0.15	21-24	69-76	33-46
Lava Overlook 3	11/2/75	Sagebrush-bunchgrass	0.14	15	59	47
Homestead Flow	6/26/75	Sagebrush-bunchgrass	12.0	21-22	69-71	23-31
Upper Ice Cave 1	6/27/75	Ponderosa pine-bitterbrush	0.7	6-16	42-61	27-62
Upper Ice Cave 2	8/22/75	Ponderosa pine-bitterbrush	0.7	24-26	76-79	21-25
Upper Ice Cave 3	11/3/75	Ponderosa pine-bitterbrush	2.0	14-19	57-67	28-50
Hovey Point	6/23/76	Sagebrush-grass	170.0	17-22	63-71	27-42
Fleener Chimneys	6/2/76	Juniper-sagebrush-bunchgrass	80.0	20-24	68-76	25-27
Little Crescent	9/20-21/76	Juniper-mountainmahogany-bitterbrush		20-23	68-73	16-28
Caldwell Loops-Upper	9/21/76	Ponderosa pine-bitterbrush		15-22	59-72	23-48
Caldwell Loops-Lower	9/21/76	Ponderosa pine-bitterbrush		15-24	59-75	17-23
Headquarters	7/7-8/77	Juniper-mountainmahogany-bitterbrush	120.0	21-28	70-82	15-25
East Caldwell	5/19/77	Ponderosa pine-bitterbrush	27.0	7-28	44-70	25-80
Gillem Camp 1	7/7/77	Juniper-sagebrush-grass	23.0	23-26	73-78	26-30
Gillem Camp 2	7/5/78	Cheatgrass	1.5	18-27	65-81	31-47
Gillem Camp 3	6/28/79	Cheatgrass	0.6	19-23	66-74	43-48
East Wildlife Overlook	9/19/78	Sagebrush-grass	12.0	14-19	57-67	21-38
Sheep Enclosure	7/5/78	Sagebrush-grass	2.0	18-23	65-74	34-47
Black Lava Flow	6/6/79	Ponderosa pine-bitterbrush	16.0	4-12	40-53	45-60
Captain Jack's Bridge	7/2-3/79	Juniper-sagebrush-bunchgrass	40.0	21-24	69-75	29-39
Schonchin	9/11-12/79	Juniper-sagebrush-bunchgrass Juniper-mountainmahogany-bitterbrush	570.0	10-15	50-85	18-43

Fuel moistures											
		Time lag class				Live					
Litter	Duff	1	10	100	1000	Foliage	Twigs	Grass	Wind	Percent burn	Comments
- - - - - - - - - - - - - - Percent								- - - - - - - - - - - - - -	km/hr		
16	--	9	7	--	--		181	137	6-16	80	
4	--	7	6	--	--		105	20	6-8		*Sitanion hystrix* 98-percent M.C.
11								128	5-10	100	
13	--	7	7	--	--		154	101	9-14	100	
9	--	14	28	--	--		136	77	0-10	100	
12	--	10	11	--	--		133	28	6-12	100	
12	--	16	--	--	--		166	109	6-9	100	
15	115	14	14	--	--	133			3-11	90	
10	34	11	14			89			2-6	100	1-2 cm rain 8/18/75
20	228	14	15			129			calm	50	Poor coverage of plot
10	--	10	9			159		36	5-12, G16	80	Line burnout 40- to 50-percent RH
		7	5			123		40	13-19		
		10	7	9		74	70	25	0-16	70	2-stage, resumed after Caldwell
13		9	12	13	12	74	66		0-8, G16		2-stage
13		9	12	13	12	74	66		0-8, G16	20	Stopped burning at 17-percent RH
		5	4			116	72	48	0-16	40	
			Destroyed in oven						0-11	80	3-stage burn; 1.1 cm rain in 3 days prior
2		7	7			194		22	0-11	30	Needed lower humidity and higher grass cure
								33	6-11	90	
								7	3-12	80	
--	--	6	7	--	--	134	--	9	0-16	90	Reburned cheatgrass 10/10/79 (2 burns)
									3-18	70	
									0-12	90	Prescribed burning workshop
7		5	4			123		21	0-11		Lines burned out at 39 to 52-percent RH
7		6	6			111		18	0-10	45	

Sapling Stands

For sapling stands up to 10 cm (4 in) diameter at breast height (d.b.h.), burning prescriptions generally must allow for cool weather, strong steady winds, and only partial consumption of large fuels. Where extensive shrubs exist under these trees, it may be necessary to burn in stages. The first stage would burn the needle drape in shrubs immediately under trees, and the second stage would burn in the needle litter under the trees. Where adjacent shrub areas exist around the trees but with no needle component, a third, drier stage may be needed. The entire sequence could generally be met in 2 days of drying following a light rain in spring or extensive rain in the autumn.

Sapling-Shrub

Season: Spring, early summer, or autumn when large fuels are wet.
Wind: 2 to 16 km/hr in stand.
Relative humidity: 60 to 85 percent.
Precipitation: Light rain 1 or 2 days previous in April to June; generally 2.5 to 4 cm precipitation in autumn.
Temperature: 7° to 20°C.
Burning pattern: Generally this will be done by lighting individual shrubs or shrub patches so the fire backs through them; general pattern of lighting is not crucial, but the easiest pattern would be a spot headfiring pattern, even though individual fires will seldom spread. The second stage of this burning would be conducted under conditions for burning sapling-pine litter below.
Fireline: In pines, wetline can be used with retardants or without only where no thick duff exists.

Sapling-Pine Litter

Season: Spring, early summer, autumn; 2.5 to 4 cm precipitation in autumn will reduce tree damage by reducing fuel consumption.
Wind: 1 to 16 km/hr in stand.
Relative humidity: 30 to 60 percent.
Precipitation: Precipitation 2 to 7 days before burning can help reduce damage where heavy duff is present.
Temperature: 5° to 25°C.
Burning pattern: Back and strip headfire; adjust flame length according to wind and temperature using Van Wagner's scorch height curves as a guideline (Albini 1976).

Mature Pine-Bitterbrush-Pine Litter

Season: Spring, early summer, autumn; after conditioning by one or two burns, summer burning should present no problems.
Wind: 1 to 16 km/hr in stand.
Relative humidity: 40 to 70 percent for first burn; 20 to 50 percent for subsequent burns.
Precipitation: In autumn, burn 2 to 4 days following 2.5 cm or more of rain after September 1.
Temperature: 5° to 25°C for first burn; 5° to 30°C for subsequent burns.
Burning patterns: Back and strip headfire for first burn, adjusting strip headfire width to get desired flame length; in conditioned stands, back outline and then strip headfire or headfire as conditions permit.

EFFECTS ON FUELS AND VEGETATION

The burns have had somewhat different effects on fuels and vegetation, depending on the season and conditions under which they were conducted. Detailed information on vegetation effects is given elsewhere (see Olson et al. in this report). The effects on fuels are supplemented by data we have collected in similar burns elsewhere.

Cheatgrass

Burns have been conducted in early summer and autumn, with sampling on fuels, measurement of cover, and bioassay of cheatgrass and other annual seeds before and after burning. Some areas have not been burned in three successive years to evaluate any cumulative effect of fire on cheatgrass cover and seed count. Some reduction in seed count has been achieved. More important, the fire seemed to restore vigor to scattered bunches of bottlebrush squirreltail, as well as encouraging new plants of this native species. The reinvigorated bunches apparently exert a strong allelopathic effect on surrounding cheatgrass, but the effect appears to diminish by the 3d year.

Prescribed burning removes almost all standing fuel in cheatgrass stands, the remaining standing fuels generally being uncured cheatgrass, bunchgrasses, or mustards. The amount of duff consumed varies depending on humidity and recent weather conditions. Fire hazard is negligible until the cheatgrass cures the following summer.

Shrub-Grass

Effects of fire on vegetation in shrub-grass types are strongly dependent on burning and vegetation conditions. Weather conditions at the time of the burn may also alter the effect of fire on vegetation. There is a limited range of conditions under which fire will spread in these types. Previous precipitation may be important in the degree of shrub sprouting.

Big sagebrush and mountainmahogany are readily killed by fire and generally do not sprout. Up to 80 percent of gray rabbitbrush plants are killed by spring and early summer fires. Up to 30 percent of bitterbrush plants may sprout when burning is conducted under cool, moist autumn conditions, lesser numbers in early summer. Green rabbitbrush, *Chrysothamnus viscidiflorus*, and blooming rabbitbrush, *Haplopappus bloomeri*, survive burning under a wide variety of conditions, and bitter cherry, *Prunus emarginata*, sprouts prolifically even after very severe wildfires.

The native bunchgrasses respond well to burning under most conditions depending on phenological stage. Bluebunch wheatgrass, *Agropyron spicatum*, Idaho fescue, *Festuca idahoensis*, bottlebrush squirreltail, and giant wildrye, *Elymus cinereus*, recover rapidly from burning. Others such as Sandberg's bluegrass, *Poa sandbergii*, may be set back considerably by burning. Uncured perennial grasses seem to be most sensitive when fire is carried by cured annuals such as cheatgrass.

Fuels in the shrub-grass type are reduced so that fire hazard is very low until the next summer. Grass and forb fuel weights are reduced from around 0.3 t/ha to around 0.1 t/ha.

Most dead shrub components, both standing and down, are consumed during burning, and many live components are converted to standing dead. In sagebrush, the partly live stems with shredded, flammable bark are often burned off, thus becoming dead and down fuel.

Fuel reduction on an area basis depends on percent shrub cover before burning. If canopy cover were 100 percent before burning, total fuel loads for sagebrush and bitterbrush are given in table 2. Fuel load for partial canopy cover can be calculated by multiplying by the fraction of area covered by shrub canopy. Most of the burns in the shrub-grass types have been designed to cover 50 to 70 percent of the area within the firelines, leaving a mosaic of vegetation. Fuel reduction and vegetation effects are measured as burned or unburned area to give more accurate indication of fire impact. The mosaics enhance wildlife habitat, improve esthetics, and approach the natural fire effects.

Pine-Bitterbrush

Season and precipitation prior to burning are very important in the effects of fire on vegetation in this type. Effects on shrub and herb vegetation are similar to that in shrub-grass types. Ponderosa pine is quite resistant to fire except as a seedling, and even larger seedlings can withstand a very light fire. The tree is killed by crown scorch or by girdling near the base. At Lava Beds, we have killed trees by girdling only when the trees were very small (less than 5-cm diameter at the base) and growing in heavy duff, or when logs or stumps were consumed next to larger trees.

Most tree mortality has resulted from crown scorch (or consumption). In the August 1975 Upper Ice Cave burn, 29 percent of the pine were killed. In no other burns at Lava Beds, has tree kill exceeded 13 percent, and these were the smaller trees in the stands (see Olson et al. in this report).

Fuels before and after burning on the East Caldwell unit in pine-bitterbrush are given in table 3. The data were from 24 samples of each, and the reductions of litter and material > 7.62-cm diameter were significant at the 99-percent level of confidence. The increasé in 0 to 0.63-cm down and dead fuel class was caused by burning off stems which fell to the ground after the fire had passed. The same phenomenon also accounted for an apparently lesser fuel reduction in the 0.63 to 2.54- and 2.54 to 7.63-cm size classes.

FIRE MANAGEMENT PLANNING

Prescribed burns at Lava Beds National Monument have been arranged in patterns to isolate parts of the Monument from others (fig. 1). By conducting burns in these patterns, the fire hazard will not be eliminated but the fuel complex will be more manageable. In shrub-grass fuels, prescribed burning has removed heavy accumulations of dead woody material, generally converting the vegetation to a grass-forb complex for several years. Although the grass-forb complex may allow for more rapid fire spread under some conditions, fire intensity and spotting potential will be reduced drastically, thus making fire control easier.

Table 2--Live and dead fuel loads for big sagebrush and antelope bitterbrush with 100-percent shrub canopy cover

	Foliage	Fuel diameter by size classes, (centimeters)			Total
		0-0.63	0.63-2.54	2.54-7.63	
	- - - - - - -	tonnes per hectare	- - - - - - -		
Sagebrush:					
Live	1.4	1.7	2.7	1.9	7.7
Dead	--	3.6	1.9	0.5	6.0
Bitterbrush:					
Live	0.2	1.8	1.1	0.2	3.3
Dead	--	4.5	3.1	0.4	8.0

Table 3--Fuels before and after burning on the East Caldwell unit in pine-bitterbrush

	Fuel size class (centimeters)									
	Preburn N = 24					Postburn N = 24				
	0-0.63	0.63-2.54	2.54-7.63	7.63+	Litter	0.0.63	0.63-2.54	2.54-7.63	7.63+	Litter
	- - - - -	- - - - -	- - - - -	- - - - -	tonnes per hectare	- - - - -	- - - - -	- - - - -	- - - - -	- - - - -
$\bar{x}$	0.272	1.1555	2.502	59.7	9.63	0.486	0.682	2.096	1.48	6.01
S_x	0.337	1.239	3.063	87.0	9.15	0.619	0.604	2.001	5.51	7.33

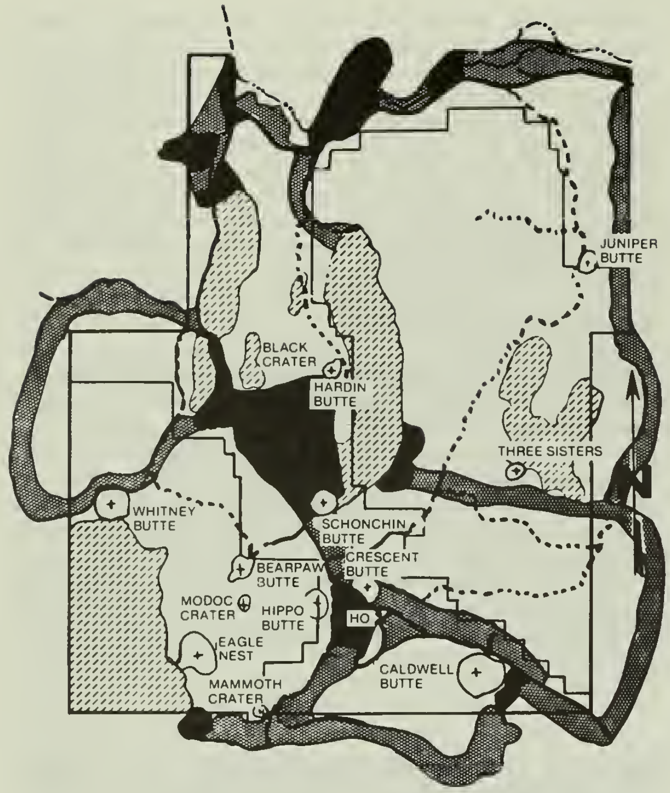


Figure 1.--Prescribed burns and wildfires (black), planned burns--fuel modification areas (cross hatching), and lava flows (dash) on Lava Beds National Monument.

Table 4--Costs of prescribed burning and wildfires recorded at Lava Beds National Monument

	Year	Area (hectares)	Total cost	Cost per hectare
		PRESCRIBED FIRES[1]		
Hovey Point	1976	170	$ 325	$ 1.91
East Caldwell	1977	27	1,389	51.44
Headquarters	1977	120	3,200	26.67
Schonchin	1979	570	2,068	3.63
		WILDFIRES		
Bighorn Fire	1973	121	$ 39,600	$ 326
Lava Fire	1973	207	132,000	638
Cougar Fire (Modoc National Forest)	1977	146	125,560	860
Strike Fire	1977	117	149,400	1,277

[1]To obtain acres from hectares, multiply by 2.47; for cost per acre, divide cost per hectare by 2.47.

In ponderosa pine stands, prescribed burning reduced fuels, making fire control relatively easy under most wildfire conditions. Potential high rate of spread and extreme fire intensity were reduced, at the same time making the pine stand quite resistant to fire.

COSTS OF PRESCRIBED BURNING

Costs of prescribed burning will be an important factor governing how much burning is done. The Monument has recorded costs on most of the large, management-sized prescribed burns and wildfires since 1976. Costs are given in table 4.

Costs of prescribed burns included the cost of preparing firelines, conducting the burns, and mop-up; not included were the costs of planning and data gathering. Planning of burns was closely tied in with general fire management planning and the two were difficult to distinguish. Sampling of fuels and vegetation, and fire documentation were considered a research function and were not included for that reason. Size of burn, type of vegetation, method and amount of line preparation, and weather variables were major factors affecting the cost of prescribed burning.

Hovey Point and Schonchin burns were in shrub-grass types. Firelines on Hovey Point were all roads or were prepared by the wetline method. Line preparation was begun by five people at 0730. By 0930, backfiring began, and the unit was burned out by 1300, with a maximum of 12 people involved. Flame lengths varied from 0.5 to 10 m, but were 2 to 5 m throughout most of the burn. Highest rates of spread were not over 2 km/hr.

The Schonchin unit required about 120 m of line preparation prior to burning. Line burnout began at 1900 one evening, continued until 0330, and resumed at 0800. The unit burn began about 1100 and was completed about 1600 with 40 percent of the unit burned. Flame lengths varied from 0.5 m in grass areas to 10 or 15 m in sagebrush and mountainmahogany thickets, with occasional western juniper ignitions reaching to about 20 or 25 m. Rates of spread were estimated to range up to 5 km/hr and depended primarily on wind and fuel conditions.

The Headquarters prescribed burn was relatively expensive for three major reasons. First, a line was cut almost one-half km through mountainmahogany-bitterbrush fuels. Second, extensive burnout was conducted on the southeast side of the burn to isolate Monument buildings and dangerous fuel concentrations. Third, two attempts to ignite the unit were unsuccessful. Unit burnout began with strip headfiring, but an alternative plan for centerfiring was used when the winds subsided. Flame lengths ranged from 2 to 10 m in sagebrush-bitterbrush fuels, 5 to 10 m in mountainmahogany, with flames to 20 m when western junipers ignited. Rates of spread up to 3 km/hr were estimated.

The East Caldwell unit required 200 m of line preparation through mountainmahogany-bitterbrush fuels. The unit contained scattered ponderosa pine and pine thickets. Most pine were saplings or poles with bitterbrush underneath. The unit was burned in three stages: (1) bitterbrush under pines were burned the morning after a light rain; (2) that afternoon the litter under the pine stands was burned; and (3) in the next 2 days, the rest of the unit was burned.

In contrast to the prescribed burns, recent wildfires in the area cost from $300 to $1,300 per ha to control, not including damages, if any. The Bighorn and Lava wildfires were both started by the same lightning storm in July 1977. Vegetation in the Bighorn fire was sagebrush-grass, and the fuel load was probably somewhat less, on the average, than that of the Hovey Point and Schonchin prescribed burns. Fuel load was definitely much less than that in the higher, wetter end of the Schonchin burn. Ratio of costs for wildfire control to prescribed burning in these vegetation types are 171:1 and 90:1.

The Lava fire burned in fuel types very similar to those of the adjacent 1977 Headquarters prescribed burn. Maximum number of people on the wildfire was 375 compared to 11 on the prescribed burn. Ratio of wildfire to prescribed burn costs per hectare are 24:1.

The Cougar and Strike fires occurred in mixed shrub and pine-shrub types most similar to the East Caldwell burn, which was small enough that it suffered from economies of scale. Still the two wildfires cost 17 and 25 times as much per hectare as the prescribed burn. The wildfires resulted in almost total loss of the sapling-pole-sawtimber stands, most of it unsalvageable, whereas only 13 percent of the trees were killed in the prescribed burn.

Presently, about 1 088 ha or 5.8 percent of the Monument's 18 720 ha have been prescribed burned. Three-quarters of the Monument, or 14 000 ha, could be burned at the cost per hectare of the Schonchin unit cost or less, or approximately $51,000. By considering the economy of burning large units, and eliminating lava areas, the remainder could probably be burned for $15 per ha or $70,000 in today's money. Thus, a program to reintroduce fire to the entire Monument could be conducted for less than the 1973 Lava wildfire, even disregarding the decreased value of the dollar.

Prescribed fires cannot eliminate the chance of wildfire and subsequent costs; but they do reduce hazard and increase the ease of control, while avoiding catastrophic wildfire. The initial costs of reconditioning fuels in the Monument will probably be much greater than costs of a maintenance prescribed burning program. Some areas of the Monument have accumulated heavy fuel loadings and may require two or three prescribed fires to reduce loadings to a manageable level. But even this would be less expensive on a per hectare basis than a catastrophic wildfire. Refined prescriptions, trained personnel, and manageable fuel complexes will enable further reductions in prescribed fire costs while approaching objectives in vegetation management.

SUMMARY

Research and management objectives have been met through the prescribed burning program at Lava Beds National Monument. Burning prescriptions and techniques have been developed and effects on vegetation measured, although more information is needed concerning effects of fire on flora and fauna. The larger burns fit into plans for fire management planning and have provided cost data for planning future burns.

LITERATURE CITED

Albini, Frank A.
1976. Estimating wildfire behavior and effects. USDA For. Serv. Gen. Tech. Rep. INT-30, 92 p. Intermt. For. and Range Exp. Stn., Ogden, Utah.

Frenzel, Richard W.
1978. The effects of prescribed burning on small mammal communities in Lava Beds National Monument. M.S. thesis, 79 p. Oreg. State Univ., Corvallis.

Frenzel, R. W., E. E. Starkey, and H. C. Black.
1979. Effects of prescribed burning on small mammal communities in Lava Beds National Monument, California. Proc. of the First Conf. on Scientific Res. in the Natl. Parks. NPS Trans. and Proc. Series 5(1):287-292.

Johnson, Arlen H., and Garrett A. Smathers.
1976. Fire history and ecology in Lava Beds National Monument. Proc. Annu. Tall Timbers Ecol. Conf. 15:102-115.

Martin, Robert E., Stuart E. Coleman, and Arlen H. Johnson.
1977. Wetline technique for prescribed burning firelines in rangeland. USDA For. Serv. Res. Note PNW-292, 6 p. Pac. Northwest For. and Range Exp. Stn., Portland, Oreg.

Martin, Robert E., and Arlen H. Johnson.
1979. Fire management of Lava Beds National Monument. Proc. of the First Conf. on Scientific Res. in the Natl. Parks. NPS Trans. and Proc. Series 5(2):1209-1217.

Schnoes, Roger S.
1977. The effects of prescribed burning on mule deer wintering at Lava Beds National Monument. M.S. thesis, 70 p. Oreg. State Univ., Corvallis.

Starkey, E. E., and R. A. Schnoes.
1979. The Columbian sharptailed grouse: with special reference to their potential reintroduction to Lava Beds National Monument. Proc. of the First Conf. on Scientific Res. in the Natl. Parks. NPS Trans. and Proc. Series 5(1):497-500.

Zezulak, David S.
1978. Northeastern bobcat study. Draft Final Rep. Calif. Fish and Game Dept. June 1978.

Effects of Prescribed Fires on Vegetation in Lava Beds National Monument

Craig M. Olson, Arlen H. Johnson, and Robert E. Martin

ABSTRACT

Prescribed fire is being used in an attempt to restore the historic vegetation sequence of Lava Beds National Monument where, prior to settlement, fires occurred every 5 to 15 years. Results of the burning will be used to develop fire plans for the Monument.

Craig M. Olson and Robert E. Martin, research foresters, U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station, Silviculture Laboratory, Bend, Oregon; Arlen H. Johnson, faculty of forestry, University of British Columbia, Vancouver, B.C., Canada.

INTRODUCTION

Fire plays an important role in determining vegetation structure and composition throughout most of the Western United States. Successional changes following fire are determined by the surviving species and proximity of potential invading species. In Lava Beds National Monument, California, dramatic changes have occurred in the plant associations with the coming of settlers and subsequent alteration of fire frequency, intensive livestock grazing, and introduction of exotic plant species. In 1974, research was begun in Lava Beds to evaluate the effects of fire on the different plant associations, to identify probable presettlement plant associations, and to recommend practices that could help reestablish presettlement plant associations.

Prescribed burning has been conducted on 22 units on the Monument from 1974 to 1979. Some required more than 1 day to complete burning while others were burned in less than 1 hour. Some were burned only once, while others were burned 2 or 3 years in succession. Research on these units was designed to: 1) evaluate the effects of various environmental conditions on fire behavior; 2) establish survival rate of grasses, shrubs, and trees; and 3) establish successional relationships following fire of the principal competitors within different plant associations. This paper discusses the effects of prescribed burning under varying conditions on the major plant associations through the first few years following fire.

Because replication of prescribed burns is difficult, if not impossible, results reported in this paper represent individual case studies. Inferences can be made though, when several burn units are located within similar plant associations.

STUDY AREA

Lava Beds National Monument is located in northeast California along the north slope of the Medicine Lake Highlands, a shield volcano. Elevation ranges from 1 200 meters (m) along Tulelake on the north to 1 700 m in the south. Annual precipitation averages 33.7 centimeters (cm), most of it falling from October to May. July daytime high temperatures average 27° celsius (C) while the daily mean low temperature for January is -6°C.

The soils in the Monument are derived from pyroclastic debris and basalt. They are relatively young with little horizon development. A stone pavement overlies shallow gravelly sand to sandy loam. There are many basalt outcrops and recent lava flows (<2,000 years old).

