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Fort Collins,
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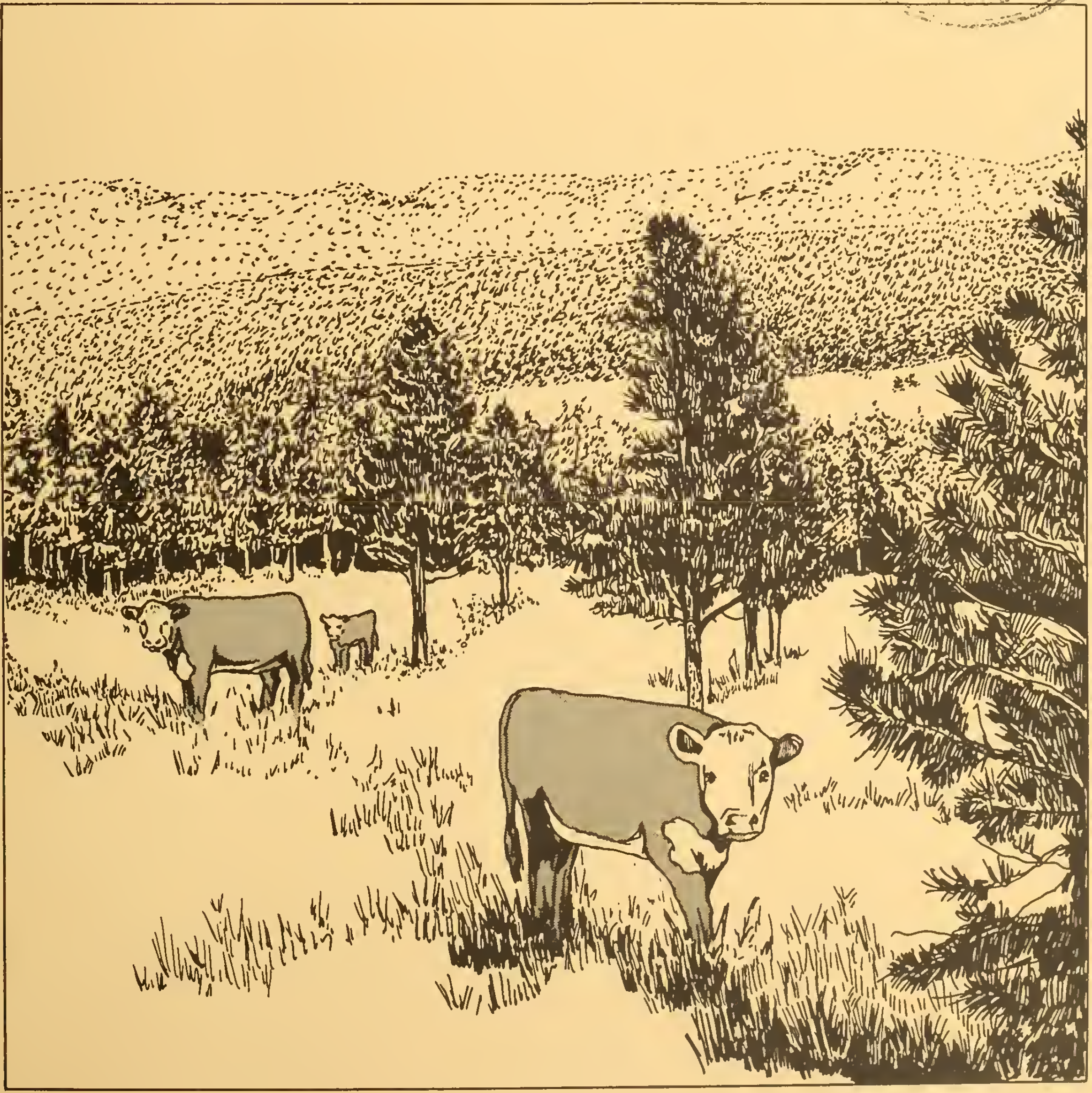
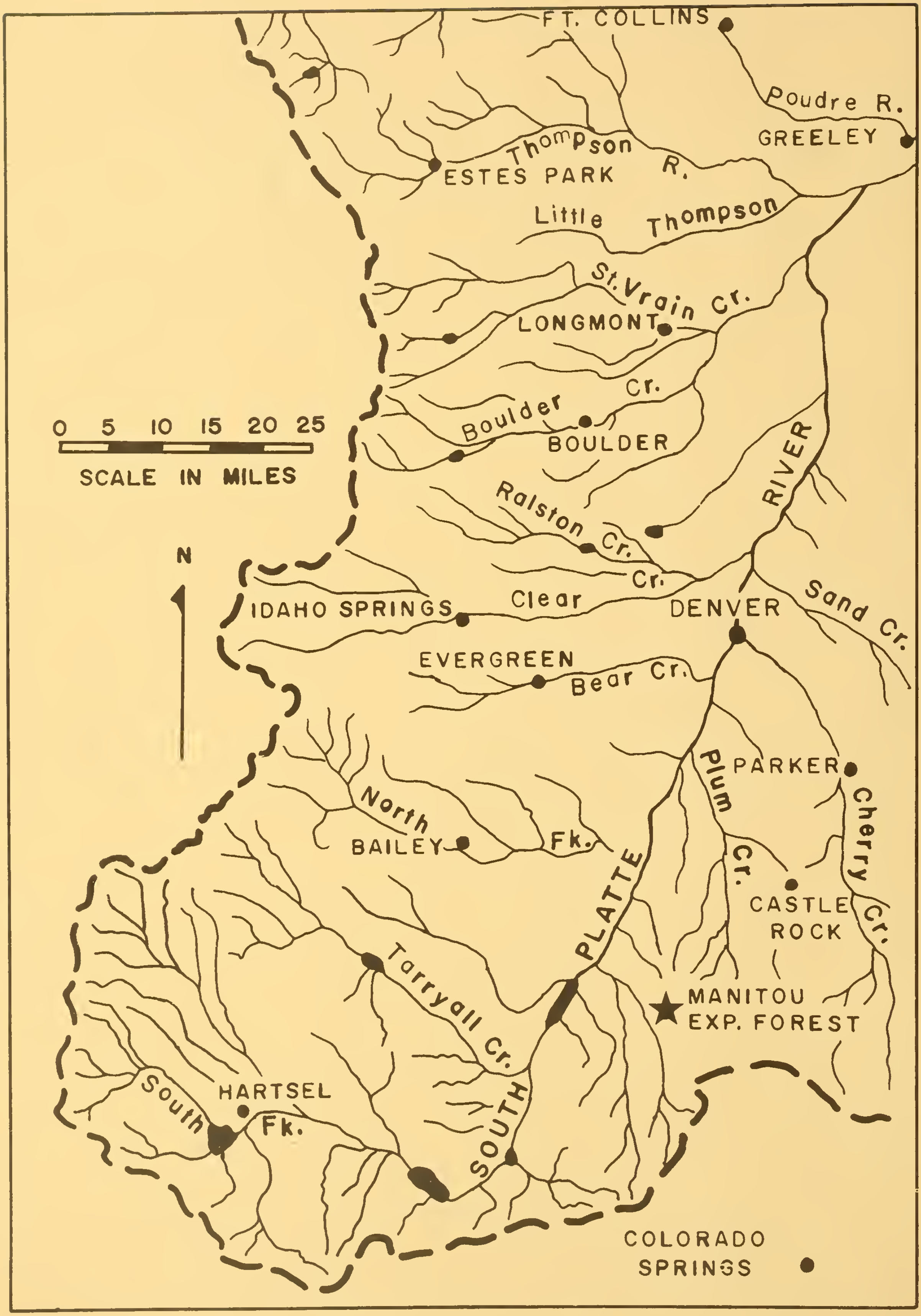
**General Technical
Report RM-116**

A Summary of Research at The Manitou Experimental Forest in Colorado, 1937 – 1983

Howard L. Gary

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PLATTE
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HARTSEL
South Fk.
SOUTH
COLORADO SPRINGS

Acknowledgments

This report draws freely from publications and unpublished data of the Manitou Experimental Forest, and especially from research completed by W. M. Johnson and Pat O. Currie. Early research by Dwight R. Smith, L. D. Love, E. J. Dortignac, E. G. Dunford and H. W. Berndt also is acknowledged. Readers are urged to consult the publication list for other research completed and to obtain greater detailed information on reported studies.

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March 198

A Summary of Research at The Manitou Experimental Forest in Colorado, 1937 – 1983

Howard L. Gary, Principal Hydrologist

Rocky Mountain Forest and Range Experiment Station[1]

Abstract

Results of selected studies for range, watershed, timber and wildlife management research are summarized to provide land managers, land-use planners, and land-use researchers with information to help evaluate consequences of land management practices in the Colorado Front Range ponderosa pine zone.

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[1] *Headquarters is in Fort Collins, in cooperation with Colorado State University.*

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Howard L. Gary

INTRODUCTION

The Manitou Experimental Forest was established in 1936 to study problems of land use as they relate to management of natural resources of the Colorado Front Range ponderosa pine zone. The Experimental Forest, administered by the Rocky Mountain Forest and Range Experiment Station, is 28 miles northwest of Colorado Springs in Manitou Park, Colorado. The Forest covers about 26 square miles in the South Platte River watershed. This large watershed supplies a major share of water consumed by Denver and other cities along the foothills of the Front Range. This watershed and similar adjacent drainages also contribute water used for irrigation in some of the most productive and intensively cultivated lands in the western United States. The Experimental Forest location in the "tension zone" between the Rocky Mountains and the Plains is characteristic of much of the land area along the Front Range in Colorado and is thus suited to study forest influences; mountain home and associated recreation development and wildlife; proper management of ponderosa pine,[2] Douglas-fir, and mountain bunchgrass types; revegetation of abandoned and submarginal farm land; erosion control; and stream improvement. This report presents selected summaries of completed and current research.

PONDEROSA PINE LANDS

The ponderosa pine zone in the Front Range of the Rocky Mountains extends from southern Wyoming to northern New Mexico and encompasses approximately 4 million acres (fig. 1). These timbered lands include grassland parks, willow fields along streams, sagebrush and oak brush areas, and scattered cultivated fields. The land, vegetation, and climate of the Forest are typical of the eastern slope of the central Rocky Mountains.

LANDFORM AND GEOLOGY

The Experimental Forest is in a fault outlier about 30 miles long and 4 miles wide, flanked by the West Creek Range on the west and the Rampart Range on the east. The Forest is bisected by Trout Creek, a small perennial stream and tributary of the South Platte River. The eastern part (western exposure) of the Forest includes rugged mountains with narrow, steep-walled canyons. The western part includes mainly broad, gently rolling valleys and plateaus. Elevation ranges from about 7,500 to 9,300 feet.

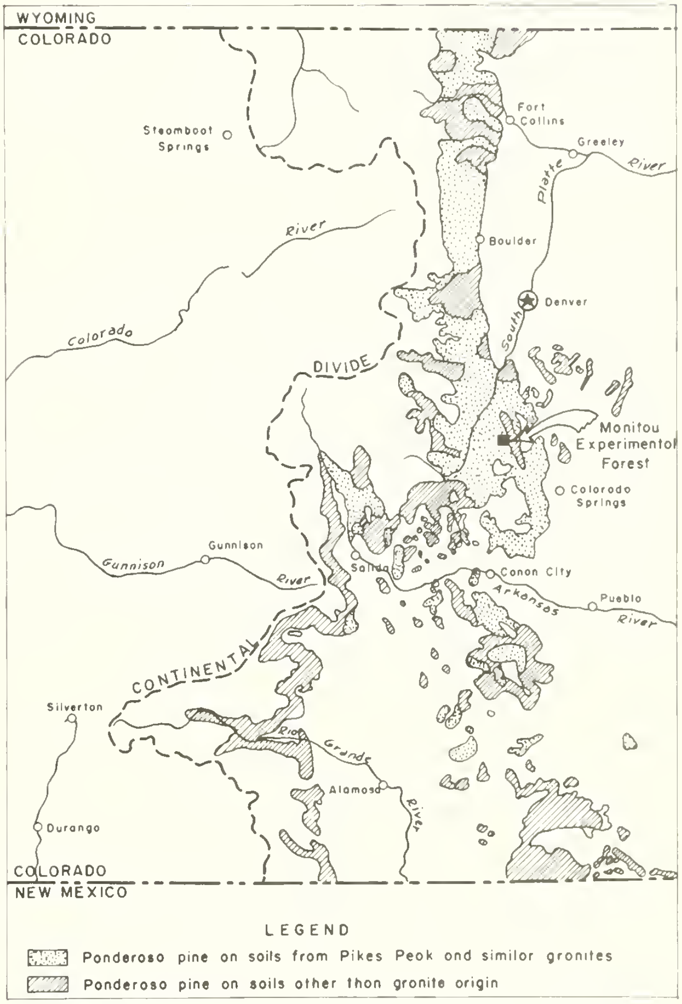

Figure 1.—Distribution of ponderosa pine in Colorado (Love 1958).

Geologic erosion has exposed three sedimentary formations. The lowermost bed is the Sawatch quartzite, the next is Madison limestone, and the topmost is Fountain arkose. The Sawatch and Madison formations outcrop on the east side of the valley within a relatively narrow band. The Fountain arkose occurs chiefly on the east side of the valley; but, erosion pedestals up to 30 feet tall are scattered throughout the western part of the forest (fig. 2). Redeposition of alluvium at lower elevations has resulted in extensive crossbedding. The basement rock is coarse-textured Pikes Peak granite.

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[2] *All plant names mentioned are listed in the appendix.*

SOILS

Soils from biotite granite are by far the most extensive and occur in the rugged eastern half of the forest.[3] The surface soils are light brown, shallow, gravelly, low in organic matter, infertile, slightly acidic, and less than 10 inches thick. The bedrock is reddish brown, disintegrating granite. Surface soils on the western side of the forest are brown to dark brown sandy or gravelly loams, ranging from 8 to 18 inches thick. Subsoils, when present, are usually reddish brown, have sandy or gravelly clay loam texture, and may extend to depths of 20 inches or more. Most soils on the forest are susceptible to severe erosion whenever vegetative cover is removed.