Vegetation associations at the lower elevations are often dominated by big sagebrush, Artemisia tridentata, or gray rabbitbrush, Chrysothamnus nauseosus, with cheatgrass, Bromus tectorum, bluebunch wheatgrass, Agropyron spicatum, Thurber's needlegrass, Stipa thurberiana, and bottlebrush squirreltail, Sitanion hystrix, as the principal grasses. Some low lying areas are dominated by cheatgrass, bottlebrush squirreltail, giant wildrye, Elymus cinereus, and needle and thread, Stipa comata. Much of the vegetation on the higher south end of the Monument is dominated by ponderosa pine, Pinus ponderosa, with an antelope bitterbrush, Purshia tridentata, understory. The transition plant association between these two areas is dominated by western juniper, Juniperus occidentalis, curlleaf mountainmahogany, Cercocarpus ledifolius, big sagebrush, and bitterbrush with Idaho fescue, Festuca idahoensis, bluebunch wheatgrass, western needlegrass, Stipa occidentalis, and cheatgrass in the understory.

During 1975, 1976, and 1977, 12 units in the four major associations were prescription burned. Permanent 10-m transects were randomly located within and adjacent to each unit prior to burning. Units dominated by cheatgrass were sampled using the point contact method with 200 points per 10-m transect (Johnston 1957). All other units were sampled using a line intercept method (Canfield 1941) recording only the crown intercept of perennial shrubs and grasses. All transects were sampled each year at approximately the same date as the preburn inventory.

On cheatgrass-dominated units burned in 1975 and 1977, litter and top soil were collected within 0.093-m^2 quadrats before and after burning to determine the number of viable cheatgrass seeds surviving the fire. The samples were replanted in a greenhouse and the number of germinants recorded. A t-test was used to compare preburn and postburn viable seed density.

Circular and rectangular macroplots were established on certain burns to count the number of sprouting and surviving shrubs by species. All shrubs greater than 20 cm but less than 2 m in height were recorded by species before and after burning.

To determine if burning was significantly changing the diameter size-class distribution of ponderosa pine trees, the diameters of all the trees within the units burned in 1975 and of all the trees within twelve 0.03-ha macroplots burned in 1977 were recorded before and after burning. A t-test was used to compare average diameter of surviving trees with average diameter of trees killed.

Complete weather and fuel-moisture-content data for each burn are listed in this publication (see Martin et al.).

RESULTS

To simplify discussion, four major plant associations are considered here. They include ponderosa pine/bitterbrush, mountainmahogany-big sagebrush, shrub/grass, and cheatgrass associations.

Ponderosa Pine/Bitterbrush Association

Four prescribed burns were conducted within ponderosa pine/bitterbrush associations, three in 1975 and one in 1977. The units burned in 1975 were dominated by old-growth ponderosa pine with an average d.b.h. of 37.5 cm and a stand density of 82 stems per ha. The unit burned in 1977 was dominated by sapling and pole-sized ponderosa pine with an average d.b.h. of 21.8 cm, an average height of 12 m, and stand density of 165 stems per ha. Preburn bitterbrush crown cover along transects ranged from 23 to 32 percent (table 1).

Table 1--Species percent cover values from burned and unburned permanent transects in various associations on Lava Beds National Monument

Burn units								Control units							
			Sample year							Sample year					
Burn date	Number of transects	Species	1975	1976	1977	1978	1979	Number of transects	Species	1975	1976	1977	1978	1979	Burn unit name
			- - - - Percent cover- - - -							- - - - Percent cover - - - -					
					Ponderosa pine/bitterbrush association										
6-27-75	4	Purshia tridentata	23.3	.0	.0	.0		1	Purshia tridentata	44.6	46.6	42.7	44.6		Upper Ice Csve I
		Haplopappus bloomeri	1.6	0.6	0.8	1.2			Sitanion hystrix	.2					
		Sitanion hystrix	.0	.0	0.2	0.1									
		Stipa thurberiana	.0	.0	0.1	.0									
8-22-75	4	P. tridentata	29.0	.0	.0	.0									Upper Ice Cave II
		H. bloomeri	3.0	1.4	3.1	5.7									
		Ribes velutinum	.0	.0	.0	0.1									
11-3-75	4	P. tridentats	32.0	.5	1.0	2.4									Upper Ice Cave III
		H. bloomeri	.0	.0	0.4	1.5									
		Ribes cereum	4.2	0.1	0.4	0.9									
		Artemisia tridentata	4.0	.0	.0	.0									
5-19-77	23	P. tridentata			28.1	2.1	6.4	1	P. tridentata			46.1	25.6	31.3	Caldwell Butte
		R. velutinum			.5	.0	1.2		Ribes velutinum			0.8	0.6	7.2	
		A. tridentata			.1	.0	.0								
		R. cereum			.1	.0	.0								
		Cercocarpus ledifolius			1.7	.0	.0								
		Eriogonum nudum			.1	.0	.0								
		Agropyron spicatum			.9	.1	.0								
		Festuca idahoensis			.1	.0	.0								
		S. hystrix			+	.2	.4								
		Stipa occidentalis			.2	+	.0								
		Carex rosii			.0	.0	.2								
					Mountainmahogany-big sagebrush association										
7-7/8-77	16	Juniperus occidentalis			5.6	1.0		9							
		C. ledifolius			13.3	4.8			Cercocarpus ledifolius			10.0	12.4		Headqusrters
		A. tridentata			11.5	1.1			Artemisia tridentata			5.0	4.8		
		P. tridentata			6.6	0.5			P. tridentata			0.5	0.4		
		R. velutinum			0.2	.0			R. velutinum			.0	0.2		
		Phlox douglasii			0.3	0.1			Chrysothamnus nauseosus			.0	0.6		
		Chamaebatiaria millefolium			0.9	0.7			Prunus emarginata			.0	0.7		
		A. spicatum			2.1	0.7			Agropyron spicatum			3.1	4.4		
		F. idahoensis			3.1	1.0			Festuca idahoensis			2.2	2.5		
		S. occidentalis			0.6	0.3			Stips occidentalis			1.2	2.0		
		Poa sandbergii			.0	0.1									
		Leptodactylon pungens			.0	0.3									

Table 1--Species percent cover values from burned and unburned permanent transects in various associations on Lava Beds National Monument (continued)

Burn units								Control units							
			Sample year							Sample year					
Burn date	Number of transects	Species	1975	1976	1977	1978	1979	Number of transects	Species	1975	1976	1977	1978	1979	Burn unit name
			- - - - Percent cover- - - -							- - - - Percent cover - - - -					
							Shrub/grass association								
6-26-75	2	P. tridentata	0.3	.0	.0	.0		2							Lava Overlook I
		A. tridentata	5.9	.0	.0	.0			A. tridentata	12.8	13.7	14.4	1.6		
		Chrysothamnus nauseosus	8.1	.0	.0	0.2			C. nauseosus	1.3	1.8	2.0	4.4		
		Chrysothamnus viscidiflorus	0.9	.0	.0	.0			Chrysothamnus viscidiflorus	.0	.0	.0	1.0		
		A. spicatum	10.9	3.4	8.4	10.1			A. spicatum	10.8	5.3	5.6	2.7		
		Poa sandbergii	9.8	1.7	8.8	5.1			Poa sandbergii	1.0	2.8	0.7	1.7		
		S. hystrix	.0	0.6	4.0	1.2			S. hystrix	.0	0.4	0.6	1.7		
		Stipa comata	.0	5.2	4.7	4.2			Stipa thurberiana	0.9	.0	0.7	0.4		
		S. thurberiana	.0	0.2	.0	1.6									
8-22-75	2	A. tridentata	12.0	.0	.0	.0									Lava Overlook II
		A. spicatum	4.4	1.0	1.5	2.4									
		S. thurberiana	12.6	7.9	10.3	13.5									
		P. sandbergii	9.1	5.0	5.1	3.6									
		S. hystrix	.0	1.6	1.7	3.3									
11-2-75	2	Tetradymia canescens	.0	0.5	2.0	3.0									Lava Overlook III
		C. nauseosus	4.0	.0	.0	.0									
		A. tridentata	6.8	.0	.0	.0									
		A. spicatum	7.0	9.0	13.5	8.4									
		S. thurberiana	.0	3.0	8.0	3.8									
		P. sandbergii	2.5	2.0	4.0	3.5									
7-6-77	5	C. nauseosus			10.4	0.5	0.4	3	C. nauseosus			9.1	7.9		Gillem's Camp II
		S. hystrix			6.4	3.9	5.4		S. hystrix			11.5	13.8		
		P. sandbergii			1.7	1.5	0.4		Bromus tectorum			8.9	38.3		
		S. thurberiana			2.1	0.5	0.8		Juncus mexicanus			2.3	2.5		
		Bromus tectorum			13.8	27.5	30.7								
6-26-75	4	C. viscidiflorus	0.3	.0	.0	.0									Homestead Flow
		A. spicatum	27.2	15.8	15.3	17.7									
		P. sandbergii	4.8	1.1	0.8	1.1									
		S. thurberiana	.0	1.8	2.2	2.2									
		S. comata	6.5	4.9	4.7	5.0									
		Elymus cinereus	5.7	3.5	3.0	3.8									
							Cheatgrass association								
6-25-75	8	B. tectorum	60.3	34.2	37.3	58.5		4	B. tectorum	58.6	33.1	21.2	42.4		West Wildlife Overlook
		Erodium cicutarium	2.9	8.9	8.6	6.1			Erodium cicutarium	1.9	2.5	7.8	9.0		
		A. tridentata	11.3	--	8.2	6.8			A. tridentata	14.1	14.4	16.7	13.8		
6-26-75	4	B. tectorum	71.4	32.9	58.4	74.8		2	B. tectorum	79.3	37.0	53.5	76.0		Gillem's Camp I
		Poa sp.	0.5	0.6	0.6	0.8			Poa sp.	.0	0.3	0.5	1.3		

Table 2--Number and percent sprouting following crown removal by fire of important shrub species in Lava Beds National Monument

Date sampled	Unit name	Date	Species	No. shrubs preburn	No. shrubs burned	No. shrubs sprouted	Percent sprout
7-8-76	Upper Ice Cave I	6-27-75	Purshia tridentata	308	308	60	19
			Haplopappus bloomeri	57	57	57	100
			Ribes cereum	1	1	1	100
8-16-76	Upper Ice Cave II	8-22-75	P. tridentata	208	208	2	1
			H. bloomeri	22	22	21	95
9-11-76	Upper Ice Cave III	11-3-75	P. tridentata	512	407	85	21
			H. bloomeri	28	24	21	88
			R. cereum	5	5	5	100
			Artemisia tridentata	10	0	--	--
6-26-79	Caldwell Butte	5-28-77	P. tridentata	855	735	43	6
			Ribes velutinum	40	40	22	55
			R. cereum	18	16	9	56
			H. bloomeri	17	16	14	88
			Chrysothamnus nauseosus	11	9	3	33
6-28-78	Headquarters	7-8-77	A. tridentata	333	246	0	0
			P. tridentata	85	61	0	0
			Cercocarpus ledifolius	17	7	0	0
			R. velutinum	2	1	0	0
			R. cereum	2	1	0	0
			Chrysothamnus viscidiflorus	3	2	0	0
			C. nauseosus	4	4	0	0
			Prunus emarginata	2	2	2	100
6-27-79	Gillem's Camp II	7-6-77	C. nauseosus	197	128	[1]58	45
			C. viscidiflorus	6	4	[1]20	100
6-27-79	Sheep Enclosure	7-5-78	C. nauseosus	44	9	0	0
			Tetradymia canescens	8	1	0	0
			R. velutinum	2	1	0	0

[1] Only crowns with live foliage above 20 cm in height were included in preburn inventory--sprouts of small plants exceeded 20 cm in postburn inventory.

Crown mortality of bitterbrush was nearly complete except on the 1977 burn where 11 percent survived. Shrub and grass cover represented between 4 and 25 percent preburn cover values within the first 2 to 3 years.

Rabbitbrush goldenweed, Haplopappus bloomeri, responded vigorously to fire. Within 3 years, its percent cover on the units burned on August 27 and November 2, 1975, exceeded preburn values.

Eighty to 100 percent of the bitterbrush crowns within 24 macroplots were killed by fire, but as much as 20 percent of these resprouted from root crowns by the following year (table 2). Shrubs burned in early summer and fall responded with higher sprouting rates.

Of the bitterbrush plants that were top killed and sprouted from root crowns, many had flowered and produced seed in the first 2 to 3 years. On the Caldwell Butte unit burned in May 1977, 65 percent of the shrubs that sprouted had produced seed by the summer of 1979. All of the 50 established bitterbrush plants examined adjacent to the burn units produced abundant seeds. Several species occurring on 0.03-ha macroplots are not known to sprout from adventitious buds or ligno-tubers, such as mountainmahogany and western juniper. Mountainmahogany does have the ability to sprout from aboveground axillary buds, however, if roots and cambium survive. Nearly all of the rabbitbrush goldenweed and wax currant, Ribes cereum, plants sprouted following crown kill on the units burned in 1975. Rabbitbrush goldenweed, wax currant, and desert gooseberry, Ribes velutinum, sprouted 88, 63, and 46 percent, respectively, the year following the 1977 Caldwell Butte fire and 88, 56, and 55 percent by two summers following burning.

Table 3--Mortality of ponderosa pine from prescribed burn on 28 May 1977, Lava Beds National Monument

	Stems per hectare	Diameter breast high $\bar{x}$	s
		------------centimeters----------	
Caldwell Butte (28 May 1977)			
Preburn live	387	21.8	7.80
Postburn live	338	23.6	8.55
Trees killed	49	13.7	7.29
Upper Ice Cave (27 June 1975)			
Preburn live	142	32.9	29.90
Postburn live	126	36.2	30.10
Trees killed	16	6.0	3.10
Upper Ice Cave (22 August 1975)			
Preburn live	69	56.6	31.70
Postburn live	49	69.2	23.50
Trees killed	20	24.5	27.20
Upper Ice Cave (3 November 1975)			
Preburn live	66	34.4	24.2
Postburn live	62	36.0	23.8
Trees killed	4	4.9	2.04

$\bar{x}$ = mean.
s = standard deviation.

Overstory ponderosa pine on all plots was not greatly affected by understory burning (table 3); generally only the smaller diameter trees were killed. Between 6 and 29 of the trees were killed by the four fires. The average d.b.h. of those trees killed was significantly less than the preburn stand average ($\alpha \leq .01$) following all four burns (table 3).

Mountainmahogany-Big Sagebrush Association

Only one prescribed burn was conducted in this association where transects and macroplots were burned. This was the Headquarters unit which was burned on July 7 and 8, 1977.

Plant crowns were killed by fire along 16 of the 25 permanent transects established prior to burning. The other nine were used as control transects.

Total perennial crown cover along the permanent transects was 35 percent before the fire (table 1). Following the fire, crown cover was reduced to 16.1 percent or 46 percent of preburn cover. Bunchgrass cover was reduced from 5.9 to 5.1 percent while shrub and tree cover was reduced from 29.1 to 11.0 percent. Mountainmahogany cover was reduced 64 percent by the fire. Western juniper cover was reduced 82 percent.

Within seven 0.03-ha macroplots, 126 of 448 perennial shrubs (28.6 percent) survived the burn (table 2). Two of the surviving shrubs were bitter cherry, Prunus emarginata, that had sprouted from root crowns. They were the only shrubs to sprout.

Although bunchgrasses appeared to have a lower mortality rate than shrubs (36.2 versus 22.1 percent), they showed poor vigor in the 1978 season and responded poorly to burning.

Shrub/Grass Association

Within the shrub/grass associations, four prescribed burns were conducted in 1975 and one in 1977. The Lava Overlook units (burned June 25, August 22, and November 2, 1975) were dominated by big sagebrush and gray rabbitbrush with bluebench wheatgrass, Sandberg's bluegrass, Poa sandbergii, and needlegrasses as principal subordinates before burning (table 1). Big sagebrush was completely killed along these transects and within the first 3 years showed no significant reinvasion. Gray rabbitbrush crowns also were nearly completely killed by these burns but showed some evidence of regrowth along burned transects.

The bunchgrass crowns on the units were consumed by the fires, but plants responded vigorously following burning compared to those on the control transects. Crown cover of bunchgrasses on the control plots declined during the 3 years following burning, while bunchgrass cover on the unit burned in November doubled by the 2d year and had greater cover than preburn. The bunchgrasses on the unit burned in August showed the least vigor following burning; crown cover was only 87 percent of preburn value by the 3d year.

Bluebunch wheatgrass and Thurber's needlegrass responded more vigorously than other bunchgrasses. On units burned in June, July, and November, cover exceeded preburn levels within the first 3 years following burning and showed significant increases compared to the control transects.

Gray rabbitbrush crowns in the Gillem's Camp II unit burned on July 6, 1977, were nearly completly killed by the fire (table 1). They showed little recovery within the first few years.

Bottlebrush squirreltail occurred along three transects on the Gillem's Camp II unit that were burned during July 6. By 1978, crown cover had regained 61 percent of preburn level; but along four unburned control transects, cover was 120 percent of the preburn level.

The percent cover of cheatgrass doubled from preburn to 1978 on the five transects in the burn units but was 430 percent of the preburn level along three control transects.

Only 35 percent of the shrubs within two 0.03-ha quadrats survived the July 7, 1977, burn (table 2). Later that summer, only two green rabbitbrush, Chrysothamnus viscidiflorus, shrubs had resprouted. Since only those shrubs greater than 20 cm in height were included in preburn inventory, small and very decadent shrubs were not included. By 1979, the number of green rabbitbrush shrubs greater than 20 cm within the macroplots was four times the preburn count.

The Homestead Flow unit, burned June 26, 1975, was dominated by bunchgrasses, principally bluebunch wheatgrass (table 1). The crowns of the bunchgrasses were removed by fire along four transects. By 1976 they had regained 61 percent of preburn cover and 67 percent by 1978. Grasses along control transects lost 45 percent of their cover from 1975 to 1978. Giant wildrye, needle and thread, and bluebunch wheatgrass all regained nearly 60 percent of preburn cover by the year following the fire, while Sandberg's bluegrass regained less than 25 percent of its preburn cover.

Cheatgrass Association

Three cheatgrass-dominated lowland units on the north end of the Monument were burned from 1975 to 1978. Two of these units were at least partially reburned the following year. All units were burned in June when seed was mature and beginning to drop. None of the units showed a significant change in cheatgrass cover compared to cover on the control area (table 1); but the number of viable seeds per square meter on the unit burned on June 26, 1975, was significantly reduced ($\alpha \leq .05$) compared to control plots (table 4).

Other annuals such as filaree, Erodium cicutarium, tumble mustard, Sisymbrium altissimum, and Draba, Draba verna, also showed no significant change in cover values.

DISCUSSION

Results from this study indicate that perennial bunchgrasses and annuals within the Monument respond vigorously following prescribed fire. On the other hand, perennial shrubs such as big sagebrush and mountainmahogany recovered very slowly. Shrubs such as bitterbursh and gray rabbitbrush had the ability to sprout from latent buds at the root collar, but the amount of sprouting depended on phenologic and climatic conditions both before and after the fires. Other shrubs in the Monument such as green rabbitbrush, elderberry, Sambucus cerulea, bitter cherry and chokecherry, Prunus virginiana, had nearly 100 percent sprouting following fire.

Mountainmahogany has a thin bark and its cambium is easily killed by fire. Western juniper and ponderosa pine, on the other hand, have relatively thick bark and are much harder to kill by fire. Ponderosa pine and western juniper have very flammable foliage; but by the time ponderosa pines reach pole-size, their crowns are high enough that they are quite resistant to surface fires, if fuels are not allowed to build up under them.

Much of the literature concerning response of vegetation to fire has been contradictory, if not misleading. This is particularly true in the case of bitterbrush. Hormay (1943) reported that bitterbrush areas in California destroyed by fire were taken over by cheatgrass and made no mention of bitterbrush's ability to sprout. Blaisdell (1950), however, reported that on the upper Snake River plains 49 percent of the bitterbrush plants sprouted on an area lightly burned, 43 percent in an area moderately burned, and 19 percent in an area heavily burned. Woolfolk (1958) reported that only one location in California is known where more than 25 percent of the bitterbrush plants sprouted, while Driscoll (1963) found that as many as 80 percent of the bitterbrush shrubs sprouted following burning in central Oregon gravelly loam soils. Soil moisture probably plays the most important role in the ability of bitterbrush to sprout following fire (Nord 1965, Britton 1979). The results of this study also suggest that soil moisture during burning determines bitterbrush survival. Therefore, spring and fall fires when soil and litter are relatively moist favor bitterbrush sprouting compared to mid-summer, when sprouting is near zero.

Soil heat transfer characteristics, phenological stage, and subspecies characteristics, however, are probably also important influences on the sprouting ability of bitterbrush following burning.

Zero to 45 percent of the gray rabbitbrush shrubs sprouted following crown removal. Additional information will be necessary to establish what determines this species' ability to sprout, since the units it occurred on were all burned at the same time of year.

Table 4--Viable seeds on burned and unburned cheatgrass (Bromus tectorum) plots[1/]

Species	Number of samples	Preburn $\bar{x}$	Preburn s	Postburn $\bar{x}$	Postburn s	Control $\bar{x}$	Control s
		Number of viable seeds per 1/10 square meter					
West Wildlife Overlook Burn (6-25-75):							
Bromus tectorum	9	486	77.4	337	425.4	529.0	380.0
Erodium cicutarium	9	136	73.3	135	80.5	90.4	37.4
Gillem's Camp II (7-6-77):							
Bromus tectorum*	11			1,149	837.2	2,516.0	6,198.2

1/ $\bar{x}$ = mean; s = standard deviation; * = significant difference ($\alpha \leq 0.05$).

Past research concerning the effects of fire on perennial bunchgrasses indicated that phenological stage at the time of burning and fire intensity were of considerable importance in determining post-fire vigor (Daubenmire 1968). The effect of clipping of bluebunch wheatgrass was negligible during early spring and late fall in Dubois, Idaho (1 670-m elevation). Reduction in production followed late May to early June clipping (Blaisdell and Pechanec 1949). In northeast Oregon, bluebunch wheatgrass showed little difference in vigor following burning at various intensities while Idaho fescue showed considerable reduction in survival with increasing intensity (Conrad and Poulton 1966). Both bluebunch wheatgrass and Thurber's needlegrass had significantly reduced leaf length the spring following an August wildfire in south-central Washington, but bluebunch wheatgrass had longer culms and spikes compared to unburned plants (Uresk et al. 1976). In this study, bunchgrasses showed the greatest increase in cover following a November fire. Bunchgrasses on the unit burned in August under hot, dry conditions showed a decrease in cover. Bluebunch wheatgrass in particular showed a dramatic increase in cover following fall burning. On the other hand, late June burning reduced cover the following year by half; but bunchgrasses regained 93 percent of their preburn cover by the 3d year following burning. Three years after an August burn, bluebunch wheatgrass cover was 55 percent of the preburn value. Evidently, the June burn reduced vigor but didn't kill the crowns; while August burning killed the crowns and lowered vigor.

On all three Lava Overlook burns, percent cover of Thurber's needlegrass had exceeded preburn levels by the 3d year following the fire. By 1978, cover of Sandberg's bluegrass was less than 60 percent of preburn values on units burned in late June, early July, and August; while on the control units, it increased during the same period. By the 2d year following the November fire, its cover exceeded the preburn value.

Cheatgrass is well adapted to fire (Klemmedson and Smith 1964, Young et al. 1976). Though the number of viable seeds and number of plants was reduced by burning in June just as seed began to drop, vigor and thus percent cover was not reduced.

CONCLUSIONS

Time of year, moisture regime, and fire intensity all must be considered when developing fire prescriptions to achieve desired results.

Bunchgrasses respond best to late summer and fall burning when heat penetration into the crown is low and nutrients are stored in the roots. Methods other than just spring burning are necessary to control cheatgrass.

Shrubs such as bitterbrush and gray rabbit brush are more sensitive to soil moisture and fire intensity than phenological condition when compared to bunchgrasses.

Both spring and fall burning can result in relatively high sprouting rates. Green rabbitbrush, rabbitbrush goldenweed, Ribes sp., and bitter cherry readily sprout following fire. Fire intensity and season of burn seem to affect bitter cherry and rabbitbrush goldenweed very little. Big sagebrush is easily killed by fire.

It is difficult to replicate conditions of a fire and individual fires are often highly variable. Additional information is necessary so managers can develop prescriptions favorable for desirable native species.

LITERATURE CITED

Blaisdell, James P.
1950. Effects of controlled burning on bitterbrush on the upper Snake River plains. USDA For. Serv. Res. Pap. INT-20, 3 p. Intermt. For. and Range Exp. Stn., Ogden, Utah.

Blaisdell, James P., and Joseph F. Pechanec.
1949. Effects of herbage removal at various dates on vigor of bluebunch wheatgrass and arrowleaf balsam root. Ecol. 30(3):298-305.

Britton, Carlton M.
1979. Fire on the range. Western Wildlands 5(4):32-33.

Canfield, R. H.
1941. Application of the line interception method in sampling range vegetation. J. For. 39:388-394.

Conrad, C. Eugene, and C. E. Poulton.
1966. Effect of wildfire on Idaho fescue and bluebunch wheatgrass. J. Range Manage. 19(3):138-141.

Daubenmire, Rexford.
1968. Ecology of fire in grasslands. Adv. in Ecol. Res. 5:209-266.

Driscoll, Richard S.
1963. Sprouting bitterbrush in central Oregon. Ecol. 44(4):820-821.

Hormay, A. L.
1943. Bitterbrush in California. USDA For. Serv. Res. Note 34, 13 p. Calif. For. and Range Exp. Stn.

Johnston, A.
1957. A comparison of the line interception, vertical point quadrat, and loop methods as needed in measuring basal area of grassland vegetation. Can. J. Plant Sci. 37(1):34-42.

Klemmedson, James D., and Justin G. Smith.
1964. Cheatgrass (Bromus tectorum L.). Bot. Rev. 30(2)226-262.

Nord, Eamor C.
1965. Autecology of bitterbrush in California. Ecol. Monog. 35(3):307-334.

Uresk, D. W., J. F. Cline, and W. H. Rickard.
1976. Impact of wildfire on three perennial grasses in south-central Washington. J. Range Manage. 29(4):309-310.

Woolfolk, E. J.
1958. Project WSTR. Crane Range restoration segment. Western Assoc. of State and Game Comm. Western Browse Res. 4(1):1-9.

Young, James A., Raymond A. Evans, and Ronald A. Weaver.
1976. Estimating potential downy brome competition after wildfire. J. Range Manage. 29(4):322-325.

Single-Year Response of Breeding Bird Populations to Fire in a Curlleaf Mountainmahogany-Big Sagebrush Community

Tamara E. Tiagwad, Craig M. Olson, and Robert E. Martin

ABSTRACT

Breeding bird territories were mapped on four 16.2-hectare (ha) grids in curlleaf mountainmahogany, Cercocarpus ledifolius,-big sagebrush, Artemisia tridentata, communities in Lava Beds National Monument, California, in the spring and summer of 1979. Grids were located in a 1973 wildfire, a 1977 prescribed burn, and control areas adjacent to each burn. Prior to burning, all areas had scattered ponderosa pine, Pinus ponderosa, and western juniper, Juniperus occidentalis, but mountainmahogany, antelope bitterbrush, Purshia tridentata, and big sagebrush dominated the vegetation.

Only one small island of original vegetation survived on the wildfire grid; the rest of the area was dominated by bunchgrasses. Vegetation structure was more varied on the control grid. The wildfire grid also showed less avian diversity than its control. Ground nesting birds dominated the burn area, but the control area had a variety of shrub and tree nesting birds.

The prescribed burn had an interspersion of burned and unburned areas; therefore, much "edge" and nesting habitat. It had a wider range of ground, shrub, and tree nesting birds than the control.

Tamara E. Tiagwad, biological aid, Craig M. Olson and Robert E. Martin, research foresters, U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station, Silviculture Laboratory, Bend, Oregon.

INTRODUCTION

In Lava Beds National Monument, California, wildfires historically played a major role in vegetation distribution and structure. Fire suppression, heavy livestock grazing, and a western pine beetle, *Dendroctonus brevicomis*, outbreak have modified vegetation patterns in the last half century. A prescribed burning program is currently being developed in the Monument to restore presettlement vegetation and reduce unnatural fuel accumulations.

Few studies have compared the response of breeding bird populations to wildfires and prescribed burns in similar habitat. The objective of this study was to document avian density, species composition, and avian diversity in wildfire, prescribed burned, and unburned areas dominated by mountainmahogany, big sagebrush, and bitterbrush.

THE STUDY AREA

The study area was located in the Lava Beds National Monument, about 48 kilometers (km) southwest of Tulelake, California. The bird census grids were located in T. 45 N., R. 4 E., Sections 27, 28, and 29, at an elevation of about 1 454 meters (m) with east-northeast aspects. Soils are derived from pumice and basalt. These relatively young soils are characterized by a stone pavement overlying gravelly sand to sandy loam with little horizon development. Soils are shallow with numerous basalt outcrops.

The Monument has a modified maritime climate with warm dry summers and cool wet winters. Weather records from the Indian Wells Weather Station located between study areas indicate an average annual precipittion of 34 centimeters (cm), July daily mean high temperatures of 27°C, and January daily mean low temperatures of -6°C.

Four 16.2-ha census grids were located in curlleaf mountainmahogany-big sagebrush communities. One of the grids was in an area burned by a 205-ha wildfire on July 11, 1973, and another was located in a 120-ha area prescribed burned on July 7 and 8, 1977. From aerial photographs and ground surveys, unburned control grids were selected approximately 0.2 km from each burned unit with plant communities similar to those characterizing the burned grids prior to the fires. Until the 1973 wildfire, no fire over one-quarter acre had occurred in the study area since the 1930's.

Although the wildfire and prescribed fire occurred at the same time of year, had similar daytime high temperatures (28° and 27°C), and had similar low humidities (20 and 18 percent, respectively), they differed significantly in winds and fuel moisture content during the fire. The wildfire followed a month with no rain and low humidity while the prescribed fire followed a month of exceptionally high rainfall (5.1 cm). Because of this, live fuels during the prescribed fire probably had much higher moisture content. Also, dead wood between 0.62- and 2.54-cm diameter had a moisture content of 3 percent during the wildfire; but during the prescribed fire, it had a moisture content of 6 percent. Winds associated with the dry lightning storm that started the 1973 wildfire were gusty and were probably around 15 to 20 kilometers per hour (km/hr) compared to winds of 0 to 12 km/hr during the prescribed fire. The combined effect of relatively high winds and low fuel moisture content significantly influenced fire behavior and subsequent vegetation patterns.

METHODS

Vegetation

Vegetation was sampled at 30 systematically located grid points on each 16.2-ha bird census grid. Alternate grid points were sampled on alternate grid lines. A rope 28.35 m long was stretched from a grid point in a randomly chosen compass direction and vegetation was sampled along the transect by two methods. First, ground cover of shrubs and trees was measured by the line intercept method (Canfield 1941). Length of the line intercept, average height, and an estimate of percent of dead crown were recorded for each shrub and tree. Dead plants, both standing and down, were not included in the sampling. Second, frequency of grasses, shrubs, and trees was determined while measuring ground surface cover as described by Daubenmire (1968). Since vegetation was sampled following the breeding season, annual forbs were beyond recognition and not included in the analysis. Fifteen subplots on each transect were sampled at 1.9-m intervals along the rope with a 20- x 50-cm steel frame placed at right angles along one side of the rope. Coverage was visually estimated for bare soil, plant litter, stones over 2-cm diameter, logs over 7.6-cm diameter, and live plants.

Constancy and frequency were calculated for all grasses, shrubs, and trees. Constancy is the percent of transects along which a species occurs. Frequency is the percent of quadrants within which a species occurs.

Bird Census

Territorial male birds were censused during the breeding season by the spot-mapping method (International Bird Census Committee 1970). Censusing began April 30, 1979, and ended July 19, 1979. All of the censuses were done between 0445 and 0900 Pacific Daylight Time and were 1 to 3 hours long. Temperature, wind speed, and cloud cover were recorded before and after each census. Sixty individual censuses were made--15 each on the wildfire and the prescribed burn control grids, 16 on the wildfire control grid, and 14 on the prescribed burn grid. Each grid was censused one or two times per week.

The square grids cover 16.2 ha, grid lines were spaced 36.6 m apart, and grid points were marked by a permanent iron rod with a letter and number corresponding to its relative position on the grid. Three of the grids had 144 (12 x 12) grid points and the wildfire control grid had 169 (13 x 13) grid points with grid lines spaced 33.5 m apart. The narrower spacing was to allow for lower bird visibility in that grid.

The censusing technique was to walk slowly along the grid lines, alternating starting points to avoid favoring a particular part of the grid, and identify and record the species, positions, and movements of all birds on a map of the grid. The daily maps were compiled on individual species maps covering the entire census period for each grid, and clumped observations were used to delineate territories. At least two separate observations of a territorial nature on separate days, such as singing or aggression toward other birds, and one of a general nature such as foraging were used as criteria for determining territories. Birds with territories only partly within a grid area were included in density and diversity calculations which would slightly inflate these values. The number of territories per 16.2 ha, was converted to territories per 40.5 ha (100 acres), a commonly used figure in bird density studies (Gashwiler 1977, Feist 1968). Diversity values were calculatd from th^ original, unconverted data using two formulas:

$$H' = \sum_{i=1}^{s} P_i \log_e P_i \quad \text{(Shannon 1948)} \qquad (1)$$

where P_i is the proportion of species i of the total number of individuals in the populations, s is the number of species, and H' is the dimensionless information index and:

$$I_p = N - \sum_{i=1}^{s} n_i^2 \Big/ N - \sqrt{N} \quad \text{(McIntosh 1967)} \qquad (2)$$

where N is the total sample size, s is the number of species i represented in the sample, n is the number of indivduals of a particular species in the sample, and Ip is the percent of theoretical maximum diversity for a particular N. In both formulas, the larger the index value, the greater the diversity. Both indices of diversity were calculated, because they provide different information.

RESULTS

Vegetation

Major differences in the estimates of cover of trees, shrubs, and grasses occurred among burned and control areas (tables 1, 2, and 3). Bunchgrasses dominated the wildfire grid except for a small island of shrubs and trees that survived the fire. The wildfire had a very high percent of rock cover and low soil cover compared to the other three areas. Dominant species on the wildfire control grid were mountainmahogany, antelope bitterbrush, and big sagebrush. The prescribed burn grid has an intersperion of burned and unburned areas. Dominant species for this grid and its control were the same as those found on the wildfire control grid, and all four areas had similar cover of litter.

1973 Wildfire Grid

Five percent of the total area within the wildfire grid did not burn. The grid was dominated by three grasses, constancy value for each were: cheatgrass, Bromus tectorum, 100 percent; bluebunch wheatgrass, Agropyron spicatum, 80 percent; needlegrass, Stipa spp., 46.7 percent. Cheatgrass had the highest frequency value (94.5). Cover of shrubs was 5.3 percent, with bitter cherry, Prunus emarginata, accounting for 73 percent of the total shrub cover.

A small area of vegatation, largely mountain-mahogany and western juniper occurring on 30 and 33.3 percent of the transects with average heights of 281 cm and 532 cm, respectively. The control grid had a total shrub coverage of 23.3 percent, with big sagebrush (10.0 percent) and bitterbrush (8.9 percent) forming 81 percent of the total.

Bluebunch wheatgrass, cheatgrass, and Idaho fescue, Festuca idahoensis, were the most abundant of the seven grass and sedge species with constancy values of 100, 96.7, and 73.3 percent, respectively. Cheatgrass had the highest frequency value (45.8), which was half that of the wildfire grid.

1977 Prescribed Burn Grid

The prescribed burn covered only 37 percent of the sampling grid, resulting in much edge and a high percent of tree and shrub cover. Mountainmahogany had a coverage of 19.3 percent and occurred on 73.3 percent of the transects. Western juniper had a coverage of 5.2 percent and a constancy of 46.7 percent. The total low shrub cover was 6.5 percent with big sagebrush, the dominant shrub, covering 4.3 percent and antelope bitterbrush 21.1 percent. They comprised 66 and 32 percent of the total low shrub cover, respectively. Of the eight grass and sedge species occurring on the prescribed burn, Idaho fescue and bluebunch wheatgrass were the most abundant with frequencies of 42.9 and 40.2 percent, respectively. These two species along with cheatgrass, Thurber's needlegrass, Stipa thurberiana, and Sandberg's bluegrass, Poa sandbergii, occurred along more than half the transects.

1977 Prescribed Burn Control Grid

Tree and tall shrub cover on the control grid was 32.5 percent, mountainmahogany covered 24.6 percent, and western juniper covered 7.9 percent of the area. The prescribed fire control grid had a tree and tall shrub cover 2.3 times that of the wildfire control grid.

Total low shrub cover on the control grid was 15.4 percent. Big sagebrush (9.2 percent) and antelope bitterbrush (6.2 percent) were the only shrubs present on the transects. The total shrub coverage on the 1977 prescribed burn control grid was 66 percent of that on the 1973 control grid.

Grasses and sedges with constancy values above 50 percent were Idaho fescue (100 percent), bluebunch wheatgrass (96.7 percent), Thurber's needlegrass (96.7 percent), cheatgrass (90 percent), and Sandberg's bluegrass (65.7 percent). Idaho fescue had the highest frequency (45.6 percent) of the nine species occurring along the grid transects.

Bird Census

Bird census data indicated some large differences in bird populations (table 4, 5, and 6). The 1973 wildfire grid had the lowest number of bird territories (41/40.5 ha), the lowest number of territorial species (6) (table 3), and the lowest diversity values (table 5). Total number of species occurring on the grid was 25. Western meadowlarks, Sturnella neglecta, rock wrens, Salpinctes obsoletus, scrub jays, Aphelocoma coerulescens, and mourning doves, Zenaida macroura, comprised 24, 24, 24, and 12 percent, respectively, of the total breeding population on the grid. Ground nesters made up 49 percent of the total breeding population (table 4).

The wildfire control grid had the highest number of bird territories (70/40.5 ha), the highest number of territorial species (14), and the highest total number of species (27) of the four areas. Tree nesters and shrub/tree nesters comprised 39 percent and 34 percent of the total breeding population. Scrub jays had the highest breeding bird density (13 pairs/40.5 ha) on the grid. This grid also had the highest diversity values (H' = .86 and Ip = 2.53) and the highest average number of species observed per census (9.9).

The number of breeding bird territories on the 1977 prescribed burn grid was 61 per 40.5 ha. Total number of species occurring on the grid was 25, with 11 species defending territories. Shrub/tree nesters made up 43 percent of the total breeding population, and tree nesters formed 36 percent of the total. Scrub jays, common bushtits, Psaltriparus minimus, and American robins, Turdus migratorius, were the most abundant species with 13, 10, and 8 pairs per 40.5 ha. The prescribed burn grid had diversity values of H' = .81 and Ip = 2.23.

The estimated number of breeding bird territories on the 1977 control grid was 49 per 40.5 ha. This control grid had the lowest total number of species occurring on the grids (23), 8 of which established territories. Shrub/tree nesting species were 57 percent of the total breeding population, and tree nesters were 22 percent of the total. More than half of the breeding birds were scrub jays or chipping sparrows, Spizella passerina. This grid had the lowest average number of species observed per census (6) and had diversity values of H' = .77 and Ip = 1.94.

DISCUSSION

Differences in breeding bird density, species composition, and diversity values between burn and control plots suggest that wildfires and prescribed burns affect habitat suitability for many avian species. Only one species, the scrub jay, nested on all four grids. Three shrub and tree nesting species, the common flicker, Colaptes avratus, common bushtit, and blue-gray gnatcatcher, Polioptila caerulea, nested on all but the 1973 wildfire grid.

Though the two control grids had similar vegetation, the vegetation analysis indicates several differences in frequency or distribution.

The 1973 control had higher percentage cover of low shrubs than did the 1977 control (23 versus 15.4 percent) and lower percentage cover values for mahogany and western juniper (14 versus 32.5 percent). Consequently, the wildfire and prescribed burn grids were not directly compared.

Breeding bird density and diversity values were considerably higher on the 1973 wildfire control grid than on the wildfire grid. The control grid also had much higher estimates for total shrub coverage and percent cover of the two most abundant shrub species. This correlates with the substantial number of shrub nesting species on the grid.

Gashwiler (1977) reported an average of 91 breeding bird territories per 40.5 ha in an area in central Oregon and shrub species and coverage similar to the wildfire control grid. In his study, average numbers of territorial species were 6.3, with Brewer's sparrows, Spizella breweri, sage sparrows, Amphispiza belli, horned larks, Eremophila alpestris, and sage thrashers, Oreoscoptes montanus, the most abundant. The wildfire control grid had 70 territories per 40.5 ha, 23 percent fewer than the average density Gashwiler (1977) found. The number of territorial species on the control grid was over twice the average number reported in the central Oregon study. Species composition was much different for the two areas. Scrub jays, common bushtits, and sparrows were most abundant on the control grid. These difference in estimates of breeding bird density could be the result of vegetative differences, seasonal fluctuation, or sampling error.

The wildfire grid had comparatively low bird density and avian diversity values. Most of the breeding birds were ground nesters. The low diversity of vegetation on the grid limited the range of niches available for nesting birds. Avian species diversity has been positively correlated with foliage height diversity by MacArthur and MacArthur (1961). Since foliage height diversity tends to increase as succession increases; avian species diversity is usually low in grassland habitats.

No trees were encountered along wildfire grid vegetation transects, yet we had two tree nesting birds breeding on the grid. One of these, a mountain bluebird, Sialia currucoides, probably used a cavity in one of the standing dead western junipers not included in our analysis. The other, a robin, nested in the patch of shrubs and western junipers spared by the fire. The dead western junipers throughout the area also provided excellent singing and roosting perches for western meadowlarks, Sturnella neglecta, mourning doves, and scrub jays.

Table 1--Cover percent, plant number, height, and percent of dead crown for the 1973 wildfire grid and its control

Species	1973 Wildfire							1973 Control						
	Number of samples	Percent cover		Height (cm)		Percent dead		Number of samples	Percent cover		Height (cm)		Percent dead	
		x̄ [1]	s [2]	x̄	s	x̄	s		x̄	s	x̄	s	x̄	s
Ground cover														
Rock	--	22.0	19.9	--	--	--	--	--	4.3	7.1	--	--	--	--
Soil	--	9.5	13.3	--	--	--	--	--	37.2	16.2	--	--	--	--
Litter	--	61.0	17.2	--	--	--	--	--	55.3	16.3	--	--	--	--
Log	--	0.6	0.5	--	--	--	--	--	--	--	--	--	--	--
Live plant	--	9.9	3.0	--	--	--	--	--	3.4	2.3	--	--	--	--
Low shrubs														
Big sagebrush	--	--	--	--	--	--	--	144	10.0	12.4	57.7	19.2	29.2	26.2
Antelope bitterbrush	2	0.2	1.1	77.5	31.8	35.5	48.8	67	8.9	9.2	127.9	53.1	23.4	23.0
Desert gooseberry	4	0.2	0.6	81.3	19.3	19.3	16.8	4	0.4	1.1	118.8	26.6	55.0	38.5
Squaw currant	1	0.1	0.3	45.0	--	5.0	--	2	1.7	5.7	70.0	28.3	37.5	31.8
Green rabbitbrush	--	--	--	--	--	--	--	11	0.5	1.8	40.5	17.2	34.3	27.0
Gray rabbitbrush	4	0.3	1.1	73.8	16.5	3.5	1.7	17	1.3	3.0	58.8	28.6	67.9	19.4
Bitter cherry	43	3.8	7.2	103.7	35.3	4.3	4.4	6	0.4	1.7	91.7	22.1	9.5	15.4
Choke cherry	3	0.5	1.6	81.7	27.5	13.3	2.9	--	--	--	--	--	--	--
Serviceberry	1	0.1	0.3	75.0	--	1.0	--	1	0.1	0.3	50.0	--	5.0	--
Total low shrubs	58	5.2						252	23.3					
Tall shrubs														
Mountainmahogany	--	--	--	--	--	--	--	31	6.2	10.4	281.1	34.6	24.5	14.7
Trees														
Western juniper	--	--	--	--	--	--	--	16	6.5	13.5	531.6	300.1	5.1	6.3
Ponderosa pine	--	--	--	--	--	--	--	1	1.3	5.0	750.0	--	10.0	--
Total trees								17	7.8					
Total trees and shrubs	58	5.2						300	37.3					

1/ x̄ = mean.

2/ s = standard deviation.

Table 2--Cover percent, plant number, height, and percent of dead crown for the 1977 prescribed burn grid and its control

	1977 prescribed burn							1977 control						
		Percent cover		Height (cm)		Percent dead			Percent cover		Height (cm)		Percent dead	
Species	Number of samples	x̄ [1/]	s [2/]	x̄	s	x̄	s	Number of samples	x̄	s	x̄	s	x̄	s
Ground cover														
Rock	--	5.0	6.5	--	--	--	--	--	6.3	6.1	--	--	--	--
Soil	--	28.3	15.1	--	--	--	--	--	28.4	13.9	--	--	--	--
Litter	--	61.7	17.4	--	--	--	--	--	59.7	13.1	--	--	--	--
Log	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Live plant	--	5.5	3.5	--	--	--	--	--	5.9	3.2	--	--	--	--
Low shrubs														
Big sagebrush	72	4.3	4.9	51.6	20.2	31.6	26.0	118	9.2	9.7	60.2	18.2	36.2	24.0
Antelope bitterbrush	26	2.1	4.2	78.5	26.9	30.2	20.8	68	6.2	6.2	82.9	24.7	42.8	20.7
Desert gooseberry	2	0.1	0.8	75.0	21.2	89.5	13.4	--	--	--	--	--	--	--
Total low shrubs	118	6.5						186	15.4					
Tall shrubs														
Mountainmahogany	97	19.3	21.3	254.5	51.3	21.9	15.1	119	24.6	20.3	265.1	63.2	27.7	17.9
Trees														
Western juniper	18	5.2	8.4	523.1	32.2	5.8	10.2	18	7.9	13.5	648.5	407.4	5.1	3.5
Ponderosa pine	1	0.7	3.5	600.0	--	20.0	--	--	--	--	--	--	--	--
Total trees	19	5.9						18	7.9					
Total trees and shrubs	234	31.7						323	47.9					

1/ x̄ = mean.

2/ s = standard deviation.

Table 3--Frequency (f) and constancy (c) values for vegetation on the 4 census grids. Mean ($\overline{x}$) and standard deviation (s) are given for frequency

	1973 wildfire			1973 control			1977 prescribed burn			1977 control		
Vegetation	c(%)	$\overline{x}$(f)	s(f)	c(%)	$\overline{x}$(f)	s(f)	c(%)	$\overline{x}$(f)	s(f)	c(%)	$\overline{x}$(f)	s(f)
Grasses and sedges												
Bluebunch wheatgrass *Agropyron spicatum*	80.0	19.4	16.8	100.0	39.8	24.0	93.3	40.2	25.1	96.7	39.1	17.9
Rush-leaved bluegrass *Poa juncifolia*	--	--	--	--	--	--	3.3	0.2	1.3	20.0	2.0	4.7
Sandberg's bluegrass *Poa sandbergii*	--	--	--	20.0	1.6	3.4	73.3	17.8	16.8	56.7	6.5	7.9
Needlegrass *Stipa* spp.	46.7	8.5	13.5	56.7	11.2	13.2	--	--	--	--	--	--
Thurber's needlegrass *Stipa thruberiana*	--	--	--	--	--	--	70.0	13.2	15.2	96.7	39.7	25.0
Bottlebrush squirreltail *Sitanion hystrix*	10.0	0.9	2.9	26.7	5.2	11.9	16.7	1.2	2.7	36.7	2.8	3.9
Ross' sedge *Carex rossii*	--	--	--	20.0	2.0	4.3	13.3	2.3	5.4	30.0	4.1	7.7
Idaho fescue *Festuca idahoensis*	13.3	1.8	5.3	73.3	12.5	14.8	80.0	42.9	30.5	100.0	45.6	23.3
Prairie junegrass *Koeleria cristata*	--	--	--	--	--	--	--	--	--	43.3	6.1	7.5
Cheatgrass *Bromus tectorum*	100.0	94.5	8.6	96.7	45.8	30.7	66.7	18.3	24.5	90.0	35.0	23.7
Low shrubs												
Big sagebrush *Artemesia tridentata*	--	--	--	63.3	22.9	23.8	63.3	14.9	15.1	70.0	19.5	19.9
Antelope bitterbrush *Purshia tridentata*	10.0	0.9	2.9	70.0	13.8	13.8	33.3	4.5	9.3	63.3	12.5	12.7
Desert gooseberry *Ribes velutinum*	10.0	0.7	2.1	13.3	0.9	2.4	3.3	0.2	1.3	6.7	0.5	1.8
Squaw currant *Ribes cereum*	--	--	--	6.7	0.5	1.8	--	--	--	--	--	--
Green rabbitbrush *Chrysothamnus viscidiflorus*	--	--	--	16.7	2.9	7.7	--	--	--	--	--	--
Gray rabbitbrush *Chrysothamnus nauseosus*	13.3	0.9	2.4	26.7	3.1	6.3	--	--	--	--	--	--
Bitter cherry *Prunus emarginata*	33.3	7.1	12.4	3.3	0.4	2.4	--	--	--	--	--	--
Choke cherry *Prunus demissa*	10.0	0.7	2.1	--	--	--	--	--	--	--	--	--
Rabbitbrush goldenweed *Haplopappus bloomeri*	--	--	--	--	--	--	--	--	--	3.3	0.4	2.4
Tall shrubs												
Mountainmahogany *Cercocarpus ledifolius*	--	--	--	30.0	7.1	12.7	73.3	22.5	21.4	80.0	29.1	24.3
Trees												
Western juniper *Juniperus occidentalis*	--	--	--	33.3	8.0	15.5	46.7	6.0	7.9	33.3	7.6	12.1
Ponderosa pine *Pinus ponderosa*	--	--	--	3.3	0.7	3.7	3.3	0.7	3.7	--	--	--

Table 4--Breeding bird territories per 40.5 ha for the 4 census grids

Species	1973 Wildfire	1973 Control	1977 Prescribed burn	1977 Control
Red-tailed hawk[a] (*Buteo jamaicensis*)	-	3	-	-
American kestrel (*Falco spraverius*)	+	+	+	+
California quail (*Lophortyx californicus*)	+	3	5	+
Mourning dove (*Zenaida macroura*)	5	+	5	+
Poor-will (*Phalaenoptilus nuttallii*)	-	+	-	-
Common nighthawk[a] (*Chordeiles minor*)	-	-	+	-
Rufous hummingbird (*Selasphorus rufus*)	+	+	-	-
Common flicker (*Colaptes auratus*)	+	5	3	3
Western kingbird (*Tyrannus verticalis*)	+	+	-	-
Ash-throated flycatcher (*Myiarchus cinerascens*)	-	+	+	-
Empidonax flycatcher (*Empidonax spp.*)	-	+	+	-
Western wood pewee (*Contopus sordidulus*)	+	+	-	+
Violet-green swallow (*Tachycineta thalassina*)	+	+	-	-
Purple martin (*Progne subis*)	+	-	-	-
Scrub jay (*Aphelocoma coerulescens*)	10	13	13	13
Black-billed magpie (*Pica pica*)	+	-	+	-
Common raven (*Corvus corax*)	+	+	+	-
Mountain chickadee (*Parus gambeli*)	-	5	+	5
Plain titmouse (*Parus inornatus*)	-	5	5	+
Common bushtit (*Psaltriparus minimus*)	-	8	10	5
White-breasted nuthatch (*Sitta carolinensis*)	+	-	-	-
Bewick's wren (*Thryomanes bewickii*)	-	+	-	+
Rock wren (*Salpinctes obsoletus*)	10	3	-	+
American robin (*Turdus migratorius*)	3	+	8	+
Hermit thrush (*Catharus guttatus*)	-	-	-	+
Mountain bluebird (*Sialia currucoides*)	3	+	3	-
Townsend's solitaire (*Myadestes townsendi*)	+	-	-	-
Blue-gray gnatcatcher (*Polioptila caerulea*)	-	3	3	3
Ruby-crowned kinglet (*Regulus calendula*)	-	3	-	-
Yellow warbler (*Dendroica petechia*)	+	-	-	-
Yellow-rumped warbler (*Dendroica coronata*)	-	+	+	+
Townsend's warbler (*Dendroica townsendi*)	-	+	-	-
Wilson's warbler (*Wilsonia pusilla*)	+	+	+	-
Western meadowlark (*Sturnella neglecta*)	10	-	3	+
Northern oriole (*Icterus galbula*)	+	-	-	-
Brewer's blackbird (*Euphagus cyanocephalus*)	+	+	3	+
Brown-headed cowbird (*Molothrus ater*)	-	+	-	-
Western tanager (*Piranga ludoviciana*)	-	-	+	-
Evening grosbeak (*Hesperiphona vespertina*)	-	-	-	+
Purple finch (*Carpodacus purpureus*)	+	3	+	-
Cassin's finch (*Carpodacus cassinii*)	+	-	+	-
Pine siskin (*Spinus pinus*)	+	-	-	-
Rufous-sided towhee (*Pipilo erythrophthalmus*)	-	5	+	5
Dark-eyed junco (*Junco hyemalis*)	-	-	+	5
Chipping sparrow (*Spizella passerina*)	-	3	+	10
Brewer's sparrow (*Spizella breweri*)	-	8	-	+
Total number territories	41	70	61	49
Total number territorial species	6	14	11	8
Total number species	25	27	25	23

a = Species with large territories.
+ = The species was present on the grid but no territories were established.