VEGETATION

Vegetation on the western part of the forest is mainly ponderosa pine in the overstory and bunchgrasses in the understory, with numerous scattered grassy openings or parks. Predominant bunchgrasses are mountain muhly and Arizona fescue. Abandoned fields have extensive stands of sleepygrass. Stringer meadows and willow thickets border Trout Creek. Similar vegetation grows on the eastern side of Trout Creek. Above about 8,000 feet elevation, the vegetation is dominated by stands of overmature ponderosa pine, Douglas-fir and aspen. Lodgepole pine grows at higher elevations along the eastern boundary of the forest. Some limber pine also is present. Engelmann spruce and blue spruce grow along the streambottoms and margins of wet meadows. Shrubs are scattered throughout the timber types.

CLIMATE

The "dry subhumid," distinctly continental climate is characteristic of most eastern slope areas in Colorado. Winters are usually dry and often cold for long periods. The highest monthly precipitation falls during the cool summers. Annual precipitation at the forest headquarters (7,740 feet elevation) for the period 1937 through 1982 averaged 15.6 inches, and ranged from 7.6 inches in 1939 to 24.1 inches in 1969 (fig. 3). Seventy percent of the precipitation falls in the primary growing season, April through August. Snow may fall from late September to late May, and accounts for about 30% of the annual precipitation. High-intensity storms, which may produce runoff and erosion, occur most frequently during July and August. Storms producing surface runoff have been recorded each month from May through September.

Figure 2.—Pedestals of Fountain arkose along the western side of the forest.

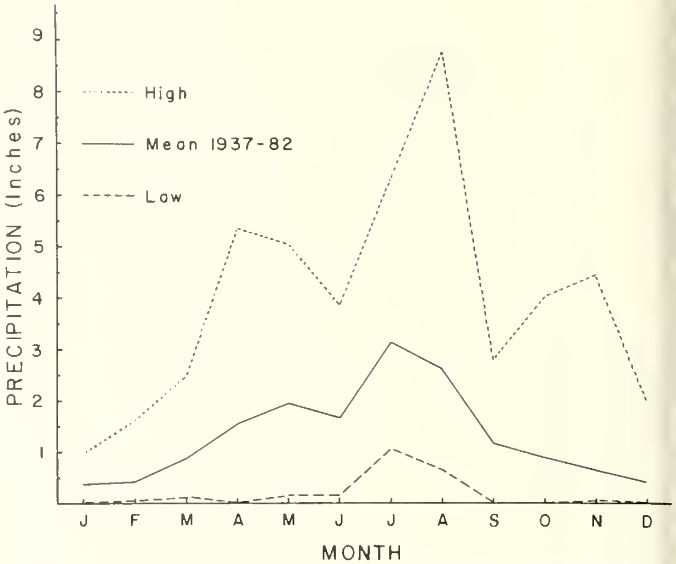

Figure 3.—Means and extremes of monthly precipitation, 1937-1982.

Yearly mean temperature for the period 1942–1958 averaged 40.6° F. Mean monthly temperatures varied from 23.0° F in January to 60.8° F in July (fig. 4). Temperatures during the summer seldom exceed 90° F and extreme winter temperatures have been −40° F. On the average, there are 113 days in the growing season, and the frost-free period extends from about May 28 to September 18.

EARLY RESEARCH

Research first sought to develop better methods for management to perpetuate and restore the natural resources for long-term productivity. Range management and seeded pasture studies specifically sought to obtain maximum livestock production on native ponderosa pine-bunchgrass range and seeded pastures consistent with wise management of other resources. The watershed studies sought to determine how to revegetate depleted ponderosa pine watersheds to minimize flood and sedimentation damages from high intensity storms and to develop methods to improve water yields.

NATURAL REVEGETATION OF ABANDONED FIELDS

Warm summers and rainfall during the growing season favor relatively rapid herbaceous plant succes-

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[3] *Retzer, John L. 1940. Soils and physical conditions of the Manitou Experimental Forest, 35 p. Unpublished manuscript, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo.*

sion on the Forest. Natural revegetation of some 600 acres of abandoned croplands began with an initial invasion of an annual forb type, progressed through perennial forbs, mixed grasses and forbs to a subclimax grass community (fig. 5). The annual forb stage lasts only a few years and is characterized by a few species occurring in great abundance. The perennial forb stage, lasting from 7 to 10 years, is characterized by an increased number of perennial grasses and forbs, such as western wheatgrass and thistles. The mixed grass and forb stage is initially characterized by an abundance of sleepygrass and slender wheatgrass and may last 10 to 25 years. In the subclimax bunchgrass stage, mountain muhly and Arizona fescue are the dominant species. Ponderosa pine probably is the potential climax vegetation for most of the abandoned fields.

GRAZING MANAGEMENT

Ponderosa pine-bunchgrass ranges have been an important vegetation type for range cattle in Colorado for more than 100 years. The optimum level of grazing in relation to range utilization, herbage production, weight gain, other plant responses and soil condition was not known in the early 1950s. The first studies were designed to determine proper grazing intensity. Later studies determined the best grazing intensity and livestock management on seeded pastures and animal-plant interactions.

Native Pastures

Six experimental ponderosa pine-bunchgrass pastures, varying in size from 254 to 309 acres, were established in 1940. Two 2.5-acre enclosures were located within each pasture. Three grazing intensities—light, moderate and heavy cattle use—were applied to each of two pastures from 1941 to 1958. Utilization goals were based mainly on mountain muhly and Arizona fescue for the three grazing intensities—less than 20% removal of herbage produced for light, 30% to 40% for moderate, and over 50% for heavy grazing. The pastures were grazed five months each year, from June 1 through October 31, using yearling heifers (Hereford or Aberdeen Angus).

Herbage Production

Production of palatable grasses and sedges over the six pastures averaged 250 pounds of air-dry forage per acre in 1938 and increased to 344 pounds per acre in 1942, the first year after beginning the grazing trials. About 43% of the herbage was mountain muhly. Near the end of the grazing study, in 1957, average herbage yields on light- and moderate-use pastures were slightly higher in 1957 than in 1942 and 1947 (fig. 6). On heavily grazed pastures, production dropped from 351 pounds per acre in 1942 to 195 pounds in 1947, and 148 pounds in 1957. Differential grazing also created marked differences in range condition (fig. 7).

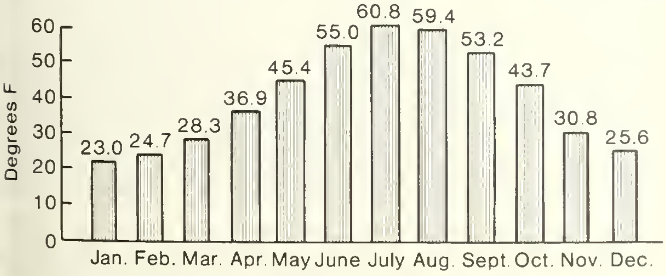


Figure 4.—Monthly mean temperatures, 1942-1958 (Berndt 1960).

Figure 5.—Natural plant succession on abandoned fields. A, *Stipa-Agropyron* community in a field abandoned 15 years; and B, Subclimax grass community on a field abandoned 62 years (Johnson 1945).

Use of Native Plants

Utilization of the six most commonly used species on the native pastures was estimated in 1950 and 1952, 6 and 8 years after starting the grazing intensity trials. Arizona fescue and mountain muhly furnished 94% of the forage on lightly and moderately grazed pastures. Little bluestem and sun sedge produced 5% of the forage. Blue grama was grazed sparingly under light and moderate grazing. Fringed sagebrush, not used under light grazing, received only 3% use under moderate grazing. Utilization of all six species on heavily grazed pastures was greater than on more lightly cropped pastures. Arizona fescue and mountain muhly received the most use; however, these species furnished only 68% of the forage. Mountain muhly was the most productive species, while Arizona fescue was considerably reduced by prolonged close grazing.

Grazing and Plant Responses

In the grassland vegetation type, perennial grass and sedge cover nearly doubled when grasslands were grazed lightly, increased by one-third under moderate use, and decreased nearly one-half under heavy grazing. Increases in perennial grasses and sedges indicated plant succession was largely responsible for changes in cover. Understory perennial grasses and forbs within both open and dense stands of timber showed a decreasing trend under all intensities of grazing, apparently in response to closure of the pine canopy.

Weight Gains on Native Pastures

Seasonal cattle gains from 1943 through 1949, under about average annual precipitation, were 231, 221, and 176 pounds, under light, moderate and heavy use, respectively (fig. 8). The years 1950 through 1955 were characterized by drought, and cattle were removed from the pastures before October. Therefore, seasonal gains for this period were less. Cattle gained most during the first 2 or 3 months of the grazing season, when nutritional value of vegetation was highest. The proportion of gain made early in the season was directly related to grazing intensity.

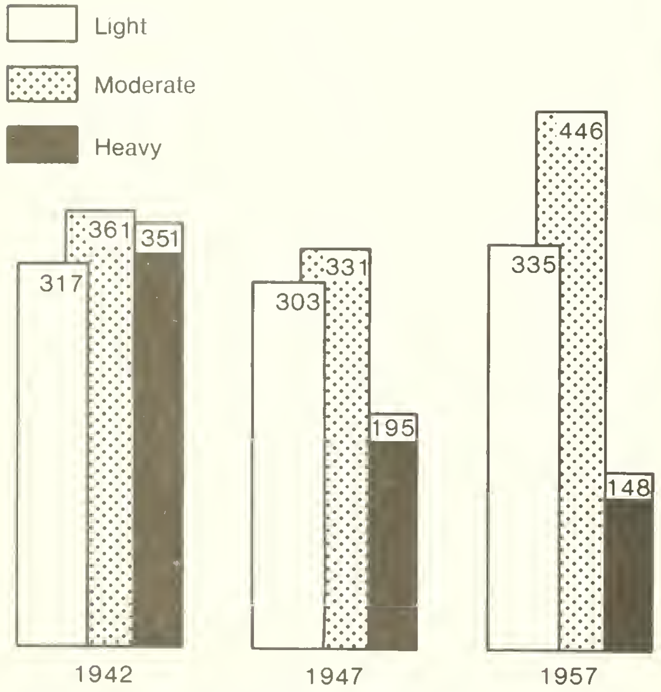


Figure 6.—Grass and sedge yield (pounds) as affected by grazing intensity (Smith 1967).

Figure 7.—Range condition on the native pastures. A, lightly grazed—one heifer per 25.5 acres; B, moderately grazed—one heifer per 14.5 acres; and C, heavily grazed—one heifer per 12.5 acres (adapted from Smith 1967).

Seeded Pastures

In the Front Range pine type, natural recovery of abandoned farmlands and depleted pastures through plant succession can take decades even with no grazing. Seeding with introduced grasses and legumes in many cases can convert abandoned farmlands and depleted ranges to productive range within a few years. Much early research dealt with planting techniques, species adaptability and grazing intensity trials.

Species Adaptability

Seedings during the fall or early spring, when moisture was available for seed germination, showed about equal success for obtaining good stands of seeded grass on abandoned farmlands and/or depleted open grassland parks. Species most promising in adaptability to climate and soil conditions 3 to 8 years after seeding were crested wheatgrass, Sherman big bluegrass, smooth brome, intermediate wheatgrass, Russian wildrye, and yellow sweetclover.

Forage Yield of Seeded Species

Maximum forage production on abandoned fields seeded to crested wheatgrass, smooth brome, intermediate wheatgrass, Russian wildrye, and a mixture of crested wheatgrass, smooth brome and yellow sweetclover was generally greatest the third to fifth year after seeding (fig. 9). Precipitation during the growing season accounted for most of the difference in forage production and may have been the main limiting variable. Average forage production from 1948 through 1959 ranged from 1,358 pounds for the mixture to 663 pounds for smooth brome. Forage production of Sherman big bluegrass seeded in 1957 ranged from 2,394 pounds per acre under 16.3 inches of moisture in 1961, to 533 pounds under 15 inches of moisture in 1965.

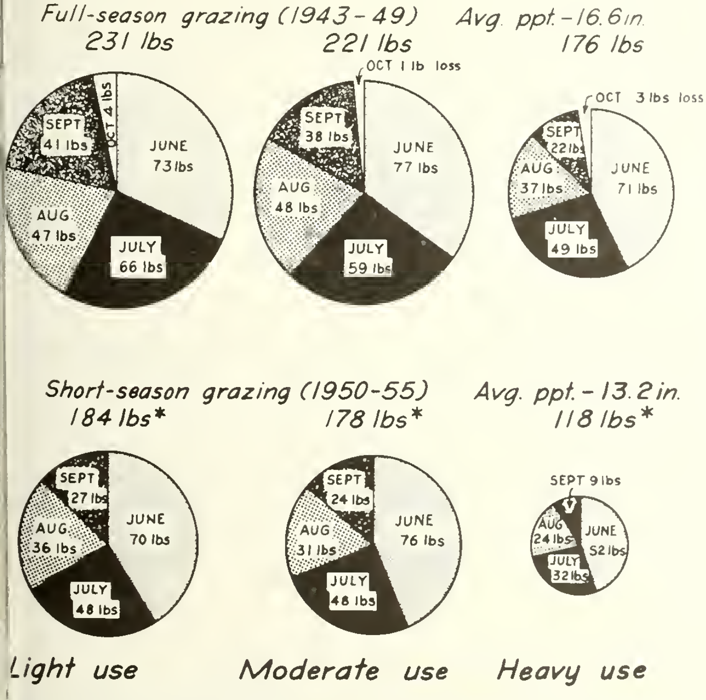


Figure 8.—Average monthly and seasonal gains under different grazing intensities (Smith 1967).

Figure 9.—A 4-year-old seeded stand of intermediate wheatgrass produced over 1,000 pounds of air-dry herbage per acre.

Grazing Intensity on Seeded Pastures

Intensity of grazing studies were conducted from 1948 through 1959 on 10-acre seeded pastures. The pastures included those seeded to crested wheatgrass, smooth brome, intermediate wheatgrass, Russian wildrye, and a mixture of crested wheatgrass, smooth brome and yellow sweetclover. Grazing use was based on average stubble heights of 1 and 2 inches, two levels of heavy use (65–85% utilization), and 4 and 6 inches, one level of intermediate (45% utilization) and light use (33% utilization), respectively.