Feist (1968) censused breeding birds on sagebrush grassland areas in central Montana in 1966 and 1967. The vegetation type reported was roughly similar to that on the wildfire grid. Feist found four species with 42.5 breeding pairs per 40.5 ha on a sagebrush range that had been sprayed with herbicide the previous year. Dominant species were the Brewer's sparrow, vesper sparrow, Poecetes gramineus, and western meadowlark. The number of species breeding on the wildfire grid was about the same as that reported in central Montana, but the species composition was much different. Dominant species for the present study were the scrub jay, rock wren, Salpinctes obsoletus, and western meadowlark with six breeding species and 41 pairs per 40.4 ha.

The prescribed burn grid had higher breeding bird density and diversity values than its control grid. Percent cover values for both trees and shrubs were considerably lower on the burn grid. The mosaic of burned and unburned areas resulted in a greater variety of ground, shrub, and tree nesting species on the burn grid. In central Oregon, Gashwiler (1977) found an average of 202.7 territories per 40.5 ha over 3 years in a western juniper type with many of the same shrub species and similar coverage values compared to the prescribed burn grid. The prescribed burn grid had 61 territories per 40.5 ha, 70 percent fewer than Gashwiler's (1977) average density. The number of territorial species was roughly the same for both studies. Gashwiler recorded an average of 13.7 species compared to 11 in this study. The most abundant species on the prescribed burn grid differed from those reported in central Oregon. Gashwiler (1977) found mostly empidonax flycatchers, Empidonax spp., house finches, Carpodacus mexicanus, chipping sparrows, mountain bluebirds, American robins, and mountain chickadees, Parus gambeli. Scrub jays, common bushtits, and American robins were most abundant on the prescribed burn grid.

SUMMARY

This report represents only 1 year's results, which indicate that conversion of shrubland to grass land by the 1973 wildfire led to a decrease in density and numbers of species of birds, a decrease in bird diversity, and a shift in bird species composition compared to unburned areas with a more varied vegetation structure.

The results also suggest that heterogeneous habitat produced by the 1977 prescribed burn led to an increase in density and numbers of bird species, an increase in bird diversity, and some shift in the species composition. Thus, prescribed burning that results in greater vegetation mosaic may produce a greater variety of ground, shrub, and tree nesting birds compared to unburned areas.

Table 5--Numbers of territories per 40.5 ha and numbers of nesting species (in parentheses) on the 4 census grids

	1973		1977	
Nesting category	Burn	Control	Burn	Control
ground	20 (2)	6 (2)	8 (2)	5 (1)
ground/shrub	--	5 (1)	--	5 (1)
ground/shrub/tree	5 (1)	8 (1)	5 (1)	--
shrub/tree	10 (1)	24 (3)	26 (3)	28 (3)
tree	6 (2)	27 (7)	22 (5)	11 (3)

Table 6--Diversity values and numbers of species observed per census for the 4 grids

		1973		1977	
Nesting category		Burn	Control	Burn	Control
Diversity:	Ip	.72	.86	.81	.77
	H'	(1.66)	(2.53)	(2.23)	(1.94)
Number of species observed per census	$\bar{x}$	6.4	9.9	8.5	6.0
	s	1.6	2.2	2.5	1.1

Ip = percent of theoretical maximum diversity for a particular sample.
H' = dimensionless information index.
$\bar{x}$ = average number of species per census.
s = number of species in a census.

Bird density and species diversity may be directly related to age of burns (Johnson 1976). Therefore, the effects of burning on breeding bird populations should be documented for several seasons before reaching conclusions about the impact of a specific wildfire or prescribed burn. Also, dramatic seasonal fluctuations of some bird populations occur even when the vegetation is not modified (Balda 1975).

Both prescribed fire and wildfire can produce highly variable vegetation structure depending on the vegetation before the fire and burning conditions. Because of this, both can change vegetation diversity and structure, and thus avian diversity and composition. Since we can pick conditions and burning patterns for prescribed fires but not for wildfires, intentioned use of fire may be the more advantageous of the two.

LITERATURE CITED

Balda, Russell P.
1975. Vegetation structure and breeding bird diversity. In Proceedings of the symposium on management of forest and range habitats for nongame birds. p. 59-80. USDA For. Serv. Gen. Tech. Rep. WO-1, Washington, D.C.

Canfield, R. H.
1941. Application of the line interception method in sampling range vegetation. J. For. 39(4):388-394.

Daubenmire, Rexford.
1968. Ecology of fir in grasslands. Advan. Ecol. Res. 5:209-266.

Feist, F. G.
1968. Breeding bird populations on sagebrush-grassland habitat in central Montana. Audubon Field Notes 22:691-695.

Gashwiler, Jay S.
1977. Bird populations in four vegetational types in central Oregon. USDA Fish. Wild. Serv. Spec. Rep., Wild. No. 205.

International Bird Census Committee.
1970. An international standard for a mapping method in bird census work recommended by the International Bird Census Committee. Audubon Field Note 24(6):722-725.

Johnson, Douglas H.
1976. Effects of grassland burning on breeding birds--preliminary report. Proc. North Dakota Acad. Sci. 30(1):24.

MacArthur, Robert H., and John W. MacArthur.
1961. On bird species diversity. Ecology 42(3): 594-598.

McIntosh, Robert P.
1967. An index of diversity and the relation of certain concepts to diversity. Ecology 48(3): 392-404.

Shannon, C. E.
1948. A mathematical theory of communication. Bell Syst. Tech. J. 27(7):623-656.

The Effects of Prescribed Burning on Mule Deer in Lava Beds National Monument

Alice Purcell, Roger Schnoes, and Edward Starkey

ABSTRACT

In the winters of 1976 and 1977, research was conducted to determine the impacts of prescribed burning on mule deer, *Odocoileus hemionus hemionus*, in Lava Beds National Monument. Visual observations, radio telemetry, and pellet-groups were used to examine deer distribution, seasonal movements, and winter food habits of deer. Individual deer occupied site-specific home ranges in the Monument. Home ranges were not abandoned or extended as a result of burning. Bitterbrush, *Purshia tridentata*, was the most important browse species to deer during the winter months. Utilization of green shoots increased, particularly in burned areas, as the winter progressed. Deer increased use of burned portions of their home ranges in spring. Due to warming trends in March, herbaceous vegetation will usually be available to does during the critical third trimester of gestation. Based on the size of home ranges, typical weather patterns, and the size and mosaic nature of prescribed burns, deer probably will not be adversely affected by burns and may benefit from them.

Alice Purcell, Roger Schnoes, and Edward Starkey, Cooperative Park Studies Unit, School of Forestry, Oregon State University, Corvallis, Oregon.

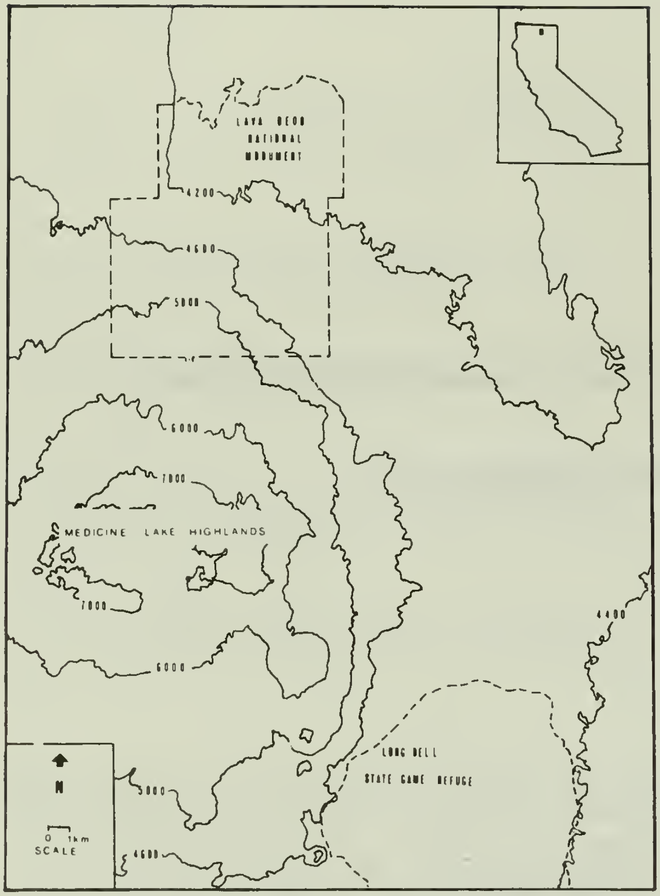


Figure 1.--Location of Lava Beds National Monument, California, and summer range of migratory deer.

INTRODUCTION

In the winters of 1976 and 1977, research was conducted to determine the impact of prescribed burning on mule deer, *Odocoileus hemionus hemionus*, in Lava Beds National Monument, California (Schnoes 1978). A second phase of the study was initiated in the spring of 1977 and continued through the spring of 1978. During the second phase, additional information was obtained on seasonal movements and use of burns by deer that wintered in the Monument. During the winters of 1976-78, data were collected on distribution and home ranges of deer in Lava Beds, movements and use of cover by deer in response to weather, and food habits of deer, especially as influenced by burns. Also, migration routes and summer range of migratory deer were located during April and May, 1978.

STUDY AREA

Lava Beds National Monument is in northeastern California, approximately 72 km south of Klamath Falls, Oregon. It is part of the Basin and Range Physiographic Province as described by Franklin and Dyrness (1973). The climate is semi-arid with a mean annual precipitation of 36.8 cm. Summers are warm and dry with a mean maximum temperature of 27°C; winters are cool with an average minimum temperature of -4.4°C. The Monument lies on the northern flank of the Medicine Lake Highlands. The land rises gradually from 1 250 m at the northeastern boundary to 1 700 m in the southwestern corner (fig. 1). Elevation continues to rise south of the Monument to over 2 100 m in the Medicine Lake Highlands.

The northern two-thirds of the monument is characteristic of a shrub-steppe habitat (fig. 2). Dominant shrubs are mountain big sagebrush, *Artemesia tridentata* ssp. *vaseyana*, rabbitbrush, *Chrysothamnus nauseosus* and *C. viscidiflorus*, and horsebrush, *Tetradymia canescens*. Endemic bunchgrasses of that area include blue bunch wheatgrass, *Agropyron spicatum*, needlegrasses, *Stipa thurberiana* and *S. occidentalis*, Sandberg's bluegrass, *Poa sandbergii*, squirreltail, *Sitanion hystrix*, and Idaho fescue, *Festuca idahoensis*. Prominent invader species are cheatgrass, *Bromus tectorum*, and tumbling mustard, *Sisymbrium altissimum*.

The southern one-third of the Monument is a dense western juniper, *Juniperus occidentalis*, and curlleaf mountainmahogany, *Cercocarpus ledifolius*, chaparral with an understory dominated by bitterbrush, *Purshia tridentata*, and mountain big sagebrush (fig. 2). The extreme southern portion supports a ponderosa pine, *Pinus ponderosa*, forest with white fir, *Abies concolor*, and incense cedar, *Libocedrus decurrens*, and an understory of snowbrush, *Ceanothus velutinus*, greenleaf manzanita, *Arctostaphylos patula*, and bitterbrush.

The climate and topography of the summer range, approximately 25 km south of the Monument, are similar to that of Lava Beds. The mean maximum temperature during the summer is 33.2°C; annual precipitation averages 135.2 cm. Elevation rises gradually into the Medicine Lake Highlands from 1 341 m on the plateau east of the Long Bell State Game Refuge (fig. 1). Lower elevations support a ponderosa pine forest similar to that in the southern porton of Lava Beds. Higher elevations support white fir and lodgepole pine, *Pinus contorta*.

METHODOLOGY

Pellet-group transects were established in 1962 and have been counted annually by Monument personnel. Each transect consisted of 10 circular plots; each plot had a radius of 3.4 m and an area of 0.004 ha. The transects were located throughout the Monument (fig. 2). Additional transects of the same design were established in 1976 in the 1973 Wildfire and the Fleener Chimneys and Hovey Point prescribed burns (fig. 3). Those transects were placed parallel to the edge of a burn and spaced 150 m apart. Two transects were placed in a burn, two were placed outside of a burn, and a

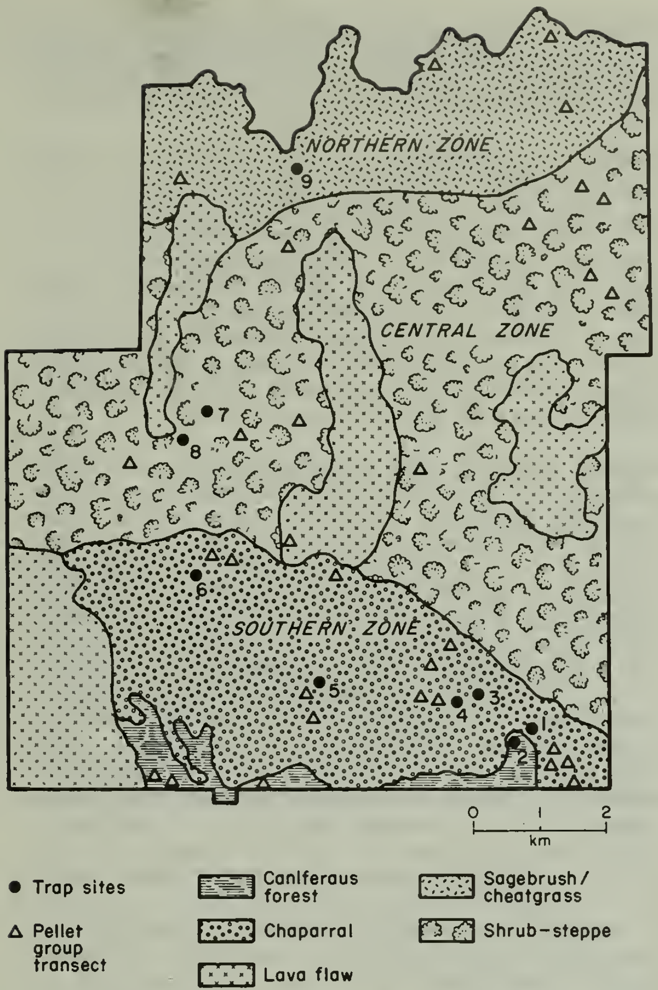


Figure 2.--Vegetation zones of Lava Beds National Monument, California. (Reprinted from Schnoes 1978).

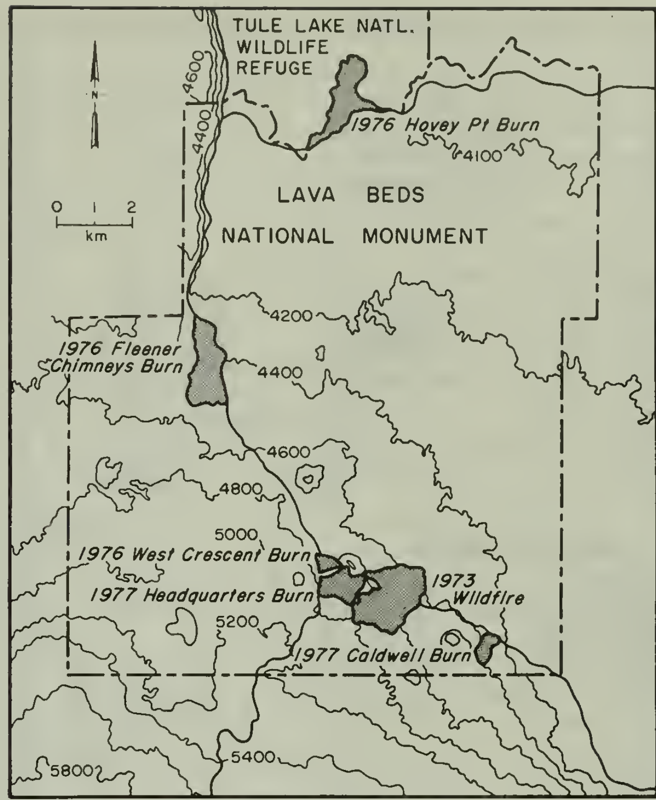


Figure 3.--Location of burns in Lava Beds National Monument, California.

middle transect was placed along the edge of a burn. Counts from those transects established in 1976 provided data on the use of those areas by deer before and after burning.

Food habits of deer during three winters were obtained by a feeding frequency method. While observing deer, we also recorded plant species and type of forage used by individual deer. For the analyses of feeding data, the Monument was divided into three zones (fig. 2); those zones reflected the type of vegetation and forage available to deer (Schnoes 1978). The southern zone roughly coincided with the juniper-mahogany chaparral and the coniferous forest. The 1973 Wildfire and the 1976 West Crescent and 1977 Caldwell prescribed burns occurred in that zone (fig. 3). Juniper and mountainmahogany occurred much less frequently in the central zone, however bitterbrush and sagebrush were common along with the bunchgrass (fig. 2). The prescribed burn at Fleener Chimneys was conducted in that zone (fig. 3). Sagebrush and rabbitbrush dominated the northern zone; cheatgrass and tumbling mustard were also frequent (fig. 2). The Hovey Point prescribed burn occurred in that zone in 1976 (fig. 3).

During all three winters, deer were trapped in Oregon single-gate traps or darted using Sernylan (Phencyclidine hydrochloride), CI-744 (an experimental drug), or a mixture of Rompun (Xylazine) and M-99 (Etorphine). Deer were ear-tagged and 12 does were fitted with radio-collars in 1977 and 1978. Radio-collared does were monitored with a truck-mounted null/peak antenna, or a four-element hand-held yagi antenna when observation of an animal was desired. The majority of data on home ranges, seasonal movements and seasonal use of burns by deer were obtained from eight radio-collared does that were still being monitored in the spring of 1978.

Home ranges were constructed according to the minimum polygon method (Mohr 1947). A composite home range was obtained for each radio-collared deer from all of the animal's locations while on the winter range. Seasonal home ranges were also constructed. The seasons were delineated as: June-August, summer; September-November, fall; December-February, winter; and March-May, spring.

The chi-square statistic was used to test for seasonal selectivity or avoidance of burns by deer, in a fashion similar to that discussed by Neu et al. (1974). Telemetry data for each animal were analyzed by season.

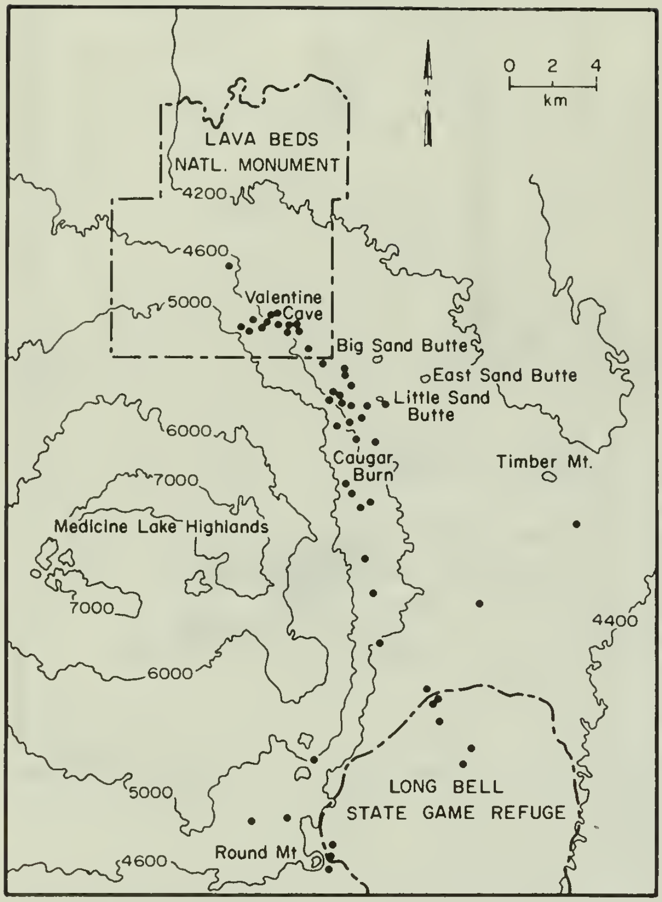


Figure 4.--Locations of radio-collared deer on the migration corridor south of Lava Beds National Monument, California, during spring 1977 and 1978.

The chi-square statistic, two-way analysis of variance, and simple and step-wise multiple regression were used in statistical analyses. The level of statistical significance was set at $p < 0.05$ in all analyses.

RESULTS AND DISCUSSION

Distribution and Home Range

Counts of pellet-group transects over an 18-year period indicated that deer use during winter was concentrated in the southern one-third of the Monument (Schnoes 1978). Based on those counts, and an assumed defecation rate of 13 pellet-groups/day, the number of deer in the Monument during winter was estimated to vary between 1,500 and 2,500 Part of the deer population was non-migratory and remained in the Monument during summer. Most of those deer occupied the northern half where the population level was low by comparison to that of the migratory population.

Migratory deer arrived in the Monument in October-December and migrated south from March-May. They left in a south-southeasterly direction moving along the lower hills of the Medicine Lake Highlands (fig. 4). During the spring migrations in 1977 and 1978, most of the migratory deer delayed briefly (usually less than 2 days) in "holding areas", as defined by Bertram and Rempel (1977). Distances travelled by deer to the summer range varied from 1.6 to 65 km. It appeared that some bucks moved to higher elevation in the Medicine Lake Highlands and did not travel great distances.

Delays were also brief for most deer during the fall migration. One doe, however, used two holding areas for 3 or 4 weeks each in the fall of 1977. She delayed in those same areas during her 1978 spring migration. Does that summered in or near Long Bell State Game Refuge initiated their fall migration early, probably due to a drought that prevailed on the summer range for a 2d year in 1977. Ashcraft (1961) documented an early fall migration for deer that summered in the McCloud Flats during the drought year of 1955.

Drought probably had the greatest influence on movements of deer while on the summer range. Home ranges of migratory deer were larger during summer than at other seasons (does S-L, table 1) and averaged 970 ha. In early August 1977, two does that summered on the southern fringe of Long Bell State Game Refuge moved to higher elevation in the Highlands (does S and Y, fig. 5). They remained there until September 25. They returned to the area south of the State Game Refuge and were located in the Monument on September 30. Since deer were monitored for only one summer, it cannot be concluded that such late summer shifts are not an annual occurrence. It is conceivable, however, that drought induced early dry forage conditions at the lower elevations, and that deer moved to higher elevations for forage in an earlier phenological stage.

In the fall of 1977, radio-collared migratory deer returned to the same home ranges in the Monument that they occupied in the winter and spring of 1977. Composite home ranges of radio-collared does ranged from 287 to 5 022 ha (table 1); seasonal home ranges of six does were largest in the fall (averaging 1 424) and smallest in the winter (averaging 671 ha).

Two-way analysis of variance showed no significant difference in size of home ranges among seasons; however, a significant difference occurred among sizes of home range of individual deer. Deer in the northern half of the Monument had significantly larger ($P < 0.05$) home ranges than those of deer in the southern half. That difference was attributed to disparity in the type of cover and forage available to deer in the two areas. The juniper-mahogany chaparral of the southern zone provided dense cover for deer. In addition, bitterbrush and mountainmahogany, two browse species selected most by deer in all three winters, were abundant in that zone. The shrub-steppe habitat of the northern and central zones provided a more open cover type for deer; bitterbrush and mountainmahogany were less abundant. Disparity in the deer population levels between the two areas probably was influenced by available cover and forage, and in turn, may have had an interactive influence on home range size.