More than twice as many heifer days of grazing per acre were obtained during a favorable growing season such as 1957 compared with a dry season such as 1954 (fig. 10). The most pronounced increase in use was on the more heavily grazed units. Crested wheatgrass, for example, was grazed from 45 to 48 days longer in 1957 than in 1954 on units grazed to 1- and 2-inch stubble heights. The mixture pasture was primarily crested wheatgrass in the final years of research. Animal days of grazing on smooth brome and intermediate wheatgrass were noticeably lower after heavy grazing in 1959 than in 1957; these species were not recommended for seeding in pure stands on depleted dry upland sites. Grazing to 3-inch stubble height was recommended for Russian wildrye, to avoid development of ungrazed wolf plants and eventual overgrazed local areas.

Weight Gains on Seeded Pastures

The mixture and crested wheatgrass pastures grazed to selected stubble heights provided the best sustained daily weight gain for yearling heifers (fig. 11). Smooth brome and intermediate wheatgrass stands provided good daily gains and per acre gains early in the study; but overall, these species gradually deteriorated under all levels of use and were not suited to seeding in pure stands. Weight gains on Russian wildrye were relatively low compared to the mixture, crested wheatgrass and big bluegrass; but, this grass provided a source of forage during early spring. Beef production on Sherman big bluegrass pastures was superior to the other seeded species for gains per acre. Gains averaged about 75 pounds more than on a nearby moderately grazed native pasture. The high potential productive capacities of seeded pastures should be considered for incorporation into Front Range livestock management programs.

Management and Grazed Plant Relations

Other studies determined cattle responses to supplemental feeding, nutritive quality of seeded and native pastures and grazing trials and forage yield.

Supplemental Feeding on Seeded and Native Pastures

The responses of weaner calves were evaluated on seeded stands of Sherman big bluegrass, with and without protein supplement; and on native ponderosa pine-bunchgrass pastures plus protein supplement during late fall, winter and early spring grazing seasons from 1967 to 1971. Calves made small weight gains on all pastures during the fall, but usually lost weight during the winter and spring. On a per acre basis, gains from big bluegrass without supplement nearly equaled those of native grass plus 0.50 pounds of protein supplement per calf per day. With either 0.25 or 0.50 pounds of protein supplement per day, gains per acre on seeded big bluegrass pastures were double those obtained on native pasture.

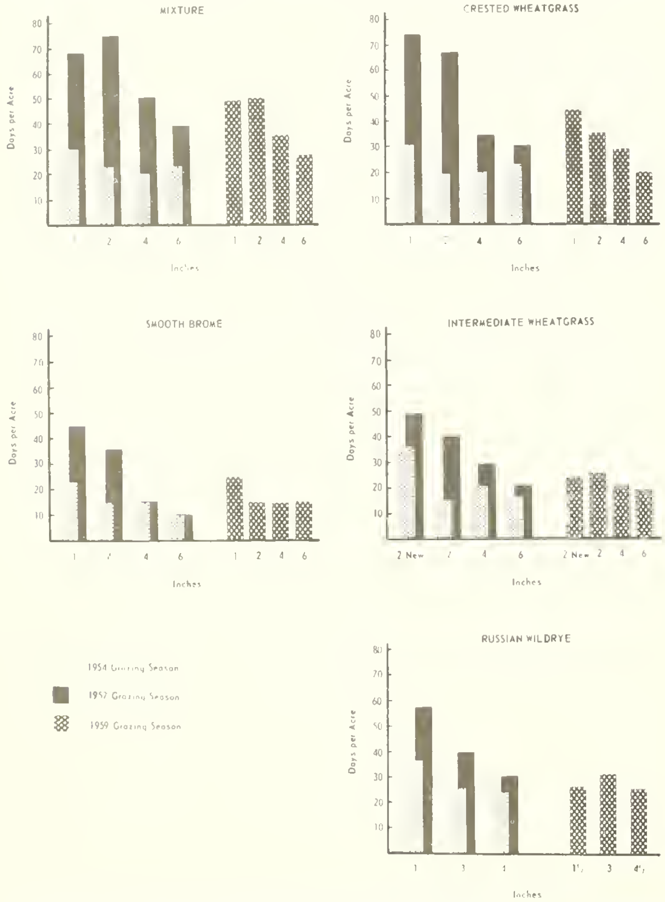
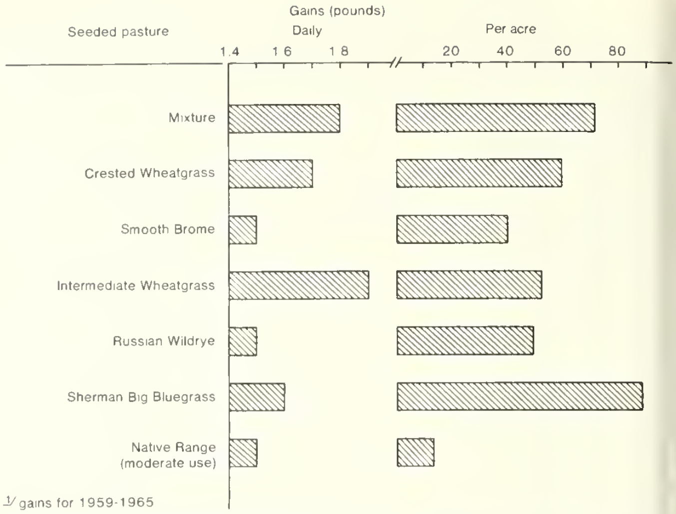


Figure 10.—Days of grazing on seeded pastures based on utilization stubble height at end of season (Currie and Smith 1970).



1/ gains for 1959-1965

Figure 11.—Average weight gains of yearling heifers on seeded pastures, 1948-1959 (adapted in part from Currie and Smith, 1970).

Nutritive Quality of Cattle Diets

The nutritive quality of forage available to two 12-cow herds on native pasture year-long and on native plus seeded pastures was determined from 1965 to 1966. One fistulated steer was incorporated into each herd. Crude protein in the diets of the two cow herds, assumed to be similar to steer diets, followed seasonal trends largely indicative of the effects of forage maturity (fig. 12). Levels were high in early spring, when forage plants were young and growing rapidly, then declined throughout the summer and autumn as the forage matured. The herd grazing the seeded pasture in the spring had an advantage of high protein levels approximately 30 days earlier than did the herd grazing native pastures. When the two herds were separated in late autumn, dietary protein levels of the herd grazing seeded Sherman big bluegrass rose sharply, whereas protein in the diet of the herd grazing native pasture continued to decline. Botanical composition of diets on the native pasture reflected heterogeneity of the pasture rather than preference for certain plant species.

Grazing Trials on Crested Wheatgrass

Forage yield differences on pastures seeded to crested wheatgrass mainly resulted from amount of

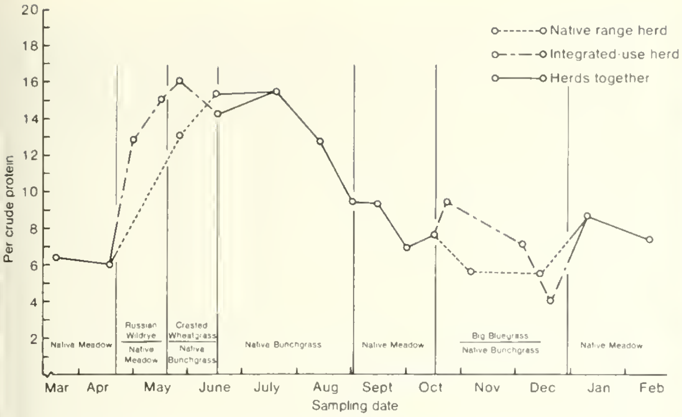


Figure 12.—Annual trends of dietary crude protein in forage samples ingested by fistulated steers (Malechek 1966).

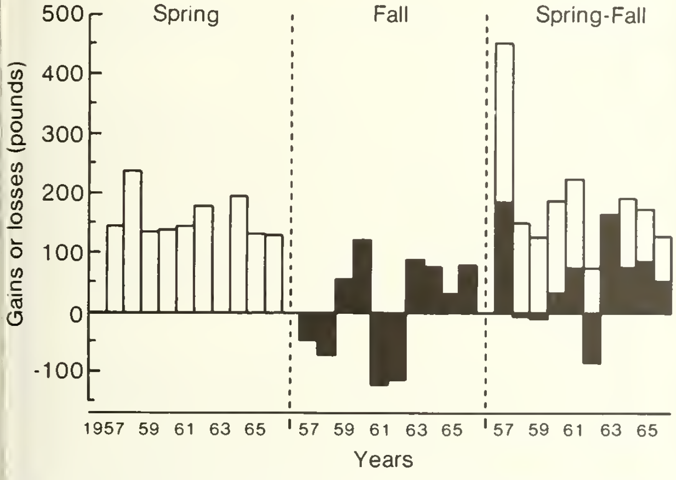


Figure 13.—Heifer response on crested wheatgrass pastures grazed seasonally (Currie 1970).

moisture received during the growing season, and not from seasonal grazing. Yields on spring-grazed pastures varied in response to April precipitation. Production on fall-grazed pastures varied in response to May–June moisture. Seasonal gains were not an intensity factor, but were related to season of grazing (fig. 13). The heifers consistently made good gains only during spring grazing.

WATERSHED MANAGEMENT RESEARCH

Because of sporadic precipitation, early watershed management studies dealt primarily with ground cover, infiltration, surface runoff and erosion from soils developed from granitic and other geologic materials.

Gully Control

Before establishment of the Experimental Forest, labor intensive erosion control measures were undertaken by the U.S. Civilian Conservation Corps. The effectiveness of their early gully control structures and deepening of gullies are of practical interest. Temporary control structures made of logs accomplished their intended objectives for many years, but eventually failed (fig. 14). Many of the check dams constructed of loose rock and mesh wire and keyed into gully banks and into the channel are still intact and have controlled gully erosion (fig. 15). Most gully systems in the forest can be traced to old wagon road ruts and cow trails in valley bottoms. Many such gullies are still active and will continue to slowly deepen and advance upslope indefinitely unless controlled (fig. 16).

1936

1981

Figure 14.—Log check dams eventually fail and trapped sediments are washed downstream (1936, 1981).

Source of Stream Sediments

Upstream channel and gully erosion contributes to the sediment load carried by Trout Creek and to sedimentation of Manitou Lake. After completing the dam for Manitou Lake in 1937, the water storage capacity of the lake was about 93 acre-feet. In 1948, the capacity had been reduced by two-thirds, and approximately 60 acre-feet of sediment had been deposited in the lake. Total sediments above and below the spillway level was about 200 acre-feet, with channel deposits as much as 1 mile upstream. The drainage area above the lake is about 69 square miles. An estimate of total sediment contribution from the drainage area is 18.2 acre-feet per year, or 0.26 acre-feet per square mile annually. An example of sedimentation and streambank cutting is illustrated in figure 17.

Bunchgrass Runoff Plots

Watershed management studies started in 1937 utilized runoff plots (fig. 18). The main purpose was to determine the influence of gravelly alluvium (outwash of Pikes Peak granite) and grazing use on surface runoff and erosion. In the period 1937 through 1952, yearly precipitation ranged from 7.6 to 24.0 inches, and averaged 15.6 inches. Annual forage production averaged about 900 pounds per acre. After a 4-year period of nonuse, runoff and erosion amounts were assessed. A heavy and moderate cattle grazing treatment was then applied. For 12 summers of grazing average runoff ranged from 0.34 inches on the heavily grazed plots to 0.11 inches on the ungrazed plots (fig. 19). Average annual soil losses varied from 134 pounds on ungrazed plots to 316 pounds per acre on heavily grazed plots. The model cloudburst storm causing erosion on the runoff plots was 0.96 inches of precipitation. Such storms occur once or twice during the summer, and produce effects shown in figure 20.

Ponderosa Pine Watersheds

Six contiguous watersheds, ranging from 1 to 2 acres in size, on granitic alluvium and draining to the west were instrumented in 1938 to determine the influence of ponderosa pine (75–100 years old) and its removal on surface runoff and sediment yields. The net result was conversion to grass cover with scattered colonies of aspen, and brush (fig. 21). Average surface runoff dur-

Figure 15.—A rock and wire check dam installed in 1936 was effective in 1983.

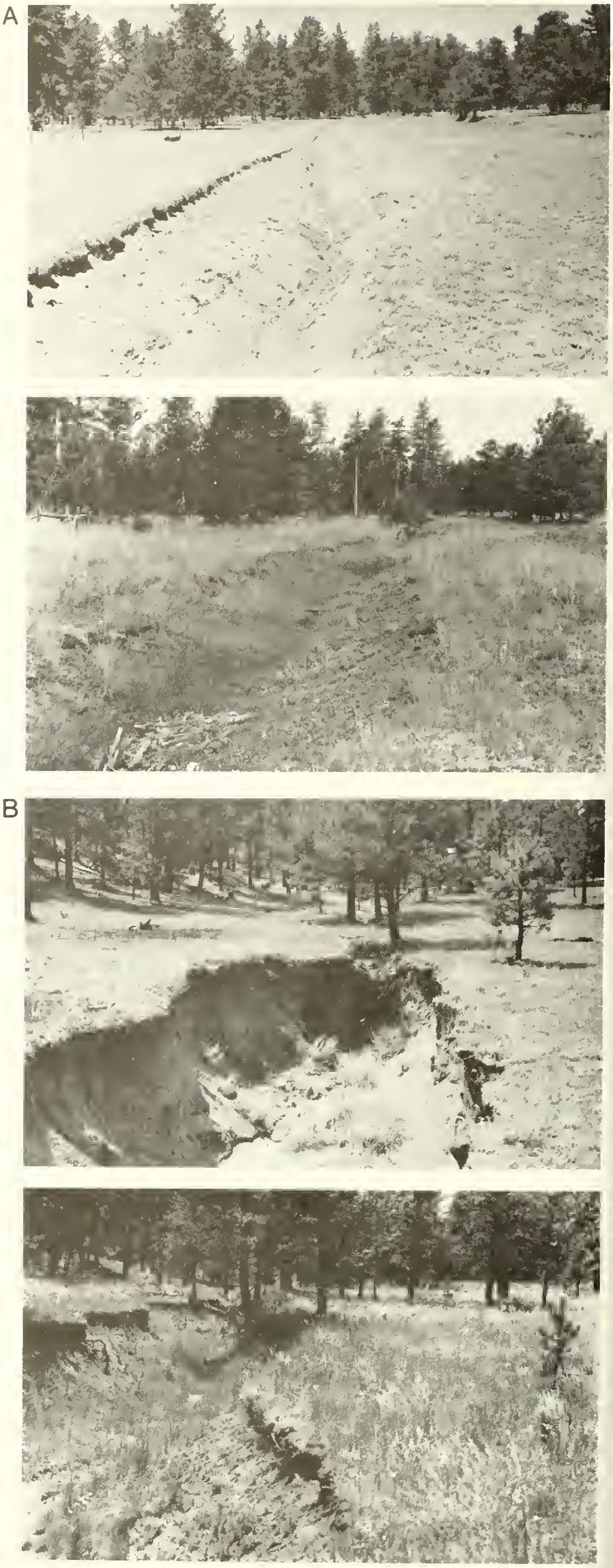
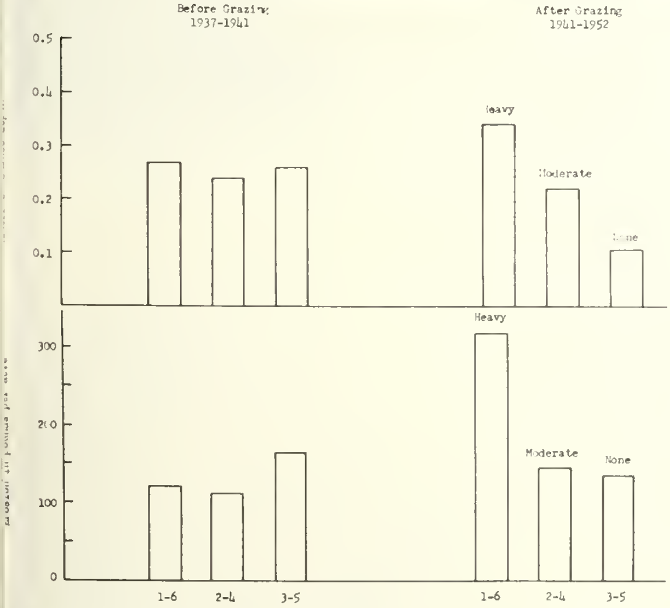


Figure 16.—Erosion problems on the Forest. A, an abandoned road; and B, active headcutting in an old cow trail. This gully has advanced 55 feet upslope in 33 years.

igure 17.—Sedimentation over the Trout Creek floodplain. The stream channel has shifted many times during floods. In 1980, remains of cross-ties for a railroad abandoned in 1887 were 3 feet below the soil surface.

igure 18.—Native bunchgrass surface runoff plots. The horizontal area of each plot is 0.01 acre.



igure 19.—Average runoff and erosion from summer storms on bunchgrass runoff plots (Dunford 1954).

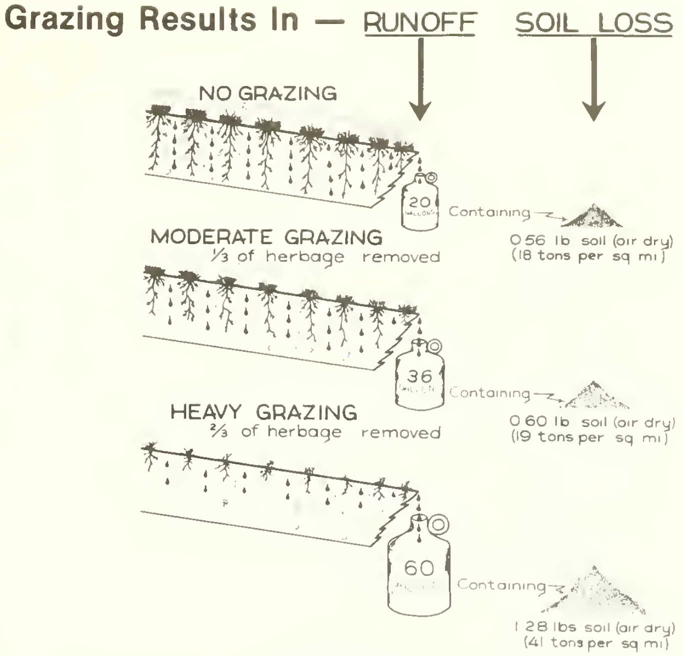


Figure 20.—Average soil loss and surface runoff from the model summer storm of 0.96 inches (Love and Johnson, 1952).

ing the first 6 years after type conversion increased from 2 to 5 times pretreatment runoff. Thereafter, the rapid increase and spread of native bunchgrasses provided almost complete protection against surface runoff and erosion. The erosion caused by rainstorms was erratic before and after type conversion and was of little practical significance. Only a small amount of sediment has been caught in runoff tanks at the mouth of the drainages in the past 30 years.

Infiltration on Native Pastures

Infiltration of precipitation was determined by rainfall-simulators (2.5 ft^2 of surface area) on six native range pastures from 1941 through 1954. The main purposes were to evaluate the relation of plant cover to infiltration and how these were affected by soil properties and cattle grazing.

Infiltration, Plant Cover and Soil Properties

Litter was the only vegetation factor consistently associated with infiltration. The value of litter in increasing infiltration and reducing surface runoff is well established. Based on 108 infiltration runs in all cover types, during 1941, 1946 and 1952, the quantity of dead organic material was significantly correlated with higher infiltration rates. Infiltration averaged 2.50, 1.78 and 1.15 inches per hour under pine-litter, pine-grass and grassland, respectively. Sand content, soil fraction passing a 2-mm screen, was the best indicator of the influence of texture on infiltration. Noncapillary pore volume was the most important soil factor related to infiltration during all years of study.

Infiltration After Protection from Grazing

Infiltration rates determined in 1941, at 24 random locations stratified by cover types, in the native pasture exclosures, and at 108 sites in the six native range pastures, were not statistically different. Differences inside and outside the exclosures in subsequent years were assumed to be the result of protection from grazing (fig. 22). Regardless of grazing intensity, infiltration rate did not materially improve under any intensity of grazing. Only complete protection from cattle grazing appeared to improve infiltration rate.

Figure 21.—Ponderosa pine watershed F. A, north aspect before treatment in 1948; B, two years after logging and slash burning, 1950; and C, in 1983.

Runoff from Missouri Gulch Watershed

Measurements of precipitation and streamflow were obtained from the Missouri Gulch watershed from 1940 through 1958, to gain information on water yield and its relation to precipitation. No other perennial streams have been gaged in the Experimental Forest (fig. 23).

Watershed Description

The watershed covers about 4,600 acres in the northeastern part of the forest, and has 6.1 miles of live channel. Elevation ranges from about 7,300 to 9,300 feet. Slopes range from 10% to 60%, and residual soils are mainly gravelly sandy loams and stony loams. Plant cover is mainly ponderosa pine and Douglas-fir, with lodgepole pine at the higher elevations, and Engelmann spruce and aspen along the streams. Scattered brush, grass, erosion pavement, and bare rock also are present.

Precipitation and Streamflow

Annual precipitation on the watershed ranged from 12.2 inches in 1950 to 27.1 inches in 1957, with a mean of 18.2 inches for 19 years of record. Seasonal precipitation was greatest during April through August (fig. 24). Streamflow was lowest during the winter and early spring, rose sharply to late spring peaks, and decreased gradually thereafter. Maximum peak flows resulting from snowmelt occurred as early as April 21 and as late as May 14. Generally, more than 60% of the seasonal runoff left the watershed in April and May, but it varied greatly from year to year (fig. 25). Proportion of water year precipitation becoming streamflow ranged from 3.4% to 13.3%, with an average of 7.9% for the period 1952 through 1958.

CURRENT RESEARCH

REGENERATION OF PONDEROSA PINE

A long-term study was started in 1980 to compare and quantify shelterwood and seed-tree cutting methods for regeneration of new even-aged patches and stands of ponderosa pine (fig. 26).[4] The information is expected to help provide management guidelines to regenerate overmature even-aged patches and stands. Scarified and unscarified site preparation treatments were used to study natural and artificial regeneration. Survival of natural seedlings after two growing seasons is presented in figure 27. Survival of planted 2–0 stock, after two grow

[4] *Personal communication with S. E. McElderry, Research Forester, Rocky Mountain Forest and Range Experiment Station, For Collins, Colo.*

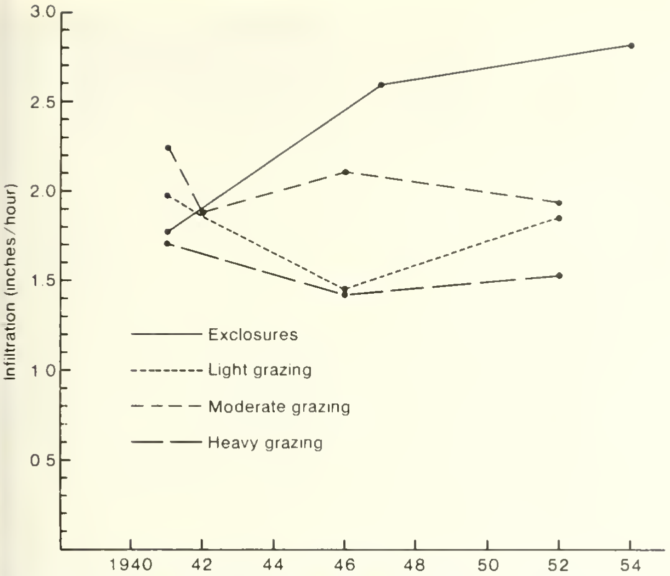


Figure 22.—Comparison of infiltration trends in exclosures with those under grazed pastures (adapted from Dortignac and Love 1961).

Figure 23.—Combination San Dimas flume and broadcrested weir gaging station near the mouth of Missouri Gulch.

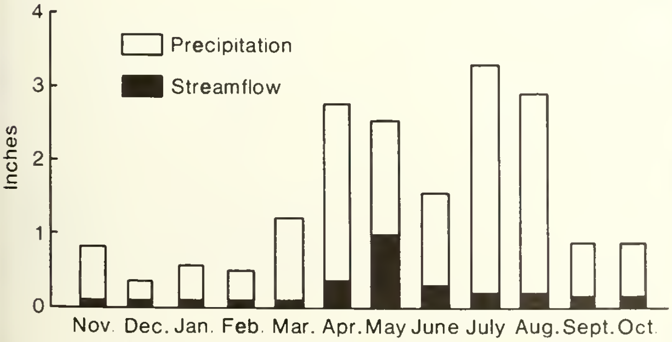


Figure 24.—Monthly mean precipitation and streamflow for Missouri Gulch watershed, 1940-1958 (Berndt 1960).

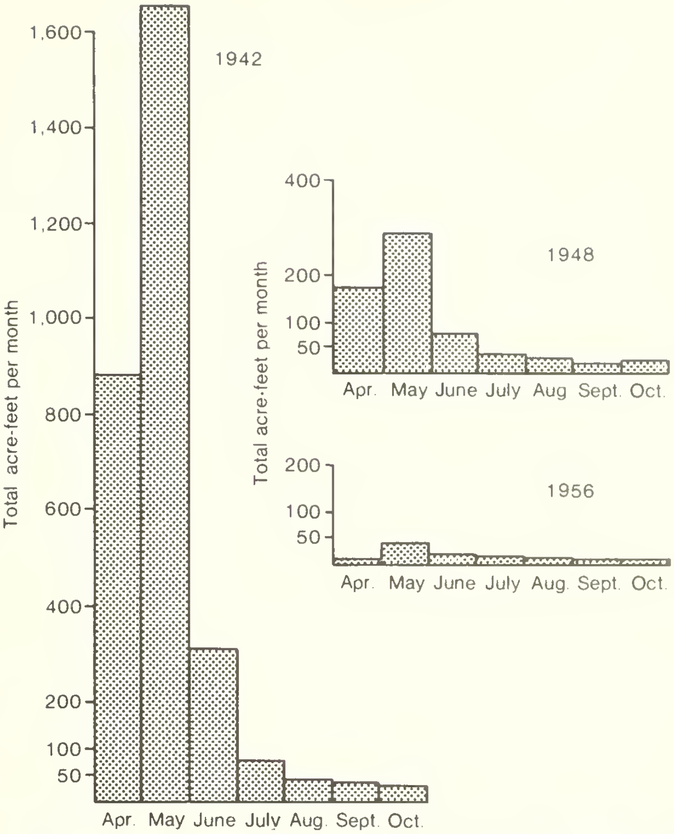


Figure 25.—Seasonal streamflow extremes for the Missouri Gulch watershed (Love 1958).

Figure 26.—Shelterwood and seed-tree plots in ponderosa pine (shelterwood, seed tree).

ing seasons, was greater on scarified plots than on unscarified plots. Seedfall and germination, determined from seed trap contents, varied greatly the first 2 years. Seedfall was two times greater the first year, and germination percentage was 38 times greater.

INITIAL TREE SPACING AND GROWTH OF PONDEROSA PINE

A long-term study was begun in 1983 to determine the effects of initial tree spacing on growth of young ponderosa pine (fig. 28).[5] Height and diameter growth as well as crown width and length will be measured for at least 30 years. Results of this study are expected to provide guidelines for optimum planting densities for artificial regeneration and for management of young, even-aged, naturally regenerated stands of ponderosa pine.

PROVENANCE TESTING OF PONDEROSA PINE

A 20-year plantation study was started in 1981 in cooperation with Colorado State University. The main objectives are to determine the relative performance and evaluate patterns of survival, growth, phenology and morphology of ponderosa pine trees derived from 75 seed collection zones delineated for Colorado. Another objective is to determine the degree to which seed can be used in other seed collection zones. Measurements during and after the growing season include height, diameter, growth cessation, and growth resumption. Other measurements include insect, disease, animal and weather damage.

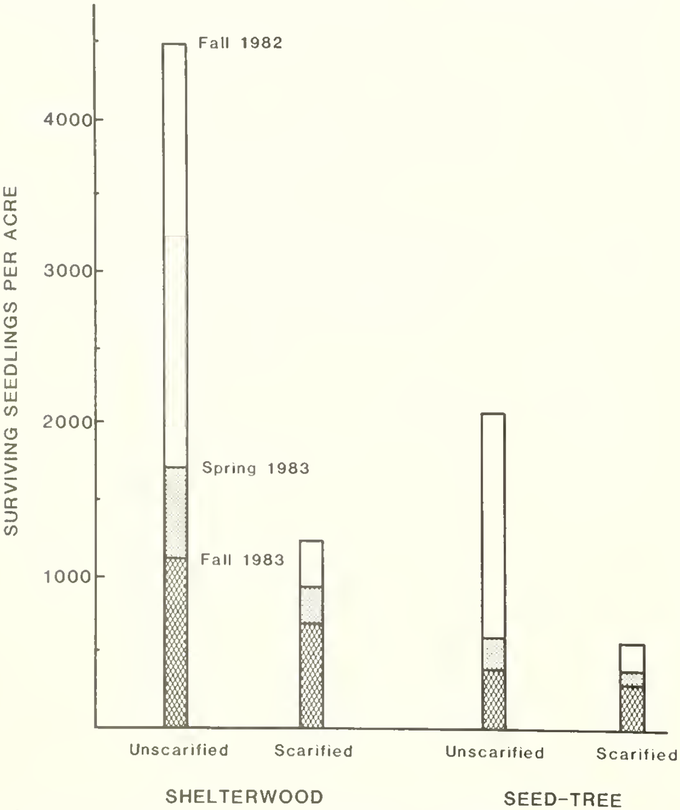


Figure 27.—Early survival of seedlings originating from 1981 seedfall.