All radio-collared deer used the same home ranges while in the Monument in 1977 and 1978; however, areas of concentrated use within individual home ranges varied between years (fig. 6). Shifts in

Table 1--Seasonal and composite home ranges in hectares of radio-collared does in Lava Beds National Monument, California[1/]

Deer	Summer	Fall	Winter	Spring	Sampling period	Composite home range
			DEER IN SOUTHERN ZONE			
A 1977	1542 (48)	--	605 (105)	369 (83)	1/77-4/77	659 (188)
1978	--	--	483 (41)	581 (88)	1/78-5/78	700 (129)
S 1977	584 (22)	491 (91)	--	152 (37)	3/77-5/78	726 (320)
1978	--	--	424 (72)	566 (109)	--	--
Y 1977	747 (27)	381 (96)	--	67 (27)	3/77-5/78	636 (301)
1978	--	--	346 (80)	581 (97)	--	--
L 1978	--	--	217 (82)	251 (120)	11/77-5/78	320 (235)
O 1977	289 (67)	186 (137)	--	354 (63)	4/77-5/78	463 (419)
C 1977	775 (34)	--	--	209 (23)	--	--
			DEER IN CENTRAL AND NORTHERN ZONES			
B 1977	406 (72)	1811 (121)	2227 (91)	2126 (132)	1/77-4/77	2873 (223)
1978	--	--	1026 (98)	1648 (72)	1/78-5/78	1917 (154)
					5/77-5/78	2563 (402)
W 1977	747 (64)	4313 (121)	--	889 (83)	4/77-5/78	4022 (437)
1978	--	--	1 (95)	1287 (71)	--	--
J 1978	--	--	623 (71)	711 (81)	1/78-5/78	922 (152)

[1/]Figures in parentheses give the number of locations.

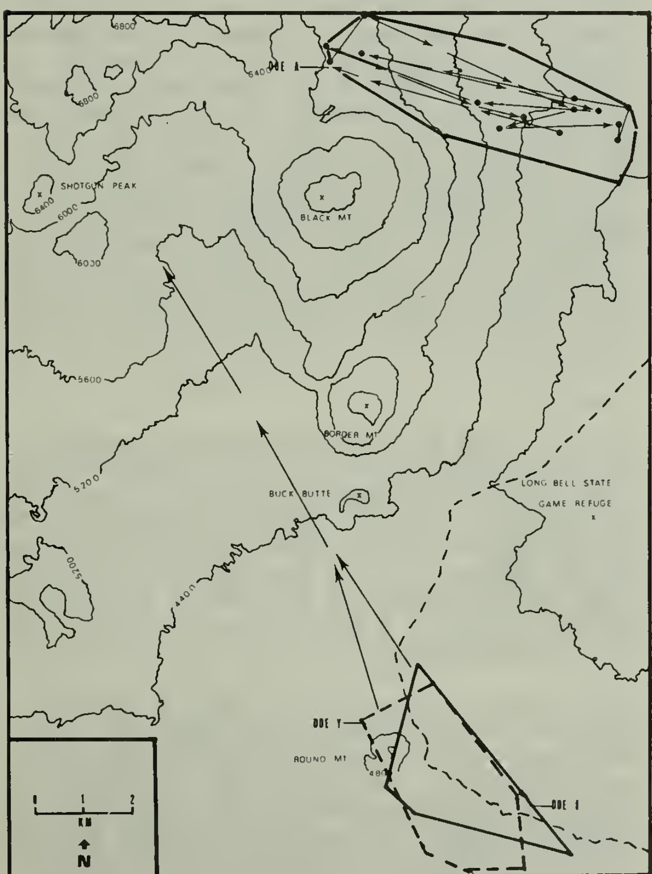


Figure 5.--Movements and home ranges of radio-collared does S, Y, and A on the summer range south of Lava Beds National Monument, California, summer 1977.

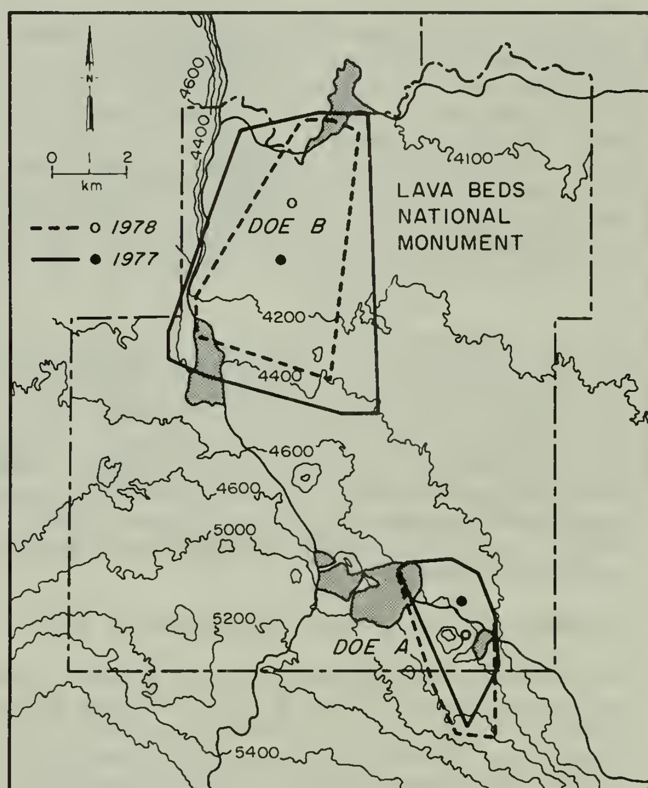


Figure 6.--Home ranges and centers of activity of radio-collared does A and B during the winter-spring period of 1977 and 1978.

Table 2--Pellet-group counts for transects established by Schnoes (1978) in three major burns in Lava Beds National Monument

Year	Burned 1	Burned 2	Edge 3	Unburned 4	Unburned 5	Five-transect total
			1973 WILDFIRE			
1976	36	35	22	39	31	163
1977	38	27	43	33	24	165
1978	32	26	31	19	36	144
			FLEENER CHIMNEYS BURN			
1976[1]	0	2	0	1	1	4
1977	1	21	0	7	15	44
1978	7	10	1	2	0	20
			HOVEY POINT BURN			
1976[1]	0	2	3	2	2	9
1977	13	17	6	15	7	58
1978	1	0	3	0	0	4

[1]Counts made before burning.

centers of activity between years probably were a result of the mild winter weather in 1978. Warm temperatures and plentiful rain resulted in an early greenup, particularly at the lower elevations in the north. Does in that area moved into burns, cheatgrass meadows, and the fields of the Tule Lake National Wildlife Refuge in mid-February. Deer continued to use those areas heavily through spring. The early and extended use of burns, meadows, and agricultural fields in 1978 resulted in the northward shift in centers of activity (doe B, fig. 6).

Centers of activity of migratory does in the southern half of the monument shifted to the south in 1978 (doe A, fig. 6). Frequency and duration of southward trips to coniferous forest by radio-collared does of the southern zone increased that year. Those trips resulted in the southward shift in centers of activity. Leckenby (1968) also reported that mule deer on the Silver Lake Range, Oregon, spent more time in ponderosa pine habitat during mild winters.

Movements and Use of Cover in Response to Burns

The winters of 1976-78 were relatively mild. There were few extended periods of below-freezing temperatures; snow accumulation remained minimal (below 18 cm). As a result, few opportunities arose to monitor the response of deer to extreme weather. During periods of inclement weather in all three winters, deer sought shelter in winds greater than 16 km/hr. Deer used topographical irregularities in addition to vegetation as wind breaks, particularly in the more open shrub-steppe habitat and the burns. During high winds, deer were often observed feeding or moving along the lee side of lava ridges or in lava depressions that interrupted an otherwise open terrain. Observations of deer in 1978 indicated that unless accompanied by high winds, rain and snow did not cause deer to seek shelter when feeding in open areas.

Data obtained from radio-collared deer confirmed such observations; no significant correlation occurred between distances traveled by does and temperature, wind, precipitation, or cloud cover ($R^2 = 0.025$, $P > 0.05$) in 1978. Results from the analyses of deer movements in the winters of 1975 and 1977 were similar (Schnoes 1978). More severe winter conditions might have revealed an association between movement patterns and general weather conditions.

Use of Burns 1976-78

There was a significant increase ($P < 0.05$) in the number of pellet-groups in the Fleener Chimneys and Hovey Point burns the 1st year after the fires (table 2). In 1978, the number of pellet-groups remained high in the Fleener Chimneys burn. A significant decline occurred, however, in the number of pellet-groups immediately outside that burn and in the Hovey Point area (table 2).

Such declines may have reflected a general dispersal of deer in both the Fleener Chimneys and Hovey Point areas, resulting from the wet, mild winter of 1978. Use within the Fleener Chimneys burn possibly remained high as a result of the greater availability of herbaceous vegetation present within the burn. The Hovey Point area, however, contained many open meadows with plant communities similar to those in the Hovey Point burn during the 2d year following the prescribed fire. In addition, agricultural fields of the Tule Lake National Wildlife Refuge lie immediately north. Herbaceous vegetation was abundant throughout the winter in all those areas. Groups of deer were often observed feeding and moving slowly through the Hovey Point burn towards the refuge in the evenings.

Seasonal Use of Burns

All does, with the exception of doe L, selected burns or used them in proportion to their availability (table 3). Deer increased use of burns in the spring of 1978 from that of the winter. An increased use of the 1978 Wildfire area by some does in the southern zone was also apparent in the fall (fig. 7). Increased use of burns in the fall and spring resulted in a shift in seasonal centers of activity toward burns (fig. 7).

The weather was exceptionally mild in 1978 while deer were on the winter range. Herbaceous forage was available throughout winter in meadows and burned areas. In such areas, deer fed predominantly on herbaceous vegetation. Availability of palatable herbaceous vegetation in burns appeared to be the primary factor influencing concentrated use of burns by deer, particularly in spring.

Table 3--Chi-square analyses[1] of seasonal use of burns, based on proportion of burn available in annual home range of radio-collared does, Lava Beds National Monument

Season	Southern zone does					Central and northern zone does		
	S	Y	O	A	L	B	W	J
Winter 1977	--	--	--	0.3 (0)	--	0.1 (0)	--	--
Spring 1977	35.3 (+)	76.1 (+)	6.2 (+)	0.1 (0)	--	0.9 (0)	78.6 (+)	--
Summer 1977	--	--	--	--	--	302.1 (+)	0.1 (0)	--
Fall 1977	21.6 (+)	121.8 (+)	157.5 (+)	1.1 (0)	22.1 (-)	65.4 (+)	93.7 (+)	--
Winter 1977-78	1.9 (0)	4.8 (+)	107.8 (+)	0.5 (0)	7.9 (-)	53.5 (+)	23.1 (+)	3.2 (0)
Spring 1978						5.9 (+)	178.9 (+)	46.2 (+)

[1]$\chi^2 > 3.84$ are significant at $P < 0.05$; (+) indicates selection for burn, (-) indicates selection against burn, and (0) indicates use of burn in proportion to its availability.

Feeding Habits

During all three winters, bitterbrush was the most important browse species and represented 75 percent of all browse feeding observations. Mountain-mahogany was the second most important browse species. In the northern zone, where bitterbrush was sparse and grasses and forbs abundant, deer diets consisted almost entirely of grass and forb species. Deer in that zone often fed in the fields of the Tule Lake National Wildlife Refuge and shrub species did not appear to play an important role in the diet.

In the southern and central zones, fire had the greatest influence on plant composition and thus, the availability of different forage classes. Effects of fire on the composition of deer diets were most evident in those zones. In the northern zone where the Hovey Point burn was conducted, cheatgrass and tumbling mustard already were very abundant; thus, rosettes and shoots of those species were available without burning. All fires that occurred in the southern and central zones resulted in invasion of cheatgrass and tumbling mustard in areas where those species were not very abundant previous to burning.

Use of green forage throughout the Monument remained high during all three winters (fig. 8). The deer in the central zone gradually increased use of green forage during winter. Low use of green forage in February 1977, in contrast to the other 2 years, was significant ($P < 0.05$) and probably was due to the very dry weather during that month, which may have caused a delayed greenup of grasses and forbs. That was particularly evident in areas outside the burn (fig. 8).

In the 1973 Wildfire, use of green forage continued to increase during February 1977 (fig. 8). Grass and forb species in the unburned portions of the central and southern zones may have had to compete with the shrub species for the little moisture that was available during that month. Inside the burn, it was probable that low shrub densities reduced that effect.

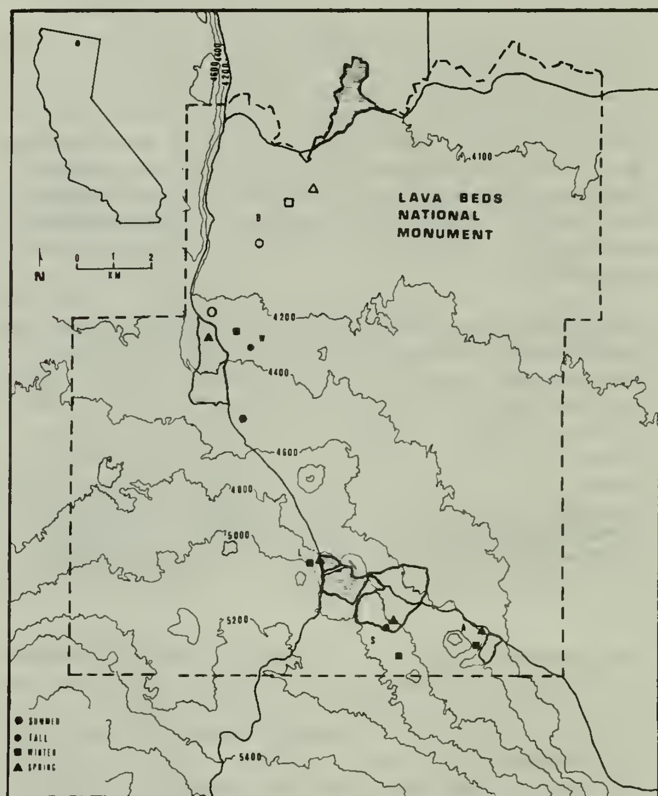


Figure 7.--Shifts in seasonal centers of activity, summer 1977 to spring 1978.

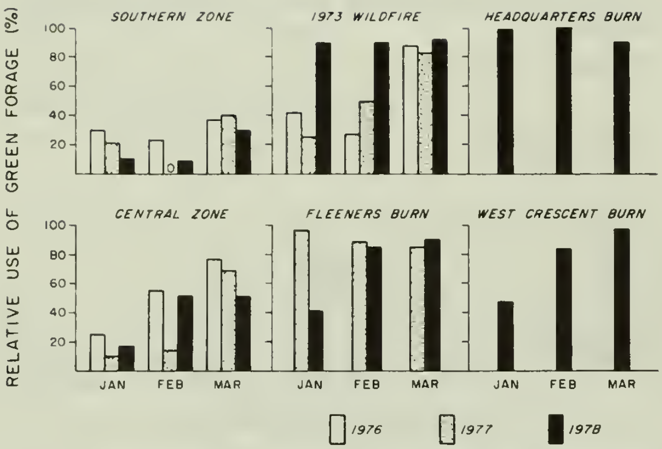


Figure 8.--Percent of relative use of green shoots by deer in the winters of 1976-78, Lava Beds National Monument.

In the southern zone, increased use of green forage was less abrupt and reached a lower peak in March than in the central zone. Again, the decline in February may have reflected a lower production in 1977. In that zone, there were large areas of very dense mountainmahogany and juniper stands, with minimal grass and forb production in the understory. The lack of availability probably was responsible for continued high use of browse in late winter (fig. 8).

In all the burns, relative use of green forage was considerably higher than in surrounding areas. Such use was extremely high in burns in the southern and central zones during the winter that immediately followed burning, despite the fact that areas of unburned vegetation remained in those burns. The second year following the Fleener Chimneys and West Crescent burns (1978), use of green forage remained high. However, there was lower use in January, as deer started to browse resprouting and unburned shrubs available in those burns (fig. 8).

Unlike other burns, the 1973 Wildfire was intense, and relatively homogeneous. Increased use of green forage was more gradual during 1976 and 1977 (fig. 8), probably due to a greater amount of snow in early and mid-winter of those years. Snowfall was high in February 1976 and January 1977. With snow accumulation reducing availability of shoots, deer in the 1973 Wildfire switched to the use of dried tumbling mustard stems protruding above the snow. Snowfall was low during winter 1978, but precipitation was normal and came in the form of rain. Green forage was available in that burn throughout winter, and deer use remained high.

Effects of Burns on Home Ranges

Migratory and non-migratory does were not displaced by recent burns within or adjacent to their home ranges. Furthermore, they did not extend their home ranges to include new burns. For example, the prescribed headquarters burn, conducted the summer of 1977, did not attract radio-collared does whose winter home ranges were adjacent to it.

Doe O, a non-migratory deer, had a small corner of her home range burned in the 1977 headquarters burn. Her use of the newly burned portion increased significantly ($P < 0.05$) from her use of that area during the previous year; however, she did not extend her home range to include a greater portion of the burn. Her spring home range of 1978 was much smaller than that in 1977. She restricted her movements to the new burn and a small area surrounding Monument headquarters that included part of the 1973 Wildfire. Apparently the new burn caused a reduction of her 1978 spring home range. Radio-collared doe A exhibited a different response to a similar situation. The 1977 Caldwell burn affected a small portion (4 percent) of her 1978 composite home range. In contrast to doe O, she neither significantly increased or decreased her use of the burned area from that of the previous year. She used the burns within her 1978 composite home range in proportion to their availability (table 3); her movements in 1978 seemed unaffected by the presence of the new burn within her home range.

Thus, deer showed a strong fidelity to their home ranges in the Monument; the presence of burns did not induce an extension or abandonment of those home ranges. Migration data in the spring of 1978 suggested that deer also returned to the same holding area on transitional ranges and home ranges on the summer range. Those data support Schnoes (1978) hypothesis of site-specific home ranges for individual deer.

Potential Impacts of Prescribed Burning on Mule Deer in the Monument

Prescribed burns that have been conducted at Lava Beds have not been detrimental to deer that winter in the Monument. General observations and evidence from four road-killed deer in the winter of 1978 indicated that animals were in excellent physical condition during that year. In addition, two bucks, which were harvested at 2.5 yrs of age during the 1977 hunting season, had four-point antlers. Such antler growth implies that those deer were on a high plane of nutrition. Mild weather prevailed during the winter of 1977-78 and placed minimal stress on deer during that period. Plentiful rainfall produced herbaceous growth in burns that remained available through the fall and spring.

An examination of weather records for the Monument over the past 18 years indicated that severe winters were not frequent in Lava Beds. Winter weather in 1976 and 1977 was milder than the 16-year average, however it closely approached it. During those winters, Schnoes (1978) reported that deer "exhibited elasticity in response to the altered environment in taking advantage of the benefits of both burned and unburned areas." Even in severe winters, herbaceous forage most likely would become available in spring prior to migration, due to warming trends in March.

The spring period, March-May, corresponds to the final 3 months of fetal development in pregnant does. Pregnancy demands additional energy and protein, particularly in the last trimester of gestation, because of rapid fetal growth rate (Moen 1973). Numerous studies have indicated that nutritional deficiencies in does during the last trimester of pregnancy result in increased neo-natal mortality of fawns (Murphy and Coats 1966, Thompson and Thompson 1953, Verme 1977).

Radio-collared migratory deer in Lava Beds remained in the Monument through mid spring in 1977 and through late spring in 1978. Thus, it appears that migratory deer have access to herbaceous forage in burns during the initial half of the third trimester of gestation. Availability of herbaceous forage in spring may increase productivity and fawn survival of deer in the Monument. Because deer return to site-specific home ranges in the Monument, it is likely that prescribed burns will have the greatest impact on those deer whose home ranges overlap burned areas.

Moderately large burns, ranging from 400 to 34 800 ha, and numerous smaller fires have occurred on the transitional and summer ranges of migratory deer, concomitantly with prescribed burns in Lava Beds. Migratory deer are on those ranges for the last half of the final trimester of gestation and during lactation. As succession proceeds in the burns south of the Monument, a seral stage of optimum cover and forage for deer will be reached. The large area impacted by those burns probably will affect a significant segment of the migratory deer population at Lava Beds. Burns on the transitional and summer ranges will have the greatest influence on productivity and fawn survival 5 to 10 years after they occur (Salwasser 1979).

An eventual increase in the deer population in the Monument appears likely in the view of the prescribed burns on the winter and early spring ranges in the Monument, and wildfires on the transitional summer ranges to the south. Therefore, periodic counts from pellet-group transects already established in the Monument should be continued. Pellet-group counts will not provide an accurate estimate of herd size, however information obtained from them will reflect general population trends. Furthermore, they will continue to provide information on distribution of deer in the Monument.

Personnel of the California Department of Fish and Game conduct annual herd composition counts in fall (bucks:does:fawns) and spring (adults:fawns). Such counts provide an index to fawn survival and thus herd recruitment and population trends. These will provide valuable information on the response of the migratory deer to changing conditions on the summer range (fall counts) and on the winter range (spring counts) and should be monitored closely.

There is also the possibility of an increase in the non-migratory segment of the deer population in Lava Beds. The present number of non-migratory deer in the Monument is relatively small when compared to the number of migratory deer. An increase in the non-migratory component, however, would result in increased use of the range. It appears that most non-migratory deer remain in the northern half of the Monument. Counts of pellet-group transects and herd composition counts of deer in the northern portion of the Monument would keep personnel informed as to the population trend of those deer.

CONCLUSIONS

The prescribed burning program in Lava Beds is still in an early stage. Relatively mild winter weather occurred during the years of this study. Severe winter weather may alter the behavioral and movement patterns of Lava Beds deer. In a more severe winter, herbaceous vegetation will not be as available and the importance of thermal cover will increase. The initial number of deer present in a burn and the size, frequency, and nature of the burns will bear directly on the response of the population in the future. To date, prescribed burns have left pockets or areas of unburned vegetation, and the size of burns has been smaller than the composite home ranges of most deer monitored in this study. Until an opportunity arises to observe response of deer to burns in a severe winter, the present burning program can probably continue without harm to the deer population. It may in fact, be beneficial to the population given typical weather conditions and recent habitat alterations that have occurred on seasonal ranges south of Lava Beds.

LITERATURE CITED

Anderson, Charles A.
1941. Volcanoes of the Medicine Lake Highlands California. Calif. Univ. Dep. Geol. Sci. Bull. 25:347-422.

Ashcraft, G. C.
1961. Deer movements of the McCloud Flats deer herd. Calif. Fish and Game 47(3):145-152.

Bertram, R. C., and Rempel.
1977. Migration of the North Kings deer herd. Calif. Fish and Game 63(3):157-159.

Franklin, J. F., and C. T. Dyrness.
1973. Natural vegetation of Oregon and Washington. USDA For. Serv. Gen. Tech. Rep. PNW-8. Pac. Northwest For. and Range Exp. Stn., Portland, Oreg. 417 p.

Leckenby, D. A.
1968. Influences of plant communities on wintering mule deer. W. Assoc. State Fish and Game Comm. 48:201-208.

Moen, A. N.
1973. Wildlife ecology: An analytical approach. W. H. Freeman and Co. 458 p.

Mohr, C. O.
1947. Table of equivalent populations of North American small mammals. Am. Wild. Nat. 37:223-249.

Murphy, D. A., and J. A. Coates.
1966. Effects of dietary protein on deer. N. Am. Wildl. Nat. Res. Conf. Trans. 31:129-138.

Neu, C. W., C. R. Byers, and J. M. Peek.
1974. A technique for analysis of utilization - availability data. J. Wildl. Manage. 38:541-545.

Salwasser, H.
1979. The ecology and management of the Devils Garden Interstate deer herd and its range. Ph.D. diss., Univ. of Calif. 377 p.

Schnoes, R. S.
1978. The effects of prescribed burning on mule deer wintering at Lava Beds National Monument. M. S. thesis, Oreg. State Univ. 71 p.

Thompson, A. M., and W. Thompson.
1953. Effect on mild yield of the ewe and growth of her lamb. Br. J. Nutr. 7:263-274.

Verme, L. J.
1977. Assessment of natal mortality in upper Michigan deer. J. Wildl. Manage. 41(4):700-708.

Fire in the Forests of Mount Rainier National Park

Miles A. Hemstrom

ABSTRACT

Infrequent, catastrophic fires have been important forces in the forests of Mount Rainier National Park. The effectiveness of topographic features as fire breaks, the relative fire resistance of forest habitat types (Franklin et al. 1979), and the natural frequency of large fires in different habitat types are examined. Ridges, valley bottoms, and lower slopes are effective fire breaks. High as well as cool, wet, and low elevations and wet habitat types are relatively fire resistant. The same habitat types seem to experience lower frequencies of large fires. This information should be useful in fire management planning in a variety of ways.

Miles A. Hemstrom, Pacific Northwest Forest and Range Experiment Station, Forestry Sciences Laboratory, 3200 Jefferson Way, Corvallis, Oregon 97331.