Figure 28.—Shaded ponderosa pine seedlings, initial spacing and growth study.

GROWTH AND YIELD OF MANAGED PLANTATIONS

Another long-term study was started in 1981 to compare growth responses of even-aged, pole-sized ponderosa pine over a wide range of growing stock levels (GSL's).[5] Diameters, basal areas, heights, volumes, numbers of live trees, growing stock levels, and dwarf mistletoe ratings will be remeasured at 5-year intervals and will be compared with changes predicted by existing growth and yield models (fig. 29). These data will provide a basis for formulating silvicultural prescriptions, management guidelines, and verification of existing growth and yield models for even-aged stands of ponderosa pine.

GROWTH AND YIELD IN UNEVEN-AGED PONDEROSA PINE

In many areas where scenic and recreation use predominate, a major management goal is to maintain uneven-aged stands of ponderosa pine.[5] The uneven-aged stands are characterized by trees of many sizes, intermingled singly or in groups. Growth predictions for these uneven-aged stands are needed to control management activities and to evaluate interactions among resources. The objective for one ongoing study is to develop a generalized technique suitable for use in simulations. The new techniques will be applicable to stands managed as uneven-aged stands, and uneven-aged stands that will eventually be converted to even-aged structure. The measurement of individual tree variables has been completed, and growth prediction functions are being developed.

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[5] *Personal communication with C. B. Edminster, Mensurationist, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo.*

DWARF MISTLETOE CONTROL IN PONDEROSA PINE

Dwarf mistletoe-infected ponderosa pine trees are removed in all timber sales on the Experimental Forest.[5] Since 1974, more than 60,000 ponderosa pine and 10,500 Douglas-fir seedlings have been planted in areas clearcut to control mistletoe. Studies are underway in past timber sale areas to determine optimum tree thinning levels to slow the spread of dwarf mistletoes, and to minimize damage from other tree diseases. A computer program, RMYLD, for ponderosa pine, provides a tool to aid foresters in managing mistletoe-infected and healthy forests.

Figure 29.—Ponderosa pine in a 1936 plantation on site index 50 land and thinned in 1981. Photographs taken 1983 (GSL-40, GSL-80, GSL-120).

PONDEROSA PINE AND UNDERSTORY PLANT GROWTH

Studies are underway to determine the long-term influence of thinning pine canopies to various basal areas on growth and production of understory vegetation.[5] Fourteen permanent plots were established in the open-timber, native range pastures on the basis of basal area of ponderosa pine and understory vegetation. Basal areas range from about 25 to 90 square feet per acre. Production of understory vegetation is estimated with a heterodyne vegetation meter and by weighing forage clipped from subplots. Production estimates and phenology are also determined from time to time for each of the major forage plants—mountain muhly, Arizona fescue, blue grama, fringed sagebrush, and sun sedge.

HABITAT USE AND REQUIREMENTS OF FLAMMULATED OWLS

Little is known about the flammulated owl's (fig. 30) habitat requirements, other than they seem to be associated with mature conifer forests, and are perhaps eliminated in logged areas where cavity trees and other elements are removed. A study has been conducted to determine breeding densities and habitat affinities in an old-growth ponderosa pine—Douglas-fir forest.[6] The owls migrate to the Experimental Forest about the first week in May, and select nest sites in cavities in old mature trees and snags. They migrate again in mid-October. They are insectivorous, and their diets include moths, beetles, grasshoppers, crickets, large flies and spiders.

Two years of telemetry study on seven nesting pairs indicated home ranges varied in size from 8 to 25 ha. Principal determinant of home range size appears to be patchiness of habitats or the intermixing of young dense stands of Douglas-fir, aspen, blue spruce along with mature ponderosa pine—Douglas-fir stands. The highest density of nesting pairs occurs in continuous stands of mature ponderosa pine—Douglas-fir. The owls tend to intensively forage in one to four open patches, about 0.1 to 1.4 ha each, within old-growth stands in their home range. The distance from forage areas to nests has ranged from 20 to 400 m. These and other data will provide a base with which to compare the ecology and population density of the owls in managed forests.

CATTLE GRAZING AND WATER QUALITY

The effect of seasonal cattle grazing on water quality is under study in pastures bisected by Trout Creek. Selected water quality parameters are measured in the stream above and below the cattle. The distribution and frequency of waste discharges and weight estimates of manure deposited near the stream have provided general evidence as to how streams may be enriched and/or

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[6] *Personal communication with R. T. Reynolds, Wildlife Biologist, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo.*

polluted by cattle. Results to date have shown minor local decreases in water quality, mainly bacteriological properties, when cattle are present. Based on moderate rates of grazing and generally adequate streamflow for manure and urine dilution, permanent removal of cattle does not appear to be necessary for good water quality maintenance.

POLLUTION INDICATOR BACTERIA IN LAKE AND STREAM WATER

Studies are underway to quantify the impact of lake-based recreation and mountain home development on surface water quality. Densities of indicator bacteria, such as total coliforms, fecal coliforms, and fecal streptococci in water, provide one measure of water quality. These bacteria are eliminated in large numbers in fecal waste, and their presence usually indicates that intestinal waste products have reached a water source.

Manitou Lake

The effect of lake-based recreation on water quality has been examined at Manitou Lake, a 12-acre reservoir, at the south end of the Experimental Forest. Daily visitor use starting in May ranges from none during stormy weather to several hundred during peak use. Recreational use at the lake (fig. 31) has not degraded water quality, based on densities of indicator bacteria. From July 1 to July 7, 1976, which included a period of major recreational use, fecal coliform densities in water entering Manitou Lake averaged 99 colonies per 100 ml of water. Fecal coliform densities leaving the lake averaged 2 colonies per 100 ml of water. Water quality actually improved from the lake inlet to the outlet, perhaps because of detention time and/or ultraviolet radiation.

Domestic Water Supply

Indicator bacteria in the domestic water supply at the forest headquarters have occasionally exceeded the state primary standard (less than 1 fecal coliform per 100 ml of water) for safe drinking water. Groundwater and streamflow from nearby Hotel Gulch is intercepted by a perforated steel pipe about 6 feet below the streambottom. The water collects in an underground concrete storage tank, and is conveyed to the headquarters through a pipeline. In mid-August counts of fecal streptococci indicator bacteria in the water supply, apparently from wildlife and insects, often averaged 150 colonies per 100 ml of water. The presence of these bacteria in the domestic water supply indicates incomplete filtering of biological pollutants through the coarse textured granitic alluvium near the water intake pipe. Incomplete filtering of biological pollutants near shallow domestic wells and springs likely occurs over a wide area of the Front Range.

Figure 30.—Flammulated owl parent and fledglings. Adult height is about 6 inches, and wingspan 14 inches (photograph courtesy of Art Wolfe).

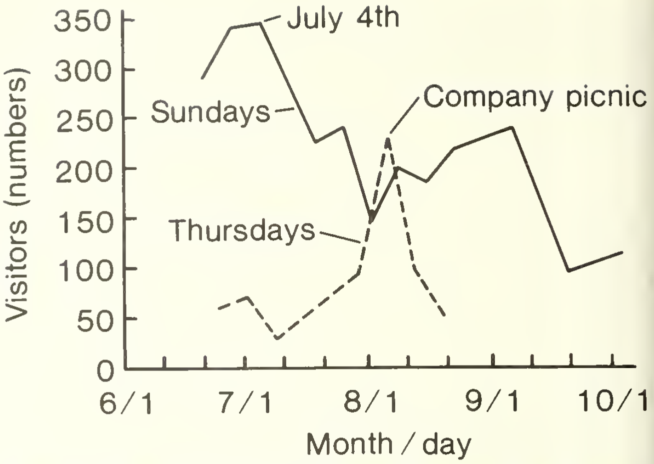

Figure 31.—Visitors at noon for selected Thursdays and Sundays at Manitou Lake, summer 1976 (Ponce and Gary 1979).

AQUATIC BIOTA IN TROUT CREEK

Surveys of aquatic biota, mainly macroinvertebrates, algae, and fish, have been conducted periodically since 1976 in Trout Creek.

Macroinvertebrates

Aquatic macroinvertebrates (underwater stages of aquatic insects) are sensitive to subtle chemical and physical changes in stream water. Because of low motility, they provide a natural monitor and quantitative means of assessing effects of erosion from road and home construction, sewage and other waste discharges, streamside shade removal, and other land uses. Most families and species of aquatic insects in the Ephemeroptera (mayflies), Plecoptera (stoneflies), and Trichoptera (caddisflies) orders are indicators of clean water conditions. Their composition in macroinvertebrate communities varies according to site (fig. 32). The absence of stoneflies below the Manitou Lake dam probably is related to the influence of the lake, because they increase with distance both above and downstream from the lake. The Diptera (true flies) order contains many families and species which tolerate a wide range of environmental conditions. A total of 78 taxa of aquatic macroinvertebrates have been collected and identified in Trout Creek.

Algae

Pollution discharges into streams may enrich water and stimulate the surface growth or "blooms" of algae and affect water use. Composition of algae in Trout Creek varies according to site and season. A total of 57 genera from Bacillariophyta, Chlorophyta, Chrysophyta, Cyanophyta, Euglenophyta and Rhodophyta divisions have been collected. Chlorophyta (green algae) is the most abundant division collected at a site 2.5 miles above Manitou Lake. The genus *Cladophora*, typical filamentous green alga, is dominant, and its presence usually indicates high nutrient concentration in streams. Rhodophyta (red algae) is the most prevalent division at the lake inlet in late summer. Bacillariophyta (diatoms) is the most abundant division collected below the lake; but, green algae is more prevalent in the fall—possibly because of cooler temperatures and reduction of diatom populations. The Chlorophyta division, mainly *Cladophora*, is also most common 1.9 miles below Manitou Lake.

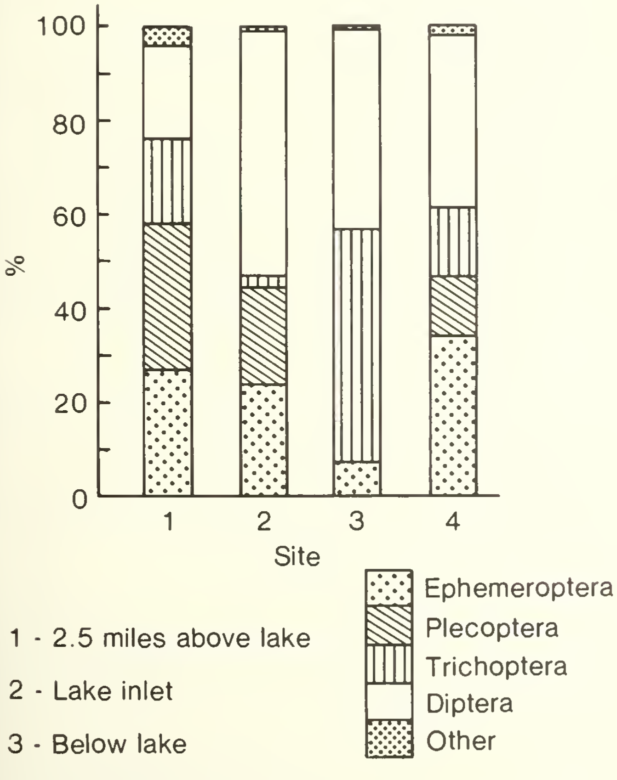

Figure 32.—Percentage composition of macroinvertebrates by density for Trout Creek above and below Manitou Park Lake (adapted from Short et al. 1978).

Fish

The abundance and composition of fish fauna in Trout Creek has been determined by DC electro-shocking and seining at selected study sites. Brook trout (*Salvelinus fontinalis*) is the dominant species 2.5 miles above Manitou Lake; but, its relative abundance is greatly reduced near the lake inlet and below the dam. Relative populations also increase 1.9 miles below the dam. Speckled dace (*Rhinichthys osculus*) and sand shiner (*Notropis stramineus*) are most common near the inlet of Manitou Lake. The greatest diversity of fish is found below Manitou Lake dam and where many western longnose suckers (*Catostomus catostomus* and white suckers (*C. commersoni*) are found.

WATER QUALITY IN THE NATURAL ENVIRONMENT

Water quality in "near pristine" streams, such as upper Hotel Gulch and Missouri Gulch on the Forest, may provide benchmarks with which to gage human impact on more highly developed land areas, such as the upstream areas along Trout Creek. Seasonal samples of stream water from the pristine streams (elevation about 8,700 feet) and from the main stream of Trout Creek (elevation about 7,700 feet), below diversely developed areas, indicate higher chemical pollution levels in Trout Creek. Low seasonal dissolved solids are associated with spring rains and/or snowmelt runoff, and high total dissolved solids with low baseflows in the fall. Fecal coliform densities in grazed sections along Trout Creek average about 14 times greater than fecal coliform densities found in the streams originating in the Hotel Gulch and Missouri Gulch natural areas.

ADMINISTRATION

The facilities of the Manitou Experimental Forest are used from time to time for training schools, graduate field work, and field meetings of forestry and conservation societies. Research at the Experimental Forest is coordinated with research elsewhere to provide knowledge about many interrelated uses of forest lands. Because research deals with the effect of use on renewable resources, it requires a long time to accomplish. Opportunities are extensive for graduate students to undertake fundamental research in the conservation and use of natural resources. Arrangements may be made through colleges, universities, foundations, or other interested groups and the USDA Forest Service on a cooperative basis. Visitors are always welcome. To obtain more detailed published information about the experimental work send requests to Director, Rocky Mountain Forest and Range Experiment Station, 240 West Prospect Street, Fort Collins, Colorado 80526.

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APPENDIX

Species List of Principal Plants[1]

Grasses and Grasslike

Common Name	Scientific Name
Crested wheatgrass	*Agropyron cristatum* (L.) Gaertin.
Intermediate wheatgrass	*Agropyron intermedium* (Host) Beauv.
Quack grass	*Agropyron repens* (L.) Beauv.
Western wheatgrass	*Agropyron smithii* Rydb.
Bearded wheatgrass	*Agropyron subsecundum* (Link) Hitchc.
Slender wheatgrass	*Agropyron trachycaulum* (Link) Malte
Redtop	*Agrostis alba* L.
Little bluestem	*Andropogon scoparius* Michx.
Pine dropseed	*Blepharoneuron tricholepis* (Torr.) Nash
Sideoats grama	*Bouteloua curtipendula* (Michx.) Beauv.
Blue gramas	*Bouteloua gracilis* (H. B. K.) Steud.
Nodding brome	*Bromus anomalus* Fourn.
Fringed brome	*Bromus ciliatus* L.
Weeping brome	*Bromus frondosus* (Shear) Woot. & Standl.
Smooth brome	*Bromus inermis* Leyss.
Water sedge	*Carex aquatilis* Wahl.
	Carex brevipes W. Boott
	Carex disperma Dewey
Needleleaf sedge	*Carex eleocharis* Bailey
Silvertop sedge	*Carex foena* Willd.
Sun sedge	*Carex heliophila* Mack.
Smallwing sedge	*Carex microptera* Mack.
Nebraska sedge	*Carex nebraskensis* Dewey
Silver sedge	*Carex praegracilis* W. Boott
Ross sedge	*Carex rossii* Boott
Beaked sedge	*Carex rostrata* Stokes
Bluejoint reedgrass	*Calamagrostis canadensis* (Michx.) Beauv.
Northern reedgrass	*Calamagrostis inexpansa* Gray
Purple pinegrass	*Calamagrostis purpurascens* R. Br.
Orchardgrass	*Dactylis glomerata* L.
Timber danthonia	*Danthonia intermedia* Vasey
Parry danthonia	*Danthonia parryi* Scribn.
Common spikesedge	*Eleocharis macrostachya* Britt.
Russian wildrye	*Elymus junceus* Fisch.
Arizona fescue	*Festuca arizonica* Vasey
Sheep fescue	*Festuca ovina* L.
Thurber fescue	*Festuca thurberi* Vasey
Tall mannagrass	*Glyceria elata* (Nash) M. E. Jones
Foxtail barley	*Hordeum jubatum* L.
Baltic rush	*Juncus balticus* Willd.
Regels rush	*Juncus saximontanus* Nels.
Poverty rush	*Juncus tenuis* Willd.
Prairie junegrass	*Koeleria cristata* (L.) Pers.
Perennial ryegrass	*Lolium perenne* L.
Mountain muhly	*Muhlenbergia montana* (Nutt.) Hitchc.
False buffalograss	*Munroa squanosa* (Nutt.) Torr.
Roughleaf ricegrass	*Oryzopsis asperifolia* Michx.
Indian ricegrass	*Oryzopsis hymenoides* (R. & S.) Ricker
	Oryzopsis pungens (Torr.) Hitchc.
Timothy	*Phleum pratense* L.
Sherman big bluegrass	*Poa ampla* Merr.
Bulbous bluegrass	*Poa bulbosa* L.
Canby bluegrass	*Poa canbyi* (Scribn.) Piper
Mutton bluegrass	*Poa fendleriana* (Steud.) Vasey

Inland bluegrass	*Poa interior* Rydb.
Fowl bluegrass	*Poa palustris* L.
Kentucky bluegrass	*Poa pratensis* L.
Tumblegrass	*Schedonnardus paniculatis* (Nutt.) Trel.
Falsemelic	*Schizacne purpurascens* (Torr.) Swallen
Panicled bulrush	*Scripus microcarpus* Presl.
Bristlegrass	*Setaria viridis* (L.) Beauv.
Bottlebrush squirreltail	*Sitanion hystrix* (Nutt.) J. & Sm.
Subalpine needlegrass	*Stipa columbiana* Macoun.
Needle-and-thread	*Stipa comata* Trin. & Rupr.
Sleepygrass	*Stipa robusta* (Vasey) Scribn.
Scribner needlegrass	*Stipa scribneri* Vasey
Green needlegrass	*Stipa viridula* Trin.

Forbs

Western yarrow	*Achillea lanulosa* Nutt.
Columbia monkshood	*Aconitum columbianum* Nutt.
Orange agoseris	*Agoseris aurantiaca* (Hook.) Greene
Pale agoseris	*Agoseris glauca* (Pursh) Raf.
Tapertip onion	*Allium acuminatum* Hook.
Nodding onion	*Allium cernuum* Roth
Geyer onion	*Allium geyeri* Wats.
Redroot amaranth	*Amaranthus retroflexus* L.
Giant ragweed	*Ambrosia trifida* L.
Rockjasmine	*Androsace septentrionalis* L.
Anemone	*Anemone multifida* Poir.
Pussytoes	*Antennaria anaphaloides* Rydb.
Field pussytoes	*Antennaria neglecta* Greene
Rocky Mountain pussytoes	*Antennaria parvifolia* Nutt.
	Aralia nudicaulis L.
Fendler sandwort	*Arenaria fendleri* Gray
Leafy arnica	*Arnica chamissonis* Less.
Heartleaf arnica	*Arnica cordifolia* Hook.
Sagewort wormwood	*Artemisia campestris* L.
Louisiana sagebrush	*Artemisia ludoviciana* Nutt.
Siskiyou aster	*Aster hesperius* Gray
Porters aster	*Aster porteri* Gray
Milkvetch	*Astragalus adsurgens* Pall.
Purple milkvetch	*Astragalus agrestis* G. Don
Alpine milkvetch	*Astragalus alpinus* L.
Milkvetch	*Astragalus miser* Hook.
Milkvetch	*Astragalus parryi* Gray
Plantainleaf kittentails	*Besseya plantaginea* (Benth.) Rydb.
	Brickellia grandiflora (Hook.) Nutt.
Gunnison mariposa	*Calochortus gunnissonii* Wats.
Marshmarigold	*Caltha leptosepala* DC.
Bluebell	*Campanula rotundifolia* L.
Wholeleaf paintedcup	*Castilleja integra* Gray
Sulfur paintedcup	*Castilleja septentrionalis* Lindl.
Starry cerastium	*Cerastium arvense* L.
	Cerastium vulgatum L.
Douglas chaenactis	*Chaenactis douglasii* H. & A.
	Chamaerhodos nuttallii (T. & G.) Pickering
Lambsquarters goosefoot	*Chenopodium album* L.
Blite goosefoot	*Chenopodium capitatum* (L.) Asch.
Slimleaf goosefoot	*Chenopodium leptophyllum* Nutt.
Common pipsissewa	*Chimaphila umbellata* (L.) Bart.
Goldaster	*Chrysopsis fulcrata* Greene
Hairy goldaster	*Chrysopsis villosa* var. *foliosa* (Nutt.) D.C. Eat.
European glorybind	*Convolvulus arvensis* L.
Spotted coralroot	*Corallorhiza maculata* Raf.

Early coralroot	*Corallorhiza trifida* Chat.
Golden corydalis	*Corydalis aurea* Willd.
Dandelion hawksbeard	*Crepis runcinata* (James) T. & G.
Cryptantha	*Cryptantha thyrsiflora* (Greene) Pays.
Cryptantha	*Cryptantha virgata* (Porter) Pays.
Branched larkspur	*Delphinium ramosum* Rydb.
Darkthroat shootingstar	*Dodecatheon pulchellum* (Raf.) Merr.
Field horsetail	*Equisetum arvense* L.
Scouring rush	*Equisetum hyemale* L.
Smooth horsetail	*Equisetum laevigatum* A. Br.
Fernleaf fleabane	*Erigeron compositus* Pursh
Trailing fleabane	*Erigeron flagellaris* A. Gray
Oregon fleabane	*Erigeron speciosus* (Lindl.) DC.
Threenerve fleabane	*Erigeron subtrinervis* Rydb.
Fleabane	*Erigeron vetensis* Rydb.
Fireweed	*Epilobium angustifolium* L.
Wing eriogonum	*Erigonum alatum* Torr.
Robust euphorbia	*Euphorbia robusta* (Engelm.) Small
Thymeleaf euphorbia	*Euphorbia serpyllifolia* Pers.
European strawberry	*Fragaria vesca americana* (Porter) Britt.
Wild strawberry	*Fragaria ovalis* (Lehm.) Rydb.
Bursage	*Frasera speciosa* Griseb.
Northern bedstraw	*Galium boreale* L.
Sweetscented bedstraw	*Galium triflorum* Michx.
Annual gentian	*Gentiana amarella* L.
Fremont geranium	*Geranium fremontii* Torr.
Parry geranium	*Geranium parryi* (Engelm.) Heller
Richardson geranium	*Geranium richardsonii* Fisch. & Trautv.
Allepo avens	*Geum aleppicum* Jacq.
Avens	*Geum triflorum* Pursh
Skyrocket gilia	*Gilia aggregata* (Pursh) Spreng.
Sticky gilia	*Gilia calcarea* Jones
Western rattlesnake plantain	*Goodyera oblongifolia* Raf.
Creeping rattlesnake plantain	*Goodyera repens* (L.) R. Br.
Northern green habenaria	*Habenaria hyperborea* (L.) R. Br.
Parry goldenweed	*Haplopappus parryi* Gray
Parry helianthella	*Helianthella parryi* Gray
Common sunflower	*Helianthus annuus* L.
Prairie sunflower	*Helianthus petiolaris* Nutt.
________________	*Helianthus pumilus* Nutt.
Common cowparsnip	*Heracleum lanatum* Michx.
Littleleaf alumroot	*Heuchera parvifolia* Nutt.
Hawkweed	*Hieracium fendleri* Sch.-Bip.
Wax currant	*Hymenoxys acaulis* (Pursh) Parker
Chicory lettuce	*Lactuca pulchella* (Prush) DC.
Stickseed	*Lappula redowskii* (Hornem.) Greene
Prairie pepperweed	*Lepidium densiflorum* Schrad.
Low bladderpod	*Lesquerella montana* (Gray) Wats.
Porter ligusticum	*Ligusticum porteri* C. & R.
Butter-and-eggs toadflax	*Linaria vulgaris* Mill.
Twinflower	*Linnaea borealis* L.
Lewis flax	*Linum lewisii* Pursh
Manyflower gromwell	*Lithospermum multiflorum* Torr.
Silvery lupine	*Lupinus argenteus* Pursh
Lodgepole lupine	*Lupinus parviflorus* Nutt.
Drummond campion campion	*Lychnis drummondii* (Hook.) Wats.
Rush skeletonplant	*Lygodesmia juncea* (Pursh) D. Don
________________	*Machaeranthera pattersonii* (Gray) Greene
Yellow sweetclover	*Melilotus officinalis* (L.) Lam.
Desert mentzelia	*Mentzelia multiflora* (Nutt.) Gray
Lanceleaf bluebells	*Mertensia lanceolata* (Pursh) A. DC.
Common monkeyflower	*Mimulus guttatus* DC.

Evening primrose	*Oenothera coronopifolia* T. & G.
Broomrape	*Orobanche fasciculata* Nutt.
Yellow owlclover	*Orthocarpus luteus* Nutt.
Bluntseed sweetroot	*Osmorhiza depauperata* Phil.
Crazyweed	*Oxytropis multiceps* Nutt.
Lambert crazyweed	*Oxytropis lambertii* Pursh
Early pedicularis	*Pedicularis canadensis* L.
Grays pedicularis	*Pedicularis grayi* Nels.
Elephanthead pedicularis	*Pedicularis groenlandica* Retz.
Crandall penstemon	*Penstemon crandallii* A. Nels.
Sidebells penstemon	*Penstemon secundiflorus* Benth.
Oneside penstemon	*Penstemon unilateralis* Rydb.
Green penstemon	*Penstemon virens* Pennell
Wandbloom penstemon	*Penstemon virgatus* Gray
	Phacelia denticulata Osterch.
	Phacelia heterophylla Pursh
	Phacelia neomexicana Torr.
Downy groundcherry	*Physalis pubescens* L.
Varileaf cinquefoil	*Potentilla diversifolia* Lehm.
Bigflower cinquefoil	*Potentilla fissa* Nutt.
Gland cinquefoil	*Potentilla glandulosa* Lindl.
Northwest cinquefoil	*Potentilla gracilis* Hook.
Horse cinquefoil	*Potentilla hippiana* Lehm.
Pennsylvania cinquefoil	*Potentilla pensylvanica* L.
Prostrate knotweed	*Polygonum aviculare* L.
	Polygonum bistortoides Pursh
Dullseed cornbind	*Polygonum convolvulus* L.
	Pseudocymopteris montanus (Gray) C. & R.
Woodland pinedrops	*Pterospera andromedea* Nutt.
Alpine pyrola	*Pyrola asarifolia* Michx.
	Pyrola chlorantha Swartz
Snowline pyrola	*Pyrola minor* L.
Sidebells pyrola	*Pyrola secunda* L.
	Pyrola uniflora L.
Littleleaf buttercup	*Ranunculus abortivus* L.
Shore buttercup	*Ranunculus cardiophyllus* Hook.
	Ranunculus macounii Britt.
Blackeyedsusan	*Rudbeckia hirta* L.
Western dock	*Rumex occidentalis* Wats.
Yellowdot saxifrage	*Saxifraga bronchialis* L.
Brittons scullcap	*Scutellaria brittonii* Porter
Stonecrop	*Sedum rhodanthum* Gray
	Sedum stenopetalum Pursh
Desert groundsel	*Senecio eremophilus* Richards
Fendler groundsel	*Senecio fendleri* Gray
Lambstongue groundsel	*Senecio integerrimus* Nutt.
	Senecio pudicus Greene
	Senecio tridenticulatus Rydb.
	Senecio werneriaefolius Gray
	Senecio wootonii Greene
Starry solomonplume	*Smilacina stellata* (L.) Desf.
Black nightshade	*Solanum nigrum* L.
Cutleaf nightshade	*Solanum triflorum* Nutt.
	Solidago decumbens Greene
	Solidago multiradiata Ait.
Baby goldenrod	*Solidago nana* Nutt.
marsh betony	*Stachys palustris* L.
Claspleaf twistedstalk	*Streptopus amplexifolius* (L.) DC.
Alpinebog swertia	*Swertia perennis* L.
Common dandelion	*Taraxacum officinale* Weber
Meadowrue	*Thalictrum fendleri* Gray
Pennycress	*Thlaspi alpestre* L.