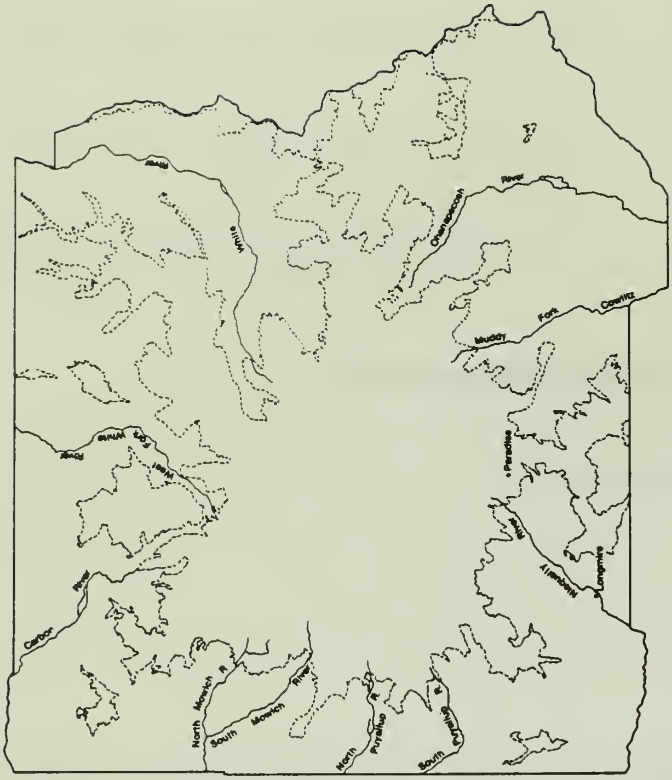


Figure 1.--Outline map of Mount Rainier National Park, Washington. Dashed line is approximate upper tree line.

To a great extent, the rich mosaics of forests in the Pacific Northwest reflect past fires. Fires initiate succession and trigger redistribution of plant and animal species. Fires respond to climatic factors, local environment, and fuel loads. Variable stages of forest recovery after fires produce mosaics of stand ages, species diversity and abundance, and forest structure. Patterns of tree ages in Mount Rainier National Park's (MRNP) relatively untouched forests reveal the presence of past large fires. Understanding the way fires have altered these forests is vital to understanding their succession, architecture, and species composition and distribution. In this paper, the roles of topography and forest habitat types as fire breaks and the effects of forest habitat type on large fire frequency are examined.

The purpose of this study was to answer several specific questions about the natural or pre-modern man role of large fires in MRNP's forest ecosystems:

1. How effective are topographic features as fire breaks?

2. How effective are different forest habitat types as fire breaks?

3. Are there differences in the frequency of large fires in different habitat types?

4. How can habitat types and topographic features help fire management planning?

Though Mount Rainier imposes strong orographic effects on weather patterns in the Park, its climate is typical of the western slope of the Cascades. Summers are warm and dry. Winters are usually wet and cool. July temperatures at Longmire and Paradise (837- and 1 682-m elevation) (fig. 1) average 16.2° and 12.1°C, respectively. January temperatures average -1.1° and -2.9°C. Most of the average annual precipitation, 205 cm at Longmire and 269 cm at Paradise, falls in the winter, accumulating as deep snowpack at higher elevations. Winter storms generally track from southwest to northeast; and because Mount Rainier causes a lee-side rainshadow, the river drainages in the Park's southern and western sectors receive more precipitation than those in the north and east (fig. 1).

Franklin et al.[1] described the Park's forest communities and habitats based on 497 sample plots and extensive field reconnaissance. The final classification defined 17 habitat and community types ranging from low elevation, wet forests through mesic to dry and high elevation forests. Plant communities and habitat types were mapped on a 1:50,000 scale whole-park USGS topographic map. The classification and map were upgraded after each of four field seasons.

The pattern of pre-modern-man fire in MRNP is representative of much of the central and northern west slope forests of the Washington and Oregon Cascades. Though stand ages range from less than 50 years to over 1,000 years, the majority of forests are over 350 years old (Hemstrom 1979). Large fires are infrequent and holocaustic. This pattern seems widespread as far south as the McKenzie River in Oregon (Franklin et al. 1979). There is some indication that large fires coincided with prolonged regional drought (Hemstrom 1979). Modern man may have increased the frequency of large fires during the late 1800's and decreased it since 1900 (Hemstrom 1979).

TOPOGRAPHIC FEATURES AS FIRE BREAKS

This study relied on maps of fire boundaries, tree ages from early seral trees, and forest habitat and community types which were produced by earlier studies in the Park (Hemstrom 1979) (see footnote 1). To examine the role of topography on fire behavior, I measured and classified the lengths of fire boundaries of recent, clearly defined burns into seven topographic classes: (1) major and secondary ridges, (2) upper slopes (within 120-m elevation of a major ridge), (3) mid slopes, (4) lower slopes (within 120-m elevation of a major valley bottom), (5) draws and valley bottoms, (6) snow avalanche tracks, and (7) other.

---

[1]Franklin, J. F., W. H. Moir, M. A. Hemstrom, and S. G. Lewis. Forest ecosystems of Mount Rainier National Park. (Manuscript in preparation.)

Table 1--Percent of total fire boundary in major topographic units from six recent, large fires at Mount Rainier National Park

Topographic feature	Percent of total fire boundary[1]
Major ridges unforested	14
Major ridges forested	10
Side ridges	12
Upper slopes	8
Mid slopes	10
Lower slopes	12
Valley slopes	15
Along fall line[2]	9
Other[3]	4

[1]Total fire boundary: 288 km.

[2]Fire boundaries running along the fall line of an otherwise featureless slope.

[3]Includes benches at various slope positions and snow avalanche tracks.

Since fire boundaries form when a fire dies, their position on topographic surfaces may reflect the effectiveness of topographic features as fire breaks. Under ideal fire conditions, a large fire burns over forested topography until it encounters major fuel breaks. Under adverse weather conditions, a large fire may stop without encountering a break or upon encountering a minor break such as a low, forested ridge. If fires spread and stop without regard to topography as long as sufficient fuel is present, fire boundaries should materialize at random with respect to all but unforested topography. The extent to which fire boundaries are concentrated on certain topographic features indicates departures of fires from random movement and, therefore, the effectiveness of those features as fire breaks.

Despite the fact that weather and chance play important parts in determining where fires stop, certain topographic features seem to act as effective fire breaks (table 1). In fact, the two most important topographic fire breaks, ridges and valley bottoms, together account for over half the total length of fire boundary. Smooth slopes account for about 30 percent of the total length. Proportion of fire boundary increases downslope; a reasonable result considering convective heat movement. Ridges and valleys both are effective fire breaks because they require vertical shifts of fire movement, often downhill or onto wetter or cooler sites. Only a small portion of fire boundary was on open, featureless slopes, oriented along the fall line; a condition indicating fires that stopped without regard to topography.

Abrupt fuel changes over short distances would seem to make avalanche tracks effective fire breaks, but only a small portion of fire boundary was along avalanche tracks. In many cases, fires seem to have burned straight across large avalanche areas. Avalanche tracks often increase in size or are rejuvenated after a fire burns anchoring vegetation (Winterbottom 1974, Hemstrom 1979). An avalanche track which should have been an effective fire break might not have been as large or even have existed at the time a fire burned through the area.

HABITAT TYPES AS FIRE BREAKS

To study the role of forest habitat types as fire breaks, I first superimposed a map of six clearly defined, recent burns on a whole-park forest habitat type map. Unfortunately, classifying fire boundary by habitat type to indicate their fire resistance presents several potential sources of error. Some habitat types are usually restricted to certain topographic features, compounding the effects of habitat type and topography. Stand age boundaries within a habitat type may also represent changes in fuel loads. In addition, habitat types represent vegetation potentials and not necessarily the vegetation actually present. They are, therefore, more accurate predictors of environment than existing fuel loads. Many of MRNP's forests, however, are over 350 years old and are, at least in terms of fuels, similar to climax stands.

Another source of error is that the proportion of the landscape occupied by particular habitat types may influence the amount of fire boundary in each habitat type, irrespective of fire resistance. To correct for this bias to some extent, I divided the percent of the total fire line in each habitat type by the percent of the total area burned which was the same habitat type. The habitat types were ranked according to this calculation of relative fire resistance. If a habitat ranked high, the length of fire line relative to burned area of that habitat was low. In other words, most of the fires which burned into that habitat also burned through it without stopping. The habitat type would therefore be relatively less fire resistant than others which rank low. Some bias may be introduced by using a ratio of a linear quantity to squared (area) quantity which might change the ratio purely on the basis of the study area size. The ranks of habitat types according to relative fire resistance should not be affected.

Another way to look at natural burning rates by habitat types is to reconstruct episodes of fire back in time and calculate burn rates by habitat; hectares burned per year per hectare of habitat type for fires larger than 100 ha. In previous reconstrucion of fires at MRNP (Hemstrom 1979), I used a somewhat arbitrary set of rules to define old burn boundaries. For this study, I modified the rules to better incorporate topographic fire barriers. I then reconstructed fires to the first significant topographic fire break in all directions. In general, the new reconstructions are more conservative than the earlier ones.

Table 2--Percent fire boundary divided by percent burned area by habitat type for six recent, large fires at Mount Rainier National Park

Habitat type[1]	F/B[2]	Rank
Tsuga heterophylla/Achlys triphylla	0.45	1
Abies lasiocarpa/Valeriana sitchensis	0.49	2
Abies amabilis and Tsuga heterophylla/ Gaultheria shallon	0.68	3
Abies amabilis/Xerophyllum tenax	0.70	4
Abies amabilis/Berberis nervosa	0.84	5
Abies amabilis/Rubus lasiococcus/ Rubus lasiococcus phase	1.00	6
Abies amabilis/Oplopanax horridum	1.04	7
Abies amabilis/Tiarella unifoliata	1.32	8
Chamaecyparis nootkatensis/Vaccinium ovalifolium	1.81	9
Abies amabilis/Erythronium montanum phase	2.00	10
Tsuga heterophylla/Polystichum munitum	2.04	11
Abies amabilis/Menziesia ferruginea	2.35	12
Abies amabilis/Rhododendron albiflorum	3.17	13

[1]Some habitat types are minor and not included. (See footnote 1 in text.)

[2]F/B is the percent of measured fire boundary in a habitat type divided by the percent of the total burned area in the same habitat type. Total fire boundary measured: 237 km. Total burned area: 14 368 ha.

Comparing the ratio of percent burn line to percent burned area and reconstructed large fire frequency allows a relatively independent evaluation of the role of fire resistance and frequency by habitat type. The first method does not rely on reconstructions but is limited to recent, well defined fires. The second method reaches much farther back in time but requires accurate reconstructions. Both approaches depend on accurate habitat type maps and tree age data.

Some habitat types appear to be significant fire breaks (table 2). The Abies amabilis/Rhododendron albiflorum (Abam/Rhal) and Abies amabilis/Menziesia ferruginea (Abam/Mefe) habitat types appear to be very fire resistant. Since both of these types tend to occur on north facing, high elevation, wet slopes, much of their fire resistance may be due to topographic position. Sites where these types occur also experience heavy snowpacks, and fuels would be wet much of the time.

At the other extreme, the Tsuga heterophylla/Achlys triphylla (Tshe/Actr), Abies lasiocarpa/Valeriana sitchensis (Abla/Vasi), Tsuga heterophylla and Abies amabilis/Gaultheria shallon (Tshe/Gash and Abam/Gash), Abies amabilis/Xerophyllum tenax (Abam/Xete) and Abies amabilis/Berberis nervosa (Abam/Bene) habitat types all seem to burn readily in large fires. The Abam/Xete and Abla/Vasi habitat types tend to occur on high elevation, exposed sites which are subject to summer lightning. They are also dominant habitat types in the White River drainage, the driest in the Park. The Tshe/Gash, Abam/Gash and Abam/Bene habitat types are typical of dry sites where fuels might be flammable early in the season. The low fire resistance of the Tshe/Actr habitat type may be an artifact of its small extent relative to the other habitat types.

FIRE FREQUENCY FROM RECONSTRUCTED FIRE HISTORY

Analysis of topographic features as fire breaks provide a basis for defining rules for reconstructing fire patterns in MRNP to 750 years ago. Calculations of burn rate for large fires and natural fire rotation for the Nisqually, Ohanapecosh, and White River drainages reveal a pattern of large fire frequencies which change between habitat types within a drainage and within habitat types between drainages (table 3). The overall pattern of large fire frequency in different habitat types strongly resembles the pattern of fire resistance by habitat types.

Over the three drainages, the Abla/Vasi, Abam/Bene, Tshe/Actr, Abam/Gash, Tshe/Gash, and Abam/Xete types experience large fires most often. The Abies amabilis/Erythronium montanum (Abam/Ermo), Abies amabilis and Tsuga heterophylla/Oplopanax horridum (Abam/Opho and Tshe/Opho), and Abam/Rhal habitat types burn least often. Except for Abam/Rhal, these were not the most fire resistant (table 2). This difference may stem from my use of the whole Park in fire resistance analysis but only three drainages in fire frequency analysis. The overall order of habitat types by fire resistance and decreasing fire frequency is remarkably similar, however.

There are some interesting, and in some cases unexplained, differences in fire frequency by habitat type between drainages. The Abam/Mefe habitat type ranks first in fire frequency in the Nisqually drainage and sixth in both the Ohanapecosh and White River drainages. The Abam/Xete habitat type ranks second in the Nisqually, third in the Ohanapecosh and tenth in the White River drainage. These examples may indicate gaps in our understanding of successional status of some of the Park's habitat types or may reflect bias from the relatively few fires sampled.

In general, the fire frequency of the same habitat type increases from the Nisqually to the Ohanapecosh to the White River drainage. The average fire frequency increases and natural fire rotation decreases from 0.0023 ha ha^{-1} $year^{-1}$ (438 years) to 0.0031 ha ha^{-1} $year^{-1}$ (324 years) from the Nisqually to the White River drainage. The average fire frequency and natural fire rotation for the three drainages is 377 years, lower than the whole Park natural fire rotation of 465 years (Hemstrom 1979).

APPLICATIONS TO FIRE MANAGEMENT PROBLEMS

This analysis provides fire managers with information useful in: (1) pointing out the most effective places to put fire lines during fire fighting operations, (2) locating areas where natural fire frequency and natural fire breaks might make let-burn management feasible, and (3) indicating areas where fires, either prescribed or natural, are frequent and necessary parts of the landscape.

Table 3--Fire frequency[1] (FF) and natural fire rotation[2] (NFR) by habitat type for the Nisqually, Ohanapecosh, and White River drainages, Mount Rainier National Park

Habitat type[3]	Nisqually drainage			Ohanapecosh drainage			White drainage			Average		
	NFR	FF	Rank	NFR	FF	Rank	NFR	FF	Rank	NFR	FF	Rank
Abies lasiocarpa/Valeriana sitchensis	NA	NA	NA	191	.0052	1	282	.0035	3	275	.0035	1
Abies amabilis/Berberis nervosa	400	.0025	4	303	.0033	3	258	.0039	2	295	.0034	2
Tsuga heterophylla/Achlys triphylla	NA	NA	NA	360	.0028	5	208	.0048	1	308	.0033	3
Abies amabilis and Tsuga heterophylla/ Gaultheria shallon	325	.0031	2	305	.0032	4	305	.0033	3	313	.0032	4
Abies amabilis/Xerophyllum tenax	348	.0029	3	273	.0036	2	490	.0020	9	323	.0031	5
Abies amabilis/Menziesia ferruginea	269	.0037	1	396	.0025	6	335	.0030	5	343	.0029	6
Abies amabilis/Rubus lasiococcus/ Rubus lasiococcus phase	667	.0015	10	400	.0025	7	318	.0031	4	367	.0027	7
Abies amabilis/Tiarella unifoliata	466	.0021	6	405	.0025	8	421	.0024	8	426	.0023	8
Tsuga heterophylla/Polystichum munitum	435	.0023	5	NA	NA	NA	NA	NA	NA	435	.0023	9
Abies amabilis/Vaccinium alaskaense and Chamaecyparis nootkatensis/Vaccinium ovalifolium	523	.0019	8	494	.0020	9	365	.0027	6	474	.0021	10
Abies amabilis/Rhododendron albiflorum	663	.0015	9	551	.0018	11	395	.0025	7	478	.0021	11
Abies amabilis/Oplopanax horridum	503	.0020	7	700	.0014	12	NA	NA	NA	535	.0019	12
Abies amabilis/Erythronium montanum	729	.0014	11	510	.0020	10	592	.0017	10	616	.0016	13

[1]Burned hectares per hectare of habitat type per year for fires over 100 ha.

[2]The time required to burn an area equal to the total area of each habitat type given its burn rate (Heinselman 1973).

[3]The areal extent of some habitat types was insignificant. These are omitted. (See footnote 1 of text.)

The most effective places to construct fire lines are located where natural topographic or vegetative fire breaks would complement artificially decreased fuel loads. It might be important not only to construct a fire line on a ridge top, as is common practice, but to place the line next to a naturally fire resistant Abam/Rhal stand. While it might be essentially useless to put a fire line through a dense Abla/Vase, Abam/Xete, Abam or Tshe/Gash or Abam/Bene stand, a similar fire line next to Abam/Rhal, Abam/Ermo, Abam/Mefe, Abam/Vaal or Abam/Opho habitat types could prove effective. There is no assurance, however, that fires will stop on ridges or in an Abam/Rhal stand if conditions for fires are favorable.

Another application is in planning fire management. In some areas, natural flammability and vegetative and topographic fire breaks provide conditions which might make possible let-burn fire management. A slope covered with Abam/Bene habitat type and bounded on three sides by ridges and fire resistant habitat types might be left to burn if weather conditions were suitable. But fires in dense Abla/Vasi stands on gentle slopes abutting valuable timber land outside the Park could easily escape. A whole Park map could be divided into units for let-burn management based on habitat type, vegetative and topographic fire barriers, and consideration of adjacent ownership.

Finally, fire frequency information by habitat type indicates where fires are most important as natural processes and where they are most likely to occur in the future. The former could provide a scale for evaluating the urgency of applying prescribed burns or let-burn management. The latter could be important to fire lookouts, to fire bosses in action, and for planning future developments such as trails or facilities.

CONCLUSIONS

1. Certain topographic features serve as effective fire breaks, especially ridges and valley bottoms.

2. Certain habitat types are more fire resistant than others. This may reflect their characteristic topographic location and environment.

3. Certain habitat types experience natural, large fires more frequently than others.

4. Both fire resistance and fire frequency vary between habitat types within river drainages and within habitat types between drainages. The driest river drainages have the highest natural frequency of large fires.

5. Natural vegetative and topographic fire breaks and differential fire frequencies between habitat types have important applications in fire management.

LITERATURE CITED

Franklin, J. F., A. McKee, F. J. Swanson, J. Means, and L. Brown.
1979. Age structure analysis of old-growth Douglas-fir stands: data versus conventional wisdom. Bull. Ecol. Soc. Am. 60:102. (Abstr.).

Heinselman, N. L.
1973. Fire in the virgin forests of the Boundary Waters Canoe Area, Minnesota. Quat. Res. 3:329-382.

Hemstrom, M. A.
1979. A recent disturbance of forest ecosystems at Mount Rainier National Park. Ph. D. thesis, Oreg. State Univ., Corvallis. 67 p.

Winterbottom, K.
1974. The effects of slope angle, aspect and fire on snow avalanching in the Field, Lake Louise, and Marble Canyon region of the Canadian Rocky Mountains. M.S. thesis, Univ. of Calgary, Alberta.

Forest Dynamics and Fuelwood Supply of the Stehekin Valley, Washington[1]

Bruce C. Larson and Chadwick Dearing Oliver

ABSTRACT

Stehekin Valley National Recreation Area in the North Cascades National Park complex of Washington is an isolated valley used by permanent residents for fuelwood (and other uses) and by seasonal recreationists. Upland forests of the Recreation Area consist of Douglas-fir, ponderosa pine, lodgepole pine, bigleaf maple, and other species. These forests at first appeared to be perpetuated by all-age succession. Examination, however, showed the forests exist in age classes which begin following large disturbances such as fire (in 1889). Small disturbances such as selection cuttings do not allow new stems to be recruited. The valley appears to go through large disturbances on 90- to 100-year cycles. Cuttings for firewood should mimic these disturbances if the natural forest patterns are to be maintained.

[1]This study was performed through the University of Washington, College of Forest Resources/U.S. National Park Service Cooperative Park Studies Unit (Contract No. CX 9000-9-0088).

Bruce C. Larson, research assistant, and Chadwick Dearing Oliver, assistant professor, College of Forest Resources, AR-10, University of Washington, Seattle, Washington 98195.

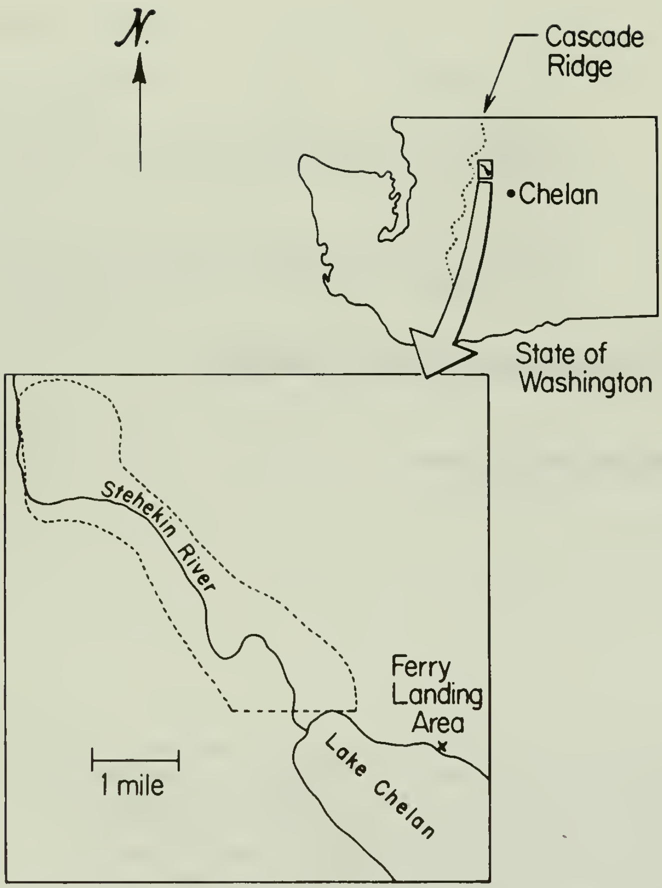


Figure 1.--Location of study area in Stehekin, Washington.

INTRODUCTION

The Stehekin Valley in the North Cascades National Park complex of Washington State is unique for a combination of geographic, social, and ecologic factors. It is a National Recreation Area (NRA) administered by the National Park Service, and management other than preservation is mandated. The Cascade Range and 55-mile (89-km) Lake Chelan provide isolation and difficult access (fig. 1). Outstanding beauty and vegetation diversity bring more than 15,000 visitors each year, although there are fewer than 130 winter residents.

The overwintering population has been expanding, and the winter residents heat with firewood cut from the NRA (to date, primarily dead wood has been taken) and private lands within the valley. The National Park Service managers needed information about the long range firewood availability and how they could properly balance the valley's natural beauty, firewood cutting, and winter population level.

The purposes of the study were to determine the potential firewood supply and how and where it could be cut. The objectives were accomplished by examining the forested areas to determine the standing volume of wood and to determine the stand dynamics--the stand development pattern--of each area.

This paper reports preliminary findings of forest stand dynamics and their importance for management considerations in one of four subareas of the Stehekin Valley. The paper describes the natural stand dynamics of the existing forest and the effects and potential effects of various cutting methods on the forest's development. The area is divided into forest types based on uniform soil substrate and the diameter, age, and species distribution. The disturbance history of each area is described.

LITERATURE REVIEW

Conventional forest inventories (Dilworth 1977, Husch et al. 1972) have often been used to determine stand volumes and growth rates. When such inventories have been used for growth rate predictions, a pattern of natural growth--either all-age or age classes following large disturbances--has been assumed.

Certain characteristics have been assumed to be indicative of an all-aged forest--the "reverse J-shape" frequency distribution of diameters, and vertical crown stratification by species (Hough 1932, Meyer and Stevenson 1943, Braun 1950, Philips 1959, Daubenmire 1968, Minckler 1974). All-aged forests have been assumed to develop naturally by the smaller (and presumably younger) stems gradually replacing the larger (and presumably older) stems. Selective cutting practices in such stands where few larger trees are taken at a time have been assumed to mimic the natural growth pattern.

Studies in other forest types in North America (Hough and Forbes 1943, Henry and Swan 1974, Oliver 1978, Stubblefield and Oliver 1978, Wierman and Oliver 1979) have examined the age structures and growth patterns in forests with diameter and stratification characteristics previously attributed to all-age stands. These characteristics were found to exist in stands in which all stems originated in a distinct time interval (age class) following a large disturbance. A stand could have more than one age class where more than one large disturbance occurred but did not eliminate all previously standing trees. Small disturbances (such as the removal of a few trees) did not create a new age class, but allowed the existing stems to increase in size (Oliver and Stephens 1977).

Forests in more mesic regions than the Stehekin Valley have been described as having periodic disturbance cycles (Loucks 1970, Heinselman 1973, Wright 1974), in which the forests became more susceptible to large disturbances (such as fire following litter buildup) as they grow old. It was not known if a similar disturbance pattern occurred in forests of the types found in the Stehekin Valley.

The patterns of development and management of stands similar to those in the Stehekin Valley have been of concern (USDA Forest Service 1978). It was unknown if the forests in the Stehekin Valley developed in an all-aged pattern or in an age-class pattern following large disturbances.