Field pennycress	*Thlaspi arvense* L.
Salsify	*Tragopogon dubius* Scop.
Vegetable-oyster salsify	*Tragopogon parvifolius* L.
Alsike clover	*Trifolium hybridum* L.
White clover	*Trifolium repens* L.
Valerian	*Valeriana capitata* Link
Edible valerian	*Valeriana edulis* Nutt.
Golden crownbeard	*Verbesina encelioides* (Cav.) B. & H.
Water speedwell	*Veronica anagallis-aquatica* L.
Hook violet	*Viola adunca* J. E. Sm.
Canada violet	*Viola canadensis* L.
Nuttall violet	*Viola nuttallii* Pursh
	Viola renifolia Gray
Mountain deathcamas	*Zigadenus elegans* Pursh

Shrubs

Rocky Mountain maple	*Acer glabrum* Torr.
Thinleaf alder	*Alnus tenuifolia* Nutt.
Saskatoon serviceberry	*Amelanchier alnifolia* Nutt.
Southwestern dwarf mistletoe	*Arceuthobium vaginatum* (Willd.) Presl.
Bearberry	*Arctostaphylos uva-ursi* (L.) Spreng.
Fringed sagebrush	*Artemisia frigida* Willd.
Creeping mahonia	*Berberis repens* Lindl.
Water birch	*Betula occidentalis* Hook.
True mountainmahogany	*Cercocarpus montanus* Raf.
Rabbitbrush	*Chrysothamus viscidiflorus* H. & C.
Rocky Mountain clematis	*Clematis pseudoalpina* (Kuntze) A. Nels.
Bunchberry dogwood	*Cornus canadensis* L.
Red-osier dogwood	*Cornus stolonifera* Michx.
Bush rockspirea	*Holodiscus dumosus* (Nutt.) Heller
Cliff jamesia	*Jamesia americana* T. & G.
Common juniper	*Juniperus communis* L.
Bearberry honeysuckle	*Lonicera involucrata* (Richards) Banks
Mountain ninebark	*Physocarpus monogynus* (Torr.) Coult.
Shrubby cinquefoil	*Potentilla fruticosa* L.
Common chokecherry	*Prunus virginiana* L.
Skunkbush sumac	*Rhus trilobata* Nutt.
Wax currant	*Ribes cereum* Dougl.
Whitestem gooseberry	*Ribes inerme* Rydb.
Gooseberry currant	*Ribes montigenum* McClat.
Arkansas rose	*Rosa arkansana* Porter
Boulder raspberry	*Rubus deliciosus* Torr.
	Rubus pubescens Raf.
	Rubus strigosus Michx.
Coyote willow	*Salix exigua* Nutt.
Pussy willow	*Salix discolor* Muhl.
Elderberry	*Sambucus racemosa* L.
Common snowberry	*Symphoricarpos albus* (L.) Blake
Rocky Mountain whortleberry	*Vaccinium myrtillus* L.
Small soapweed	*Yucca glauca* Nutt.

Trees

Engelmann spruce	*Picea engelmannii* Parry
Blue spruce	*Picea pungens* Engelm.
Lodgepole pine	*Pinus contorta* Dougl.
Pinyon	*Pinus edulis* Engelm.
Limber pine	*Pinus flexilis* James
Ponderosa pine	*Pinus ponderosa* Laws.
Quaking aspen	*Populus tremuloides* Michx.
Douglas-fir	*Pseudotsuga menziesii* (Mirb.) Franco

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[1] *Plant names mentioned in publications and reports from the Manitou Experimental Forest.*

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Gary, Howard L. 1985. A summary of research at the Manitou Experimental Forest in Colorado, 1937–1983. USDA Forest Service General Technical Report RM-116, 24 p. Rocky Mountain Forest and Range Experiment Station, Fort Collins. Colo.

Results of selected studies for range, watershed, timber and wildlife management research are summarized to provide land managers, land-use planners, and land-use researchers with information to help evaluate consequences of land management practices in the Colorado Front Range ponderosa pine zone.

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U.S. Department of Agriculture
Forest Service

Rocky Mountain Forest and Range Experiment Station

Rocky Mountains

Southwest

Great Plains

The Rocky Mountain Station is one of eight regional experiment stations, plus the Forest Products Laboratory and the Washington Office Staff, that make up the Forest Service research organization.

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Research programs at the Rocky Mountain Station are coordinated with area universities and with other institutions. Many studies are conducted on a cooperative basis to accelerate solutions to problems involving range, water, wildlife and fish habitat, human and community development, timber, recreation, protection, and multiresource evaluation.

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Tempe, Arizona

*Station Headquarters: 240 W. Prospect St., Fort Collins, CO 80526

United States
Department of
Agriculture

Forest Service

**Rocky Mountain
Forest and Range
Experiment Station**

Fort Collins,
Colorado 80526

**General Technical
Report RM-117**

Silvical Characteristics of Blue Spruce

Gilbert H. Fechner

Abstract

This report summarizes information on distribution, botanical description, habitat conditions, life history, special uses, and genetics of blue spruce.

USDA Forest Service
General Technical Report RM-117

April 1985

Silvical Characteristics of Blue Spruce

Gilbert H. Fechner, Professor of Forest Genetics
Colorado State University[1]

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[1] *This report was prepared under cooperative agreement between the Rocky Mountain Forest and Range Experiment Station (MFRWU-1252) and Colorado State University, both in Fort Collins, Colo.*

Contents

Silvical Characteristics of Blue Spruce

Gilbert H. Fechner

Blue spruce (*Picea pungens* Engelm.)[2] is one of seven species of spruce indigenous to the United States. Other common names include Colorado blue spruce, Colorado spruce, silver spruce, and pino real.

DISTRIBUTION

Blue spruce is primarily restricted to the central and southern Rocky Mountains of the western United States. Its range extends across 15° 04′ of latitude (33°50′ to 48°54′ N.), a distance of about 1,050 miles, and 9° 15′ longitude (104°45′ to 114°00′ W.). Blue spruce is found from southern and western Wyoming, southwestern Montana, and eastern Idaho, south to Utah, northern and eastern Arizona, southern New Mexico, and central Colorado. It also has been reported in isolated locations in north-central Montana (Strong 1978) and in north-central (Coconino County) Arizona (Jones and Rietveld 1974) (fig. 1).

Approximately one-half of the blue spruce distribution is in the mountains of Colorado. In Idaho it is restricted to the Wasatch and Caribou Mountains, the Snake River Range, and the extreme northeastern part of the state.

In addition to the recently reported locations in Arizona, blue spruce is found on the Kaibab Plateau and in the Lukachukai and White Mountains. In New Mexico, it grows from the Sacramento Mountains and the Sangre de Cristo Range westward in scattered locations. Blue spruce is not abundant in Utah, although it grows over a wide range from Iron County to the Uinta Mountains along the mountain backbone of that state, and also in the Deep Creek Mountains near its western boundary (Erdman 1970).

BOTANICAL DESCRIPTION

Leaves.—Leaves are straight, 4-angled, about 1 to 1-1/4 inches long; they are yellow green to bluish green o silvery-white, often with a glaucous bloom. The stiff, harp-pointed leaves extend nearly at right angles to the wig. When chewed, they have a sharp, acid taste.

Twigs.—The stout, stiff, shiny twigs are greenish brown, becoming orange brown to grayish brown; they re usually glabrous.

Buds.—The buds are pointed, about 1/2 inch long, ght chocolate brown; the scales are usually reflexed.

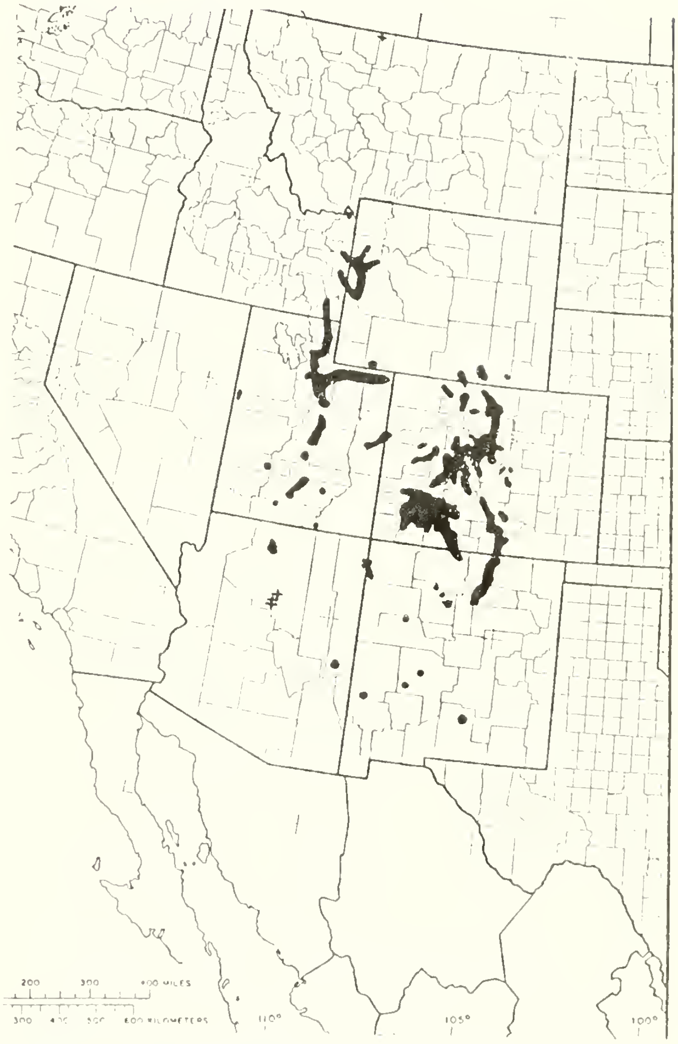

Figure 1.—Natural distribution of blue spruce (*Picea pungens* Engelm.). Adapted from Little 1971.

Conelets.—Blue spruce is monoecious. Male conelets are yellow, tinged with red, and the female, light pink to bright scarlet; occasionally conelets of both sexes are light yellow green.

Cones.—The cones are oblong to cylindrical, and usually 2-1/2 to 3-1/2 inches long, but sometimes up to 4-1/2 inches. They are green, tinged with red, but become straw-colored at maturity. The unstalked or short-stalked cones have scales that are thin, diamond-shaped, tough, wrinkled, with straight or ragged margins and flat tips, with the broadest point of the scale below the middle. Maturing in August and September, some cones fall during the first winter, but many remain on the tree for 2 to 3 years after seeds have been released. Cones are concentrated in the upper third or less of the crown.

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[2] *Scientific and common names of trees used in this report are om Little (1979); names of other plants follow Nickerson et al. 976). For plants not included in either of these publications, the ame used by the author of the reference has been adopted.*

Bark.—The gray bark is tinged with red. It is scaly when young, becoming furrowed, with rounded ridges. Epicormic branches frequently develop along the trunk.

HABITAT

Climate

Blue spruce grows in a climatic zone that is generally cool and humid. It may be classified as a microthermal to taiga temperature province and a subhumid to humid moisture province, characterized by low summer temperatures and low winter precipitation (Thornthwaite 1948).

Local temperature data within the range of blue spruce are sparse. Mean annual temperatures, where blue spruce is most commonly found in Colorado and the Southwest, are as follows:

	Mean temperatures °F
Annual	39–43
January	25–27
January minimum	12–16
July	57–59
July maximum	70–72

The frostfree period from June to August is about 55 to 60 days (Bates 1924, Pearson 1931).

Precipitation data are also sparse. Average annual precipitation where blue spruce most commonly occurs varies from 18 to 24 inches. Winter precipitation is usually low; less than 20% of the annual moisture falls from December through March. Fifty percent of the annual precipitation falls as rain during the growing season (Baker 1944, Bates 1924, Pearson 1931).

Soils and Topography

The soils on which blue spruce is found vary considerably, but frequently they consist of rich, moist, fairly fertile, sandy to gravelly loams in streambottoms, in valleys, and on low, moist soils or on subirrigated, gentle slopes. Depending on the location, these soils may be alluvial or fluvial deposits derived from a variety of parent materials, including limestone, quartzite, sandstone, or shale. The soils are approximately neutral to slightly alkaline (pH 6.8 to 7.2) (Dixon 1935).

In Arizona and New Mexico, blue spruce is found on gentle upland slopes and in well-watered tributary drainages, extending down intermittent streams, and on lower northerly slopes. Soils there may consist of sponsellar loam, sponsellar gravelly silt loam, or deep alluvial soils derived from limestone (Moir and Ludwig 1979). Similarly, in many localities in Utah, blue spruce is found on loamy sands, loams, and clays, with some gravel present. Most of these soils are derived from calcareous parent materials (Mauk and Henderson 1984, Pfister 1972). In a few localities in Utah, blue spruce may be found on swampy sites; the species i considered to be the pioneer tree species in wet soil (Dixon 1935).

In general, the soils and the landforms of the mixe conifer forest of the central Rocky Mountains, of whic blue spruce is often a part, are similar to those of th spruce-fir type at higher elevations and the ponderos pine type at lower elevations, although the sites o which blue spruce grows are more moist than those ponderosa pine and warmer than those of Engelman spruce and subalpine fir (Alexander 1974) (fig. 2).

Blue spruce is characteristically found at elevatior between 6,000 and 9,000 feet in the northern part of i range, and from 7,000 to 10,000 feet in the souther part. At the most northerly extent of its reporte distribution in Montana, it occurs at 6,960 feet (Stror 1978). In northern Colorado, it is mostly found betwe 6,000 and 8,500 feet, occasionally to 9,000 feet (Fechn 1980). In Utah, most of the blue spruce usually grov between 6,560 and 8,530 feet, but an island populati has been reported at 9,840 feet and occasional tre grow to timberline (Dixon 1935, Johnson 1970). Arizona, this species commonly is found from 8,300 9,100 feet on the Kaibab Plateau; in the White Mou tains, it occasionally grows up to 11,000 feet and dov streams to 8,000 feet (Little 1950, Peattie 1953). In Ne Mexico, blue spruce is found between 7,800 and 8,1 feet, and it is found up to 9,100 to 9,500 feet in t Sangre de Cristo Mountains and similar elevations the San Juan Mountains of southwestern Colorado (M and Ludwig 1979).