Management by selective cutting assumes the all-aged pattern of stand development can occur. Management by more intensive cutting assumes new stems begin after large disturbances mimicked by the cutting. Conditions following each type of cutting may be different in several ways:

(1) Successional pattern: One cutting pattern would follow the natural stand dynamics and produce stands similar to those naturally there; the other cutting pattern could produce forests of quite different species and appearances.

(2) Volume growth: The tree growth for firewood may prove quite different if the stands were managed on an age-class basis or on an all-age basis.

(3) Regeneration: For forests of the same type to be perpetuated in the valley, any cutting must mimic the natural stand development pattern enough to allow trees to regenerate.

It is important, therefore, to understand how each forested type develops--either in age classes following large disturbances or by all-aged gradual stem recruitment--within the valley if the forests are to be manipulated and perpetuated for natural beauty, recreation, and firewood uses.

PROCEDURES

Study Area

The study area was approximately 4,000 acres, (1 600 ha) about 15 percent of which is private ownership. It could be divided roughly into four forested subgroups: river floor plain, moist alluvial, upland, and steep sidewall forests. This paper describes the results from the upland (nonflooding) subgroup--a highly accessible area and therefore desirable for firewood cutting.

The valley is typed as Abies grandis and Pseudotsuga menziesii zones by Franklin and Dyrness (1973). The dominant tree species are Douglas-fir, Pseudotsuga menziesii [Mirb.] Franco, and ponderosa pine, Pinus ponderosa Dougl. ex Laws. The flood plain areas also have cottonwood, Populus trichocarpa Torr. and Gray, bigleaf maple, Acer macrophyllum Pursh, red alder, Alnus rubra Bong., grand fir, Abies grandis [Dougl. ex D. Don] Lindl., and western redcedar, Thuja plicata Donn. ex D. Don.

Miners and trappers frequented the valley in the 19th century using some wood for houses and fuel. Regular steamboat service and tourist trade from Chelan began in 1888. Fuelwood for the boat was cut in the lower portion of the study area in contiguous patches that eventually resembled clearcuts. A large, hot fire swept the valley in 1889. After 1900, selective cuttings were done continuously in many areas. Larger fire remnant trees were removed for housebuilding and small trees were thinned for firewood.

The U.S.D.A. Forest Service managed much of Stehekin Valley until the late 1960's, at which time management was assumed by the National Park Service.

This glacial valley is typically U-shaped, 1 to 2 miles (1.5 to 3 km) wide, with steep side walls. The glacial drift has been resorted by the Stehekin River. Upland stands lie on river terraces indicating a once large and shifting glacial river. Several creeks originating from large empty cirques enter the valley from the side walls. The creeks moved much glacial material into raised alluvial fans of loose rubble on the valley floor when the mountain glaciers were retreating. The streams now are fed by snowmelt and no longer are powerful enough to flow over the large fans. They flow to one side before joining the Stehekin River.

Elevation of the study area ranged from 1,140 to 2,463 ft (348 to 751 m). Upland areas studied in this paper were located between 1,300 and 1,600 ft (396 and 488 m). Rainfall ranges from 34 to 40 in (86 to 102 cm) (lowest in southeast)--most falls as snow in winter; summers are very dry. Average temperature is 49°F (9°C). On the average, the maximum temperature is below 32°F (0°C) during 49 days each year and the maximum exceeds 95°F (35°C) during 9 days (Donaldson and Ruscha 1975).

Field Procedures

The valley was studied during the summer of 1979 by stratified sampling techniques. The area was mapped into stand types (Dilworth 1977) using: 1978 true color aerial photographs; interviews with residents and National Park Service personnel for disturbance information; and visual inspection noting tree species, lesser vegetation, evidence of disturbance, and information from soil pits.

Variable size (prism) plots were established in each type using a 10-factor prism. Trees 7.0 in (17.8 cm) or less in diameter at 4.5-ft (1.4-m) d.b.h. were sampled using a fixed plot 30 ft (7.2 m) in radius. Data were collected in one of two ways. "Simple" plot data included: diameters and subjective crown classes (Smith 1962) of trees, representative codominant heights, notes of lesser vegetation; and evidence of past disturbance including charcoal, fire scars, wind breakage or blowdown, and stumps, and notes of evidence of past forest stand structure including down wood and litter searches. "Complete" plots included all above information plus the heights of all trees and increment cores of two trees from each 2 in diameter class, if possible. Increment cores were brought back to the laboratory and their ages determined using a dissecting microscope.

Data Analysis

Stems per acre were calculated by species and diameter class. Averages of four or more plots were used in each type. Age structure of stands was determined. Proportion of trees sampled in each 10-year age class was calculated by species.

RESULTS AND DISCUSSION

The upland, accessible forest subgroup described in this study was subdivided logically into four types based on uniformity of soils. Characteristics of each area are shown in table 1 and are discussed below.

Table 1--Characteristics of upland, accessible forest types in Stehekin Valley

Type	Tree species	Area (approx.)	Soil	Disturbances	Diameter range	Age range (years)	Peak age classes (years)
1. Moist conifer stand on lower terraces	Douglas-fir bigleaf maple ponderosa pine	5 acres (2.0 ha)	excessively well-drained glacial rubble, much sorting	extensive fire 1889 much cutting prior to 1900	1 - 44 in (2.5 - 1118 cm)	40-170	65
2. Transition zone between fans and up-land terraces	Douglas-fir bigleaf maple	30 acres (12.1 ha)	excessively well-drained glacial rubble	extensive fire 1889	1 - 44 in (25 - 111.8 cm)	50-180	75, 155
3. Glacial drainage fans	Douglas-fir ponderosa pine bigleaf maple	250 acres (101.2 ha)	excessively well-drained glacial rubble, many large boulders	extensive fire 1889 numerous small fires	1 - 40 in (2.5 - 101.6 cm)	30-375	65, 155, 255
4. Upland terraces	Lodgepole pine Douglas-fir bigleaf maple willow	75 acres (30.4 ha)	excessively well-drained glacial rubble, some sorting	extensive fire 1889	1 - 40 in (2.5 - 101.6 cm)	50-130	85
5. Upland terraces		175 acres (70.8 ha)	excessively well-drained glacial rubble, some sorting	extensive fire 1889			
a. uncut	Douglas-fir ponderosa pine bigleaf maple			some cutting in	1 - 40 in (2.5 - 101.6 cm)	30-150	65, 125
b. partially cut	dogwood	75 acres (30.4 ha)		4b, occasional snowslides	1 - 42 in (2.5 - 106.7 cm)	30-80	65

Moist Stand Type

The type consisted of excessively well-drained material; moistness resulted from close proximity of water table. This area was cut over prior to 1900 and burned in 1889. Some burned wood was collected for steamboat fuel after the fire.

Figure 2 shows the species distribution by diameters and ages. The large range of diameters and "reverse-J-shape" diameter distribution showing many small stems and few large ones can give the appearance of an all-aged stand, with the smaller trees gradually replacing the larger (and presumably older) ones. The age distribution, however, shows that the stems invaded during an interval after 1889, the time of the large fire. As has been found in more mesic forests in other parts of North America, stems have not been continuously invading the area, but invaded in a distinct wave following the disturbance.

Transition Zone Type

The type represented a transition between moist stands and extremely dry glacial alluvial fans. This area was not cut over, but selective cutting was a continual influence.

Figure 3 shows a similar diameter distribution to the moist type. The age structure shows two age groups, or classes: one after the fire of 90 years ago and one approximately 150 years old.

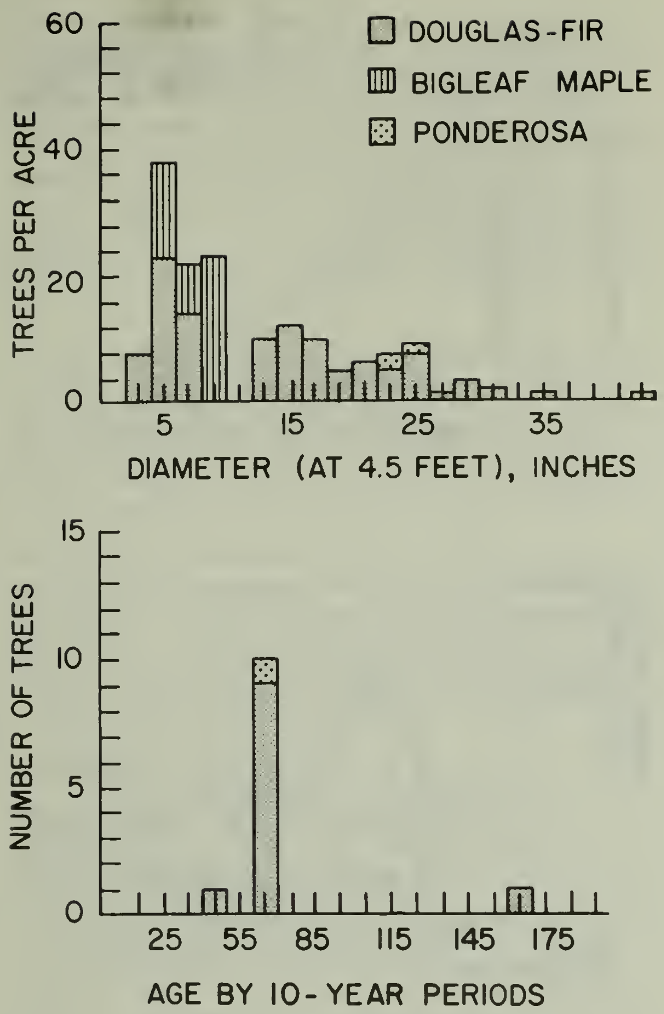


Figure 2.--Diameter and age distributions by species for "Moist conifer stand on lower terraces" type.

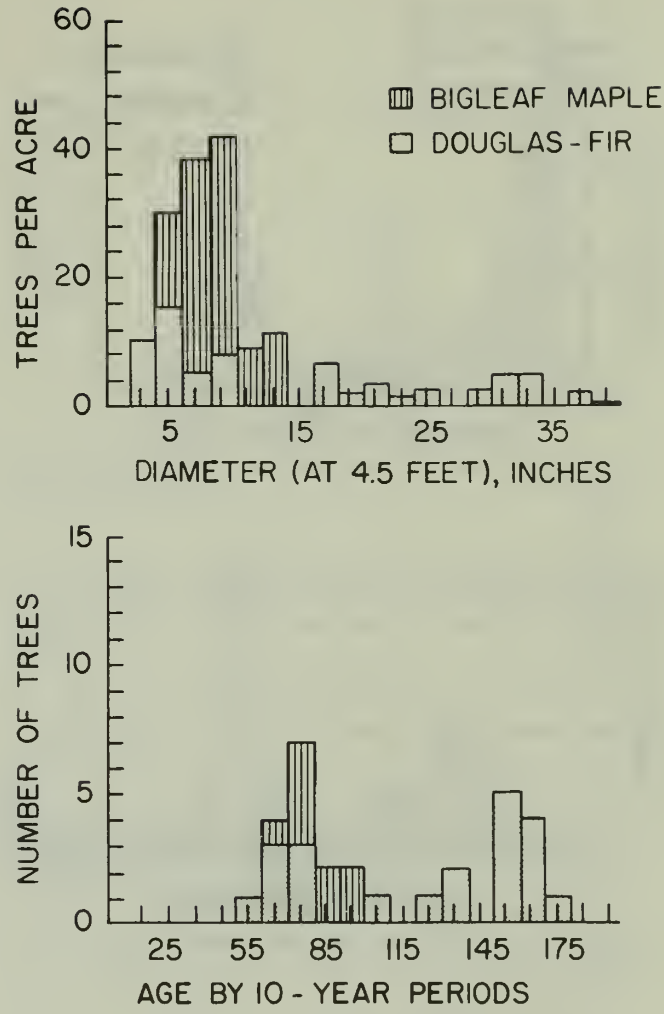


Figure 3.--Diameter and age distributions by species for "Transition zone between fans and upland terraces" type.

Glacial Fan Type

This type was also low elevation, but driest because the glacial drift consisted of large rocks and was excessively well drained. Dryness resulted in aggregated and somewhat open stands. Lesser vegetation was primarily grasses, Arctostaphylos, and Ceanothus.

Figure 4 shows a strong "reverse J-shape" diameter distribution for each species as well as the combination of species. Age structure shows three age groups, or classes. The age distribution within each "group" is quite broad, probably because it took several decades for trees to grow large enough to exclude later arriving ones. Examination of a small recent burn (1967) on a similar soil showed new tree stems were still invading the area in 1979.

Many trees remain in the pre-1889 age groups, probably beause the lack of fuels on this dry site kept the fire incomplete.

Upland Terraces with Lodgepole Pine Type

The type was located on higher, sandy terraces with north aspects. Dense, small diameter stands consisted primarily of lodgepole pine with a large component of Douglas-fir. Stands average over 195 trees per acre of 6- to 8-in (15.2- to 20.3-cm) d.b.h. and 130 trees of 4- to 8-in (10.2- to 20.3 cm) d.b.h. All trees over 12-in (30.5 cm) d.h.b. were Douglas-fir.

The age distribution was very narrow. Sixty percent of trees whose ages were determined (all species) were aged 70 to 90 years. Over 90 percent of lodgepole pines were 70 to 90 years. The pine component was post-1889 (fire) origin.

The stands were located in a cold air drainage, which may partally explain the lodgepole pine. The terraces showed similar age and diameter distributions to other types but with different species.

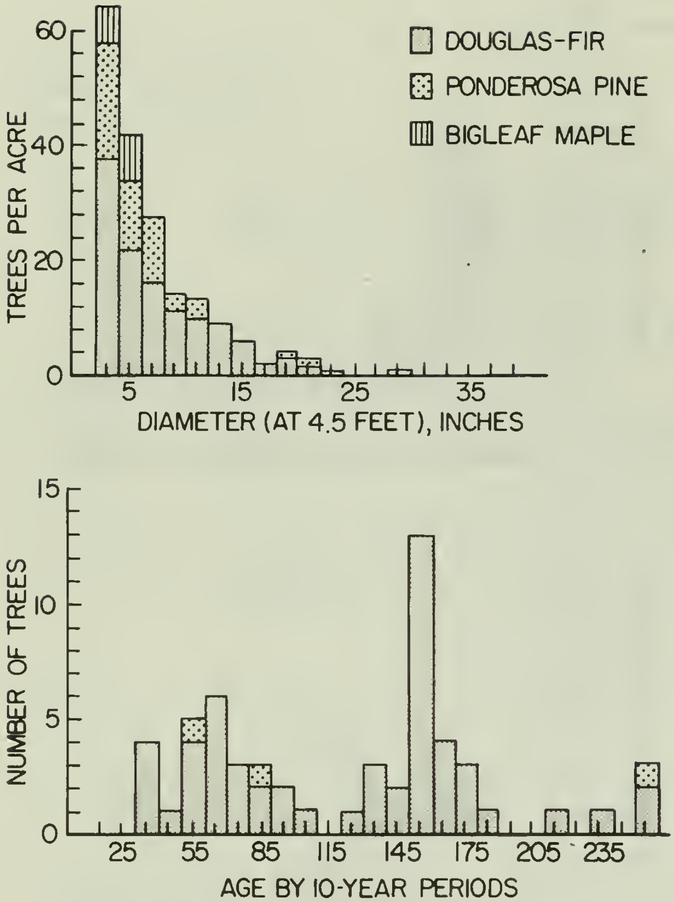


Figure 4.--Diameter and age distributions by species for "Glacial drainage fans" type.

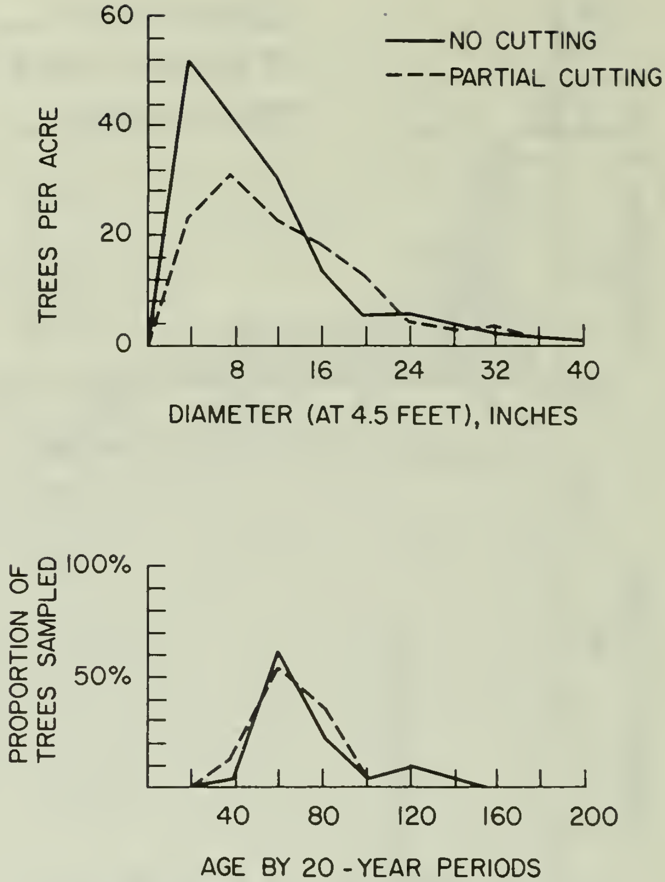


Figure 5.--Diameter and age distribution of all species for "Upland terraces" type, comparing cut and uncut stands.

Upland Terraces of Douglas-fir

The type included most upland terraces in the valley and consisted of two age groups. Some stands had never been cut, others had been partially cut (most about 20-30 years ago). The cutting was selective removal of some large fire remnant trees and some thinning of other, smaller diameter stems, primarily for firewood. Many stumps were 10- to 14-in (25- to 35-cm) diameter and some exceeded 20 in (50.8 cm). The cut stands had essentially returned to crown closure.

Figure 5 shows the diameter and age distribution of both cut and uncut stands of this type. Again, a distinct peak of ages is evident indicating a wave of regeneration after the 1889 fire and an exclusion of later stems. No fires had occurred in this area to eliminate possibly younger trees, apparently the selective cutting done in these stands was not a suitable disturbance to allow new stems to become established. This indicates that it may be unfeasible (as well as unnatural) to perpetuate the stand in an all-aged condition.

GENERAL DISCUSSION AND CONCLUSIONS

Stand Dynamics

The age distribution for all stands is shown in figure 6. Distinct age classes, indicating waves of regeneration, are apparent. As a whole, the area was multi-aged but not all-aged.

The greatest proportion of trees originated in a wave beginning after the last documented major disturbance (fire of 1889). This wave is also the only one still to contain nonfire-resistant species (such as hardwoods and lodgepole pine).

Although the stands originated in distinct age classes, they had an all-age appearance because of the diameter distribution. This appearance is also the result of vertical crown stratification (Smith 1962). This age class structure has been found elsewhere (Hough and Forbes 1943, Oliver and Stephens 1977, Oliver 1978, Stubblefield and Oliver 1978) but has been hard to identify in dry, east Cascade slope stands. A long stem recruitment time following the disturbance and a lack of data have misled observers to conclude that the stands are all-aged.

Previous waves of regeneration may have been coincidental with either major disturbances (such as fire or perhaps catastrophic insect defoliations) or favorable climatic conditions during good seed years. Several factors suggest fire was the cause: (1) favorable climate and seed crop conditions probably would have lasted for a shorter time; therefore the age range within each "class" would not have been as broad; (2) fires have been a factor in the valley for a long time; buried soil horizons were found to contain charcoal.

A fire cycle dependent on the buildup of fuel such as has been found in less dry forests of the Midwest (Heinselman 1973) probably exists. Figure 6 indicates a possible 90- to 100-year cycle of fire in the valley. At present, 90 years after the fire of 1889, a large fuel buildup again presents a fire danger.

The partially cut stands shown in figure 5 indicate that regeneration does not follow minor disturbances (no trees less than 25 years old were found here). Peaks of regeneration following major disturbances and no regeneration following minor ones also have been documented in the New England forests (Oliver and Stephens 1977).

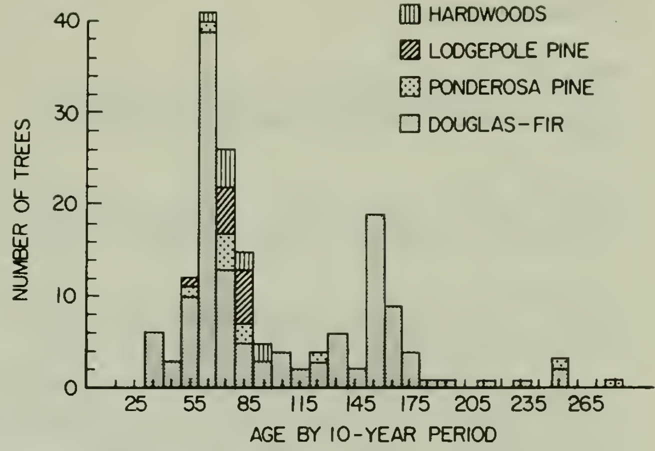


Figure 6.--Age distributions for all species, all forest types.

In the past, new stems appeared following major fires; heavy disturbance, whether natural or man-made, appeared to be necessary to obtain new stems again.

MANAGEMENT IMPLICATIONS

The findings to date are preliminary. More analyses will be made of the data collected; however, the study appears to contain several important management implications:

1. Forest fires may be a real hazard in the valley at present because fuel has accumulated since the last cyclic fire. Past natural disturbances were widespread and catastrophic. It is possible that the fuel buildup rate exceeds what the residents could remove if all dying and down material were useable and firewood collection were restricted to downed wood.

If a selection cutting policy is adopted, minor disturbances may have to be supplemented with management tools such as prescribed burning to prevent natural and dangerous major fires from destroying the community.

If the management plan contains heavy cuttings---shelterwood, seed tree, or clearcutting (Smith 1962)--mimicking large disturbances on specific areas, these ares could be spread throughout the valley and might act as buffers, breaking up the continuous forests susceptible to fires.

2. The type of firewood cutting will have a major impact on the volume available and the species composition of the stands. This will affect both the firewood supply and the esthetics, two prime concerns of the National Park Service. Continual cuttings removing a few trees each time will not promote young trees in the valley. As shown in figure 5, no regeneration occurred after small disturbances. Seedlings appear, but never reach the 2-in (5.1-cm) diameter class. In fact, field observations indicate such small openings promote grasses and shrubby species which may later exclude new tree stems even if large disturbances occur.

3. The type of cutting will have an impact on the species composition and composition changes within the valley.

Providing forest fires are avoided, continual removal of a few stems will change the species composition, since the present forests were the result of relatively large disturbances. It is probably necessary to mimic such disturbances to ensure intolerant trees will predominate within the valley.

If a large forest fire is not avoided and much of the area is burned, early successional species (such as cherry, Prunus, will appear dominant for several decades. It will take 90 years for the forest to appear again as it does now.

Heavier cutting (perhaps followed by slash burning) could mimic the natural disturbances and could be done at regular intervals on scattered areas throughout the valley. This would result in some parts of the valley containing vegetation representative of different times following a major disturbance.

4. It is important for forest managers not only to know the volume and growth rates of the forest stands but also to know the stand dynamics of each forest community. Forest inventories unaccompanied by knowledge of past disturbances and present growth rates may lead National Park Service managers to cut in a manner that would change the species composition and even the area of forest. Proper interpretation of forest stand dynamics may allow managers to manipulate the area so that management mimics natural growth patterns.

LITERATURE CITED

Braun, E. L.
1950. Deciduous forests of eastern North America. The Blakiston Company, Philadelphia. 596 p.

Daubenmire, R.
1968. Plant communities: A textbook of plant synecology. Harper and Row, New York. 300 p.

Dilworth, J. R.
1977. Log scaling and timber cruising. O.S.U. Book Stores, Inc., Corvallis, Oregon. 473 p.

Donaldson, W. R., and C. Ruscha.
1975. Washington climate for Chelan, Douglas, and Okanogan Counties. Coop. Ext. Serv., Washington State Univ., Pullman, Washington.

Franklin, J. F., and C. T. Dyrness.
1973. Natural vegetation of Oregon and Washington. USDA For. Serv. Gen. Tech. Rep. PNW-8.

Heinselman, M. L.
1973. Fire in the virgin forests of the Boundary Waters Canoe Area, Minnesota. Quat. Res. 3:329-382.

Henry, J. D., and J. M. A. Swan.
1974. Reconstructing forest history from live and dead plant material--an approach to the study of forest succession in southwest New Hampshire. Ecology 55:772-783.

Hough, A. F.
1932. Some diameter distributions in forest stands of northwestern Pennsylvania. J. For. 30:933-943.

Hough, A. F., and R. D. Forbes.
1943. The ecology and silvics of forests in the high plateaus of Pennsylvania. Ecol. Monogr. 13:299-320.

Husch, B., C. I. Miller, and T. W. Beers.
1972. Forest mensuration. Ronald Press. New York. 410 p.

Loucks, O. L.
1970. Evolution of diversity, efficiency, and community stability. Amer. Zool. 10:17-25.

Meyer, H. A., and D. D. Stevenson.
1943. The structure and growth of virgin beech-birch-maple-hemlock forests in northern Pennsylvania. J. Agric. Res. 67:465-484.

Minckler, L. S.
1974. Prescribing silvicultural systems. J. For. 72:269-273.

Oliver, C. D.
1978. The development of northern red oak in mixed species stands in central New England. Yale Univ., Sch. of For. and Envir. Stud., Bull. No. 91.