Associated Forest Cover

Blue spruce is characteristically a species of the m tane zone in the central and southern Rocky Mountai It is the principal species of the blue spruce cover ty (SAF Type 216) (Society of American Foresters 19 and is a minor associate in four other forest cover typ

SAF Type Number	**Type**
206	Engelmann Spruce—Subalpine Fir
210	Interior Douglas-fir
235	Cottonwood—Willow
237	Interior Ponderosa Pine

In the central and southern Rocky Mountains of C rado, Utah, and southern Wyoming, where most of blue spruce grows, Rocky Mountain Douglas (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco) a Rocky Mountain ponderosa pine (*Pinus ponderosa* v *scopulorum* Engelm.) are perhaps the most persist tree associates of blue spruce. Blue spruce never gr in extensive stands, but it is often the only conifer p ent on streamside sites.

The most common hardwood associate of blue spr in the central Rocky Mountains is narrowleaf cot wood (*Populus angustifolia* James) (fig. 3). Quaking as (*Populus tremuloides* Michx.) is also a frequ associate, and blue spruce will invade quaking as stands, especially in moist, protected locations. Occasionally balsam poplar (*Populus balsamifera* L.) is found with blue spruce. Smaller streamside trees and common shrub associates of blue spruce in the central Rocky Mountains include water birch (*Betula occidentalis* Hook.), mountain alder (*Alnus tenuifolia* Nutt.), shrubby cinquefoil (*Potentilla fruticosa* L.), common snowberry (*Symphoricarpos albus* (L.) Blake), chokecherry (*Prunus virginiana* L.), and various species of willow (*Salix* L.). Herbaceous plants in the montane zone streambottom locations often include Richardson geranium (*Geranium richardsonii*) Fisch. & Trautv.) and grasses, such as foxtail barley (*Hordeum jubatum* L.), Kentucky bluegrass (*Poa pratensis* L.), timothy (*Phleum pratensis* L.), nodding brome or Porter brome (*Bromus anomalus* Fourn.), and bluejoint reedgrass (*Calamagrostis canadensis* (Michx.) Beauv.) (Hess 1981, Mauk and Henderson 1984).

On north-facing slopes adjacent to streambottom sites where blue spruce is found, Rocky Mountain Douglas-fir may form dense stands, and near the upper limits of the montane zone, that species may be replaced by lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.). White fir (*Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr.) is also associated with blue spruce on mesic sites in the central Rocky Mountains but not north of approximately 42°30′ N. latitude. On the north-facing slopes, blue spruce may extend somewhat up the slope in direct mixture with the above-named species, but is rarely found more than 30 to 40 feet above the streambottom or drainage bottom. Associated small trees and shrubs on these cool, moist sites include Rocky Mountain maple (*Acer glabrum* Torr.), western serviceberry (*Amelanchier alnifolia* (Nutt.) Nutt., common juniper (*Juniperus communis* L.), red-osier dogwood (*Cornus stolonifera* Michx.), and bearberry or kinnikinnick (*Arctostaphylos uva-ursi* (L.) Spreng.) (Fechner 1964, Hess 1981).

Forests of the south-facing slopes near the blue spruce streambottom sites of the montane zone in the central Rocky Mountains, or at the lower altitudinal extent of blue spruce, characteristically consist of open stands of Rocky Mountain ponderosa pine and perhaps Rocky Mountain juniper (*Juniperus scopulorum* Sarg.). Common shrubby vegetation on these sites include antelope bitterbrush (*Purshia tridentata* (Pursh) D.C.), alderleaf cercocarpus (*Cercocarpus montanus* Raf.), and wax currant (*Ribes cereum* Dougl.). Common herbaceous plants are hairy goldaster (*Chrysopsis villosa* (Pursh) DC.) and grasses, such as needleandthread (*Stipa comata* Trin. & Rupr.), blue grama (*Bouteloua gracilis* (H.B.K.) Steud.), and bottlebrush squirrel tail (*Sitanion hystrix* (Nutt.) J. G. Smith).

Figure 2.—Stand of blue spruce (*Picea pungens* Engelm.) in north-central Colorado.

Figure 3.—Typical streamside habitat of blue spruce in Colorado. Major hardwood associate shown is narrowleaf cottonwood.

At 8,500 to 9,000 feet in the central Rocky Mountains of northern Colorado, blue spruce contacts the lower extent of the subalpine life zone, which is dominated by Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.). Blue spruce may mingle with these two species on moist sites, such as lower, north-facing slopes, or with lodgepole pine on somewhat dry sites or on disturbed sites. Quaking aspen is also a common associate of blue spruce in the lower subalpine life zone on moist, disturbed sites. Rocky Mountain maple, common juniper, russet buffaloberry (*Shepherdia canadensis* (L.) Nutt.), bearberry honeysuckle (*Lonicera involucrata* (Richards.) Spreng.), and creeping mahonia (*Berberis repens* Lindl.) are common shrubs. Herbaceous associates in the lower subalpine zone include heartleaf arnica (*Arnica cordifolia* Hook.), sagebrush or wormwood (*Artemisia* spp.), cinquefoil (*Potentilla* spp.), and spreading thermopsis (*Thermopsis divaricarpa* A. Nels.); grasses may be bearded wheatgrass (*Agropyron subsecundum* (Link) Hitchc.) and Thurber fescue (*Festuca thurberi* Vasey) (Hess 1981, Mauk and Henderson 1984, Pfister 1972).

In the southern part of the blue spruce range (southwestern Colorado, Arizona, and New Mexico), blue spruce is a component of several habitat types, and it also occurs in the widespread and complex mixed conifer forest (Jones 1973, Moir and Ludwig 1979). These habitat types are relatively diverse, the blue spruce series constituting topoedaphic climaxes bordering meadows and in streambottoms. In general, blue spruce dominates in habitats that are too warm and dry for Engelmann spruce and subalpine fir and that are wetter than those typically occupied by ponderosa pine, although all three of these species are associates of blue spruce. Blue spruce forms ecotones with types dominated by subalpine fir, white fir, and Rocky Mountain Douglas-fir, and it also forms ecotones with the deciduous riparian forest and the woodland riparian types (Layser and Schubert 1979). Additionally, southwestern white pine (*Pinus strobiformis* Engelm.) is a common component of the mixed conifer forest containing blue spruce.

Typical shrub associates of blue spruce in the southern part of the range include alders and willows in the most moist situations, and Rocky Mountain maple, western serviceberry, chokecherry, common juniper, and Gambel oak (*Quercus gambelii* Nutt.) in somewhat drier situations. Western thimbleberry (*Rubus parviflorus* Nutt.), Utah honeysuckle (*Lonicera utahensis* Wats.), bearberry or kinnikinnick, and twinflower (*Linnaea borealis* L.) may also be found associated with blue spruce in some habitats.

Common herbaceous associates in various habitats of the southern part of the blue spruce distribution are fleabane (*Erigeron superbus* Rydb.), wild strawberry (*Fragaria ovalis* (Lehm.) Rydb.), groundsel (*Senecio cardamine* Greene) and sharpleaf valerian (*Valeriana acutiloba* Rydb.). Also associated with blue spruce may be sedges (*Carex* spp.) and grasses, such as Arizona fescue (*Festuca arizonica* Vasey), screwleaf muhly (*Muhlenbergia virescens* (H.B.K.) Kunth), fringed brome (*Bromus ciliatus* L.), and Kentucky bluegrass, the latter sometimes constituting up to 70% of the ground cover (Moir and Ludwig 1979).

In the northern part of the blue spruce range (northern Wyoming, Idaho, and Montana), the species occurs only in scattered locations. It may be found reproducing on cobble bars in the upper montane and lower subalpine zones, such as under established stands of narrowleaf cottonwood and among scattered ponderosa pines. Large shrub associates here include mountain alder, water birch, bearberry, honeysuckle, and various species of willow. Associated herbaceous plants include red baneberry (*Actea rubra* (Ait.) Willd.), sweetscented bedstraw (*Galium triflorum* Michx.), starry solomon plume or starry smilac (*Smilacina stellata* (L.) Desf.) and mountain bluebells (*Mertensia ciliata* (James) G. Don), especially in moist locations; Kentucky bluegrass and sedges are common grass and grasslike associates. Flats and benches may be dominated by big sagebrush (*Artemisia tridentata* Nutt.), whereas most adjacent slopes are predominantly covered with Engelmann spruce, and south-facing sites are dominated by lodgepole pine, as are disturbed Engelmann spruce forests (Mogren, personal communication 1981, Steele et al. 1979).

In the extreme northern extent of the blue spruce distribution, associates of this species are Engelmann spruce and white spruce (*Picea glauca* (Moench) Voss) (Strong 1978).

Blue spruce occurs in various seral stages, from pioneer to climax, in 32 currently recognized habitat types. These habitat types are summarized in the Appendix.

LIFE HISTORY

Reproduction and Early Growth

Flowering and Fruiting

Blue spruce is monoecious. Male strobili occur throughout the living crown of the tree, although they are usually more frequent in the upper one-half of the crown. They commonly develop in whorls of three to five at the base of the current vegetative growth, or singly in subterminal or terminal positions. Female strobili of blue spruce develop in the upper 10% to 25% of the live crown of mature trees. They usually occupy terminal positions on lateral branchlets (Fechner 1964, 1974).

The male strobili of blue spruce mostly are rose-red colored at the time that they emerge from the buds.[3] A single male strobilus, containing approximately 100 sporophylls, may produce about 370,000 pollen grains. The female strobili consist of 175 to 225 scales and thus have a potential to produce 350 to 450 seeds per cone. Pollen is shed in May and June, depending upon altitude (fig. 4) (Fechner 1964, 1974).

For a short period of time following emergence from the bud, the scales of the female strobili are greenish yellow. However, as peak receptivity is reached, the scales become light pink to red, the scales are reflexed 90 degrees or more toward the base of the strobilus, and the strobili become erect on the twig (fig. 5). Within approximately two weeks following initial receptivity, the female strobili change from erect to a position about +45° above horizontal. In another week, approximately 50% of the cones are −45° to pendent; during the fourth week, all remaining cones become pendent and reach approximate full size (Fechner 1964, 1974). Phenological events of blue spruce are summarized in table 1.

Seed Production and Dissemination

Blue spruce is generally considered to be a good to prolific seed producer; full crops of cones occur about every 2 or 3 years (Safford 1974, Sudworth 1916) but some intermediate years are complete failures (Fechner 1964). Seed production begins at approximately 20 years, and optimum seed-bearing age is reached between 50 to 150 years (Vines 1960). Cones mature in August of the first year, and seed shed begins from early to late September, depending on altitude, and continues into the winter (Fechner 1974, Safford 1974). Seed set may reach 198 sound seeds per cone, averaging about 85, on open-pollinated trees. However, self-pollination, which may reach 18% in natural stands, depresses seed set by as much as 75% (Cram 1983a, 1984b). The seed is wind-disseminated, and seedfall diminishes rapidly as distance from the source increases. Most seeds fall within 300 feet of the upwind timber edge (Alexander 1974).

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[3] *Some trees bear yellowish-green strobili, but these trees occur in relatively low frequencies. Male and female strobili on a given tree are the same color, whether red or green.*

igure 4.—Male strobili of blue spruce (*Picea pungens* Engelm.) at pollen shedding.

Figure 5.—Female strobili of blue spruce (*Picea pungens* Engelm.) at peak receptivity.

Table 1.—Notes on the phenology of blue spruce in the Bennett Creek area, Larimer County, Colorado (40°40′ N.; 105°30′ W.; 7,600 to 7,800 feet altitude) (Fechner 1964).

Date	Blue spruce			Associated species
	Male strobili	**Female strobile, cones**	**Vegetative development**	
April				
1-10	Internal and external growth becomes measurable	Strobilus buds appear dormant	Buds appear dormant	Quaking aspen (*Populus tremuloides* Michx.) male catkins begin to emerge from buds
10-20	Strobilus growth continues			Quaking aspen male catkins reach woolly stage
20-30	Strobilus growth continues			Quaking aspen pollen is shed. Wax currant (*Ribes cereum* Dougl.) vegetative buds burst
May				
1-10	Meiosis; strobilus growth obvious	Buds show measurable but not obvious growth	Buds show measurable but not obvious growth	American pasqueflower *Anemone patens* L. in full bloom. Quaking aspen and wax currant leaves emerging
10-20	Many strobili begin to emerge from buds; microspore stage; airsacs developing, but pollen sinks in water		Buds show definite internal development	American pasqueflower waning. Quaking aspen leaves 1/3 inch. Rocky Mountain ponderosa pine (*Pinus ponderosa* var. *scopulorum* Engelm.) shows obvious vegetative elongation
20-30	Most strobili have broken bud, most red (yellow-green on some trees); size increase is regular. Branches may be excised for pollen forcing	Strobili buds elongating; becoming erect, all scales intact; early free nuclear gametophyte stage. Time for flower isolation in breeding programs		Wax currant in full bloom. Rocky Mountain ponderosa pine vegetative elongation continues
June				
1-10	Strobili show sharp increase in length	Strobili elongating, bud scales pushing off, strobili scales greenish to reddish	Buds continue swelling	Wax currant still in bloom. Rocky Mountain ponderosa pine shows pronounced candling

Table 1.—Notes on the phenology of blue spruce in the Bennett Creek area, Larimer County, Colorado (40°40′ N.; 105°30′ W.; 7,600 to 7,800 feet altitude) (Fechner 1964).—Continued

10-20	Pollen is shed	Strobili become receptive; most red (yellow-green on some trees); erect, ca. 40 mm long, scales reflexed to about 90°; starch deposition heavy in nucellus; pollen tube emergence begins on nucellus	Buds burst, leaves unfold, and elongation begins after pollen is shed	Wax currant and American pasqueflower fruit begins to swell. Quaking aspen leaves reach 3/4 inch in diameter
10-30	Strobili desiccate and abscise	Strobili scales close, red; strobili begin to turn down	Elongation is rapid, new branchlets are green	
July 1-10		Strobili become completely pendent, red color fading; egg forms in archegonium; sperm nuclei formed; penetration of nucellar