Oliver, C. D., and E. P. Stephens.
1977. Reconstruction of a mixed species forest in central New England. Ecology 58:562-572.

Phillips, E. A.
1959. Methods of vegetation study. Holt, Rinehart, and Winston, Inc. New York. 107 p.

Smith, David M.
1962. The practice of silviculture. John Wiley and Son, Inc., New York. 578 p.

Stubblefield, G., and C. D. Oliver.
1978. Growth of a mixed red alder-hemlock-redcedar-Douglas-fir stand and its silvicultural implications. In Utilization and management of alder. USDA For. Serv. Gen. Tech. Rep. PNW-70:307-320.

U.S. Department of Agriculture, Forest Service.
1978. Uneven-aged silviculture and management in the United States. Timber Manage. Res. Washington, D. C.

Wierman, C. A., and C. D. Oliver.
1979. Crown stratification by species in even-aged Douglas-fir/western hemlock stands of coastal Washington. Can. J. For. Res. 9:1-9.

Wright, H. E., Jr.
1974. Landscape development, forest fires, and wilderness management. Science 186:487-495.

Optical Properties of Crater Lake, Oregon: Variation in Secchi Disk Transparency, 1937-79

Douglas W. Larson and Mark E. Forbes

ABSTRACT

Since 1937, the Secchi disk transparency of pristine Crater Lake, Oregon, has tended to decrease. Secchi readings during the summers of 1968 and 1969 averaged 36.6 m which was about 2 m less than the 1937 average (38.3 m). Recent Secchi measurements (1978 through 1979) averaged 29.3 m (range: 23 to 31 m) which indicated further decline in lakewater visibility. Cause of the change is uncertain, but an increase in suspended particulate matter such as phytoplankton is suspected.

Douglas W. Larson, limnologist, Hydrology Section, U.S. Army Corps of Engineers, Portland District, Portland, Oregon; and Mark E. Forbes, resource management specialist, Crater Lake National Park, USDI, National Park Service, Crater Lake, Oregon.

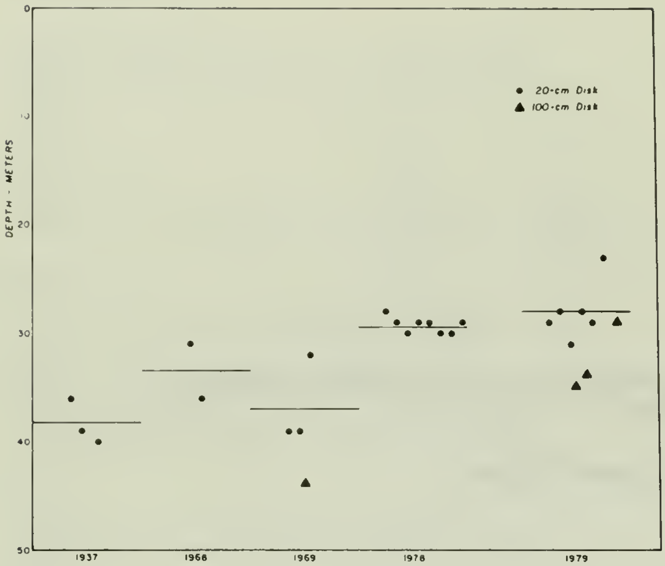


Figure 1.--Secchi disk readings, Crater Lake, Oregon, 1937-79. Horizontal lines represent the average values for 20-cm disk readings.

INTRODUCTION

Crater Lake, Oregon, the deepest lake in the United States at 589 m, is one of the clearest lakes in the world (Smith and Tyler 1967, Smith et al. 1973). Secchi disk transparency measurements, indicating the degree of lakewater clarity, were 36, 39, and 40 m in August 1937 (Hasler 1938). Secchi readings in 1968 and 1969 were slightly less (average: 36.6 m), although a larger disk measuring 100 cm in diameter was still visible at 44 m (Larson 1972). Other lakes with exceptionally high Secchi readings include Lake Masyuko in Japan (41.6 m, 20-cm disk diameter), Lake Baikal in the U.S.S.R. (40.6 m, 20-cm disk diameter) and Lake Tahoe in northern California (36 m, 20-cm disk diameter) (Thomasson 1956).

Limnological studies were resumed at Crater Lake in 1978 after a hiatus of nearly 10 years. The work included Secchi measurements which we present in this report.

PROCEDURES

Use of the Secchi disk at Crater Lake was under the most favorable conditions possible (i.e., midday readings, clear sky, calm lake surface), with two and frequently three persons making each observation. Considerable effort was made to avoid typical operator errors (Tyler 1968) and to be consistent when using the disk.

Secchi readings were taken by lowering the disk (20- and 100-cm diameters) into the lake until it disappeared. The disk was then raised carefully until it reappeared. The average distance between the two sightings was called the Secchi depth (Welch 1948). Readings were taken only during summer months.

RESULTS AND DISCUSSION

Secchi measurements of Crater Lake in 1978 and 1979 indicated that lakewater clarity had diminished since 1969. Whereas 20-cm Secchi readings in 1937 and 1969 averaged 38.3 and 36.6 m respectively, the average value for 1978-79 was 29.3 m (fig. 1). For the 100-cm disk, decline in visibility was even more pronounced--from 44 m on July 16, 1969 (Larson 1972), to 35 and 34 m on July 16 and August 1, 1979, respectively (fig. 1).

These values, representing a reduction in lake-water clarity of about 25 percent since 1937, suggest that the lake has become less transparent due to an increase, perhaps, in the amount of suspended particulate matter capable of scattering subsurface light and reducing Secchi transparency or visibility. The nature of the particulate matter is not known (assuming that this is the source of the problem); but it is possible that the lake has become more productive biologically as the result of subtle increases in algal nutrients or water temperature. Either factor, singly or in combination, could conceivably increase phytoplankton biomass, which is often the cause of reduced Secchi transparency in lakes (Wetzel 1975), and is regarded as a precursor of accelerated eutrophication in oligotrophic systems (Hasler 1969).

The Secchi disk is an inexpensive, easily developed limnological tool. Nevertheless, its use can reveal much about the quality and evolution of a lake, especially when Secchi measurements span a period of several years (or decades) and are compared with data from lakes featuring different levels of eutrophication. The seasonal nature and sharp numerical fluctuations of lake algae and other light scattering particulate matter requires, however, that Secchi measurements be recorded frequently and consistently throughout the year to avoid inaccurate lake assessments resulting from sporadic monitoring. Reliable Secchi records, capable of yielding data for predicting trends, can usually be obtained even under a financially austere lake management program. Such a program would seem to be consistent with National Park Service goals to preserve those natural resources with which the agency is charged.

ACKNOWLEDGMENTS

We thank J. Rouse, D. Sholley, B. Wadlington, and R. Kirschner, Crater Lake National Park, for their valuable assistance and cooperation. J. Bradley, Corps of Engineers, and T. Thomas, National Park Service, assisted in the field.

LITERATURE CITATIONS

Hasler, A. D.
1938. Fish biology and limnology of Crater Lake, Oregon. J. Wildl. Manage. 2:94-103.

Hasler, A. D.
1969. Cultural eutrophication is reversible. Bioscience 19:425-431.

Larson, D. W.
1972. Temperature, transparency, and phytoplankton productivity in Crater Lake, Oregon. Limnol. Oceanogr. 17:410-417.

Smith, R. C., and J. E. Tyler.
1967. Optical properties of clear natural water. J. Opt. Soc. Am. 57:589-595.

Smith, R. C., J. E. Tyler, and C. R. Goldman.
1973. Optical properties and color of Lake Tahoe and Crater Lake. Limnol. Oceanogr. 18:189-199.

Thomasson, K.
1956. Reflections on arctic and alpine lakes. Oikos 7:117-143.

Tyler, J. E.
1968. The Secchi disc. Limnol. Oceanogr. 13:1-6.

Welch, P. S.
1948. Limnological methods. McGraw-Hill, New York. 381 p.

Wetzel, R. G.
1975. Limnology. W. B. Saunders, Philadelphia. 743 p.

Species Composition and Vertical Distribution of Pelagic Zone Phytoplankton in Crater Lake, Oregon: 1940-79

Douglas W. Larson and N. Stan Geiger

ABSTRACT

Phytoplankton studies at Crater Lake, Oregon, in 1940 and 1978-79 are compared. Contrary to the earlier work, (1) diatoms are the predominant phytoplanktonic form, (2) Anabaena sp. is not present, (3) surface waters contain an abundance of phytoplankton, particularly Nitzschia gracilis, (4) taxa diversity is greater, with more than 60 species of phytoplankton identified, (5) the vertical distribution of phytoplankton varies among species, (6) equally large numbers of organisms occur at various depths throughout the vertical water column, and (7) phytoplankton smaller than 10 μm appear to be dominant.

Disparity between the two studies might be attributed to either differences in limnological sampling techniques or changes in lake quality.

Douglas W. Larson, limnologist, Hydrology Section, U.S. Army Corps of Engineers, Portland District, Portland, Oregon; and N. Stan Geiger, senior aquatic biologist, Beak Consultants, Portland, Oregon.

INTRODUCTION

Crater Lake, Oregon, is recognized as one of the deepest, clearest, most oligotrophic lakes in the world (Hasler 1938, Byrne 1965, Larson 1972). Yet, little is known about the biology of this unusual body of water, including the limnologically important phytoplankton which occupies the surface-to-200-m stratum and may extend even deeper.

Brief, cursory surveys of phytoplankton were conducted in 1913 (Kemmerer et al. 1924), 1940 (Utterback et al. 1942), and 1959 (Thomasson 1962). More recent studies (Hoffman and Donaldson 1968, Larson 1972) measured rates of phytoplankton primary production and made biomass estimates based on chlorophyll a determinations. Here we report on other aspects of the phytoplankton community, including taxa identifications and the distribution and relative abundance of various species through the vertical water column. The work is intended as a point of reference for future limnological studies.

PREVIOUS STUDIES

The 1913 plankton survey by Kemmerer et al. (1924) was probably the first of its kind for the lake. Although these investigators reported only two species of phytoplankton, *Mougeotia* sp., and a diatom, *Asterionella* sp., they discovered that phytoplankton and zooplankton were distributed to great depths, reaching maximum abundance between 60 and 200 m.

Limnological studies of the lake in 1940 (Utterback et al. 1942) indicated that (1) phytoplankton was most abundant between depths of 75 and 150 m, (2) virtually no phytoplankton existed in the surface-to-20-m stratum, or in the deepest sample taken at 425 m, (3) most phytoplankton consisted of filamentous, blue-green algae, *Anabaena* sp., and (4) diatoms constituted only about 15 percent of the total phytoplankton collected. Samples were obtained by hauling a No. 20 mesh plankton net (mesh aperture = 79μm) vertically through the water column, or by casting a Kemmerer bottle to discrete depths, retrieving the sample, and then centrifuging the water to extract the phytoplankton. Population densities reportedly ranged from $1X10^3$ to $3X10^6$ cells per liter, but no indication is given as to the meaning of the term "cells". The work provided a sketchy taxonomic list, including, in addition to *Anabaena* sp., the diatoms *Nitzschia* sp., *Asterionella* sp., *Navicula* sp., and the filamentous alga *Mougeotia* sp. identified earlier by Kemmerer et al. (1924).

Thomasson (1962) listed about a dozen species, one of which, *Ceratium hirundinella*, suggested that the samples were collected from sheltered shoreline locations rather from the pelagic region of the lake (sampling locations were not reported). Thomasson noted that the plankton were "very sparse" on the day he visited the lake (July 14, 1959), and identified a rather abundant filamentous alga as *Tribonema* sp. which earlier investigators may have mistakenly called either *Mougeotia* sp. (Kemmerer et al. 1924) or *Anabaena* sp. (Utterback et al. 1942).

MATERIALS AND METHODS

The work reported here was completed during the summers of 1978 and 1979. Water samples were collected with a 2.5-liter (volume) Van Dorn polyvinyl chloride, messenger-activated bottle from selected depths extending from lake surface to 200 m. Samples were retrieved and emptied individually into an extremely fine mesh ultraplankton net (10- m-mesh aperture). The collected materials, called "net" samples, were contained in plastic bottles and preserved with 3-percent formalin. Filtered water (about 500 ml) was also collected, preserved with formalin, and later Millipore-filtered (HA-type filters, 0.45-μm pore diameter) to determine the fraction of phytoplankton small enough to escape the 10-μm net.

The composition of the net samples was first determined by examining material at various magnifications with an inverted microscope (Wild M40). Samples were then Millipore-filtered (HA-type) and examined microscopically (oil immersion, 1000X magnification). Counts were made of 100 discrete algal particles (a "particle" was represented by a single cell, a cluster of cells, or an entire algal filament) on randomly selected areas of both the net sample filters and the filters containing the $<$ 10-μm portion of the phytoplankton. Brightfield and phase microscopy were used for counting and identification (Keating 1976). Only cells or groups of cells with distinctive chloroplasts were considered. Standard taxonomic references for diatoms were used (Archibald 1972, Patrick and Reimer 1975) in addition to Sovereign's work (1958) on Crater Lake periphyton.

Water samples for chlorophyll a determinations were also collected with a Van Dorn bottle and Millipore-filtered (HA-type). Extraction and determination of chlorophyll a was done in accordance with Strickland and Parsons (1965). Percent absorbance by pigment extracts was measured on a Bausch and Lomb spectronic spectrophotometer.

RESULTS AND DISCUSSION

The phytoplankton of Crater Lake is dominated by 6 to 10 species, although 63 species have been identified in 250 of the 350 samples collected to date (table 1) and 51 species are diatoms, 15 of which belong to the genus *Nitzschia*. Some species

Table 1-- Twenty of the more common species of phytoplankton in Crater Lake, Oregon, 1978-79

Species	
Synedra mazamaensis	*Nitzschia latens*
S. delicatissima	*N. frustulum*
S. rumpens	*N. innominata*
S. vaucheriae	*N. perminata*
Nitzschia gracilis	*Stephanodiscus hantzschii*
N. demota	*S. astraea*
N. serpenticula	*Asterionella formosa*
N. recta	*Tribonema* CL1
N. mediocris	*Gomphonema* CL1
N. silica	*Melosira italica*

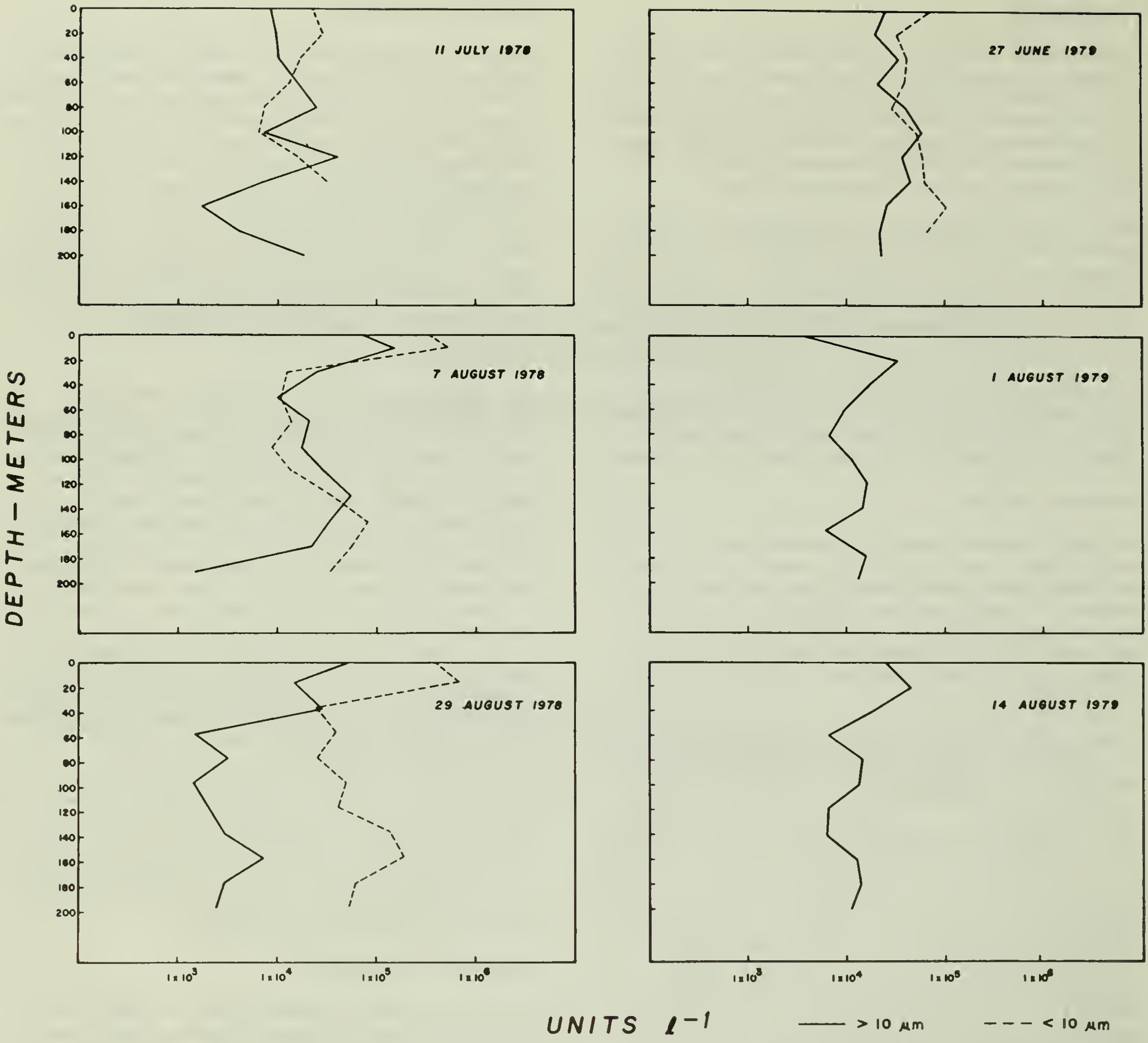


Figure 1.--Vertical distribution of phytoplankton in Crater Lake, Oregon, 1978-79. Sampling intervals are 20 m.

are periphyton, washed from benthic substrates and shoreline rocks into the pelagic zone of the lake.

Anabaena sp. was not present. The organism identified earlier as Anabaena (Utterback et al. 1942) was probably Tribonema sp. which we found to be relatively abundant (i.e., averaging 70 percent of the standing crop at several depths) and similar in size to the Tribonema described by Thomasson (i.e., 5-µm-wide filaments).

The vertical distribution of phytoplankton in Crater Lake is characterized, generally, by three maxima: at the surface (0-20 m), at middepth (80-120 m), and near the bottom of the profile (180-200 m) (fig. 1). Surface waters usually contain large numbers of phytoplankton, particularly organisms smaller than 10µm. Nitzschia gracilis is by far the most abundant phytoplankter in the 0-20-m stratum (table 2), and its numerical increase through summer appears to be related to an increase in surface temperatures which reach maximum levels in late July or early August (Larson 1972). Conversely, phytoplankton in the 180-200-m stratum is dominated by the small (5-8-µm diameter) centric diatom Stephanodiscus hantzschii (table 2).

In the middepth region, described earlier as the lower limit of the photic zone as well as the zone of maximum productivity (Larson 1972), Tribonema sp. usually outnumbers all other species present (table 2). A chlorophyll a maximum also develops at middepth, but does not correspond well to particle counts (fig. 2).

Table 2--Relative abundance of the three most common species of phytoplankton in Crater Lake, Oregon, 1978-79

Date	Net fractions	Surface			100 m			200 m		
		S.h.	N.g.	T.	S.h.	N.g.	T.	S.h.	N.g.	T.
	μm	- - - - - - - - - - - Percent - - - - - - - - - - -								
1978:										
July 11	> 10	8	17	37	5	0	83	53	1	35
July 25	> 10	1	77	0	4	0	85	37	4	34
August 7	> 10	0	96	0	9	3	71	18	7	17
	< 10	9	89	0	38	2	9	96	1	2
August 29	> 10	0	96	0	0	0	88	9	10	22
	< 10	2	90	2	10	8	55	87	4	0
1979:										
June 27	> 10	1	10	70	1	0	66	7	10	36
	< 10	73	19	0	55	25	3	71	12	0
August 1	> 10	0	55	19	2	15	42	5	10	18
August 14	> 10	0	79	8	2	7	54	10	9	22

S.h. = Stephanodiscus hantzschii; N.g. = Nitzschii gracilis; and T. = Tribonema CL1.

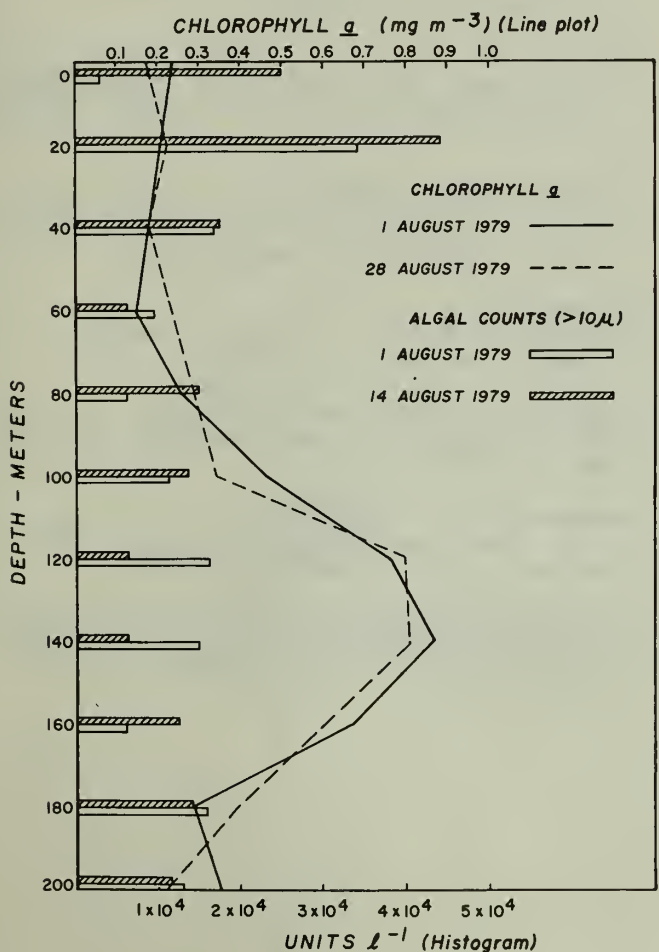


Figure 2.--Vertical distribution of chlorophyll a and phytoplankton in Crater Lake, Oregon, 1979.

Dissimilar findings between the 1940 and 1978-79 studies are due, possibly, to (1) different sampling and analytical techniques, or (2) alteration in lake quality, especially with regard to certain physical and chemical properties capable of influencing the composition, size, and depth distribution of phytoplankton populations.

The composition and quantity of lake phytoplankton are often used to characterize the existing state of lake eutrophication. A continuous, lengthy record of phytoplankton species types and species abundance can be valuable in determining the historical condition of the lake as well as the rate at which the lake is eutrophying. A marked change in species composition or a growing abundance of a particular species (or set of species) could be indicative of a significant shift in lake quality, perhaps toward an irreversible degraded condition. Conceivably, through phytoplankton monitoring, these shifts could be anticipated and averted by controlling the factors that are potentially harmful to lake environments.

ACKNOWLEDGMENTS

We thank J. Rouse, M. Forbes, D. Sholley, B. Wadlington, and R. Kirschner, Crater Lake National Park, for their valuable assistance and cooperation. J. Bradley, Corps of Engineers, and T. Thomas, National Park Service, assisted in the field. E. Mulvihill, Beak Consultants, kindly provided laboratory space and equipment. Without those facilities, this work could not have been done.

LITERATURE CITATIONS

Archibald, R. E. M.
1972. A preliminary key to the fresh and brackish water species of the genus Nitzschii in South Africa. News Letter, Limnol. Soc. South Africa 18:33-46.

Byrne, J. V.
1965. Morphometry of Crater Lake, Oregon. Limnol. Oceanogr. 10:462-465.

Hasler, A. D.
1938. Fish biology and limnology of Crater Lake, Oregon. J. Wildl. Manage. 2:94-103.

Hoffman, F. O., and J. R. Donaldson.
1968. Zooplankton population dynamics, Crater Lake, Oregon. Crater Lake Rep. 2., Natl. Park Serv. Pub. 12 p.

Keating, K. I.
1976. Algal metabolite influence on bloom sequence in eutrophied freshwater ponds. EPA-600/3-76-081, Environ. Prot. Agency, Washington, D.C.

Kemmerer, G., J. F. Bovard, and W. R. Boorman.
1924. Northwestern lakes of the United States: Biological and chemical studies with reference to possibilities in production of fish. U.S. Bur. Fish. Bull. 39:51-140.

Larson, D. W.
1972. Temperature, transparency, and phytoplankton productivity in Crater Lake, Oregon. Limnol. Oceanogr. 17:410-417.

Patrick, R., and C. Reimer.
1975. The diatoms of the United States. Exclusive of Alaska and Hawaii. Vol. 2, Part 1. Acad. Nat. Soc., No. 13, Philadelphia.

Sovereign, H. E.
1958. The diatoms of Crater Lake, Oregon. Trans. Am. Micros. Soc. 77:96-124.

Strickland, J. D. H., and T. R. Parsons.
1965. A manual of seawater analysis. Fish. Res. Bd. Can. Bull. 125.

Thomasson, K.
1962. Planktological notes from western North America. Arkiv für Botanik 4:437-463.

Utterback, C. L., L. D. Phifer, and R. J. Robinson.
1942. Some planktonic and optical characteristics of Crater Lake. Ecology 23:97-103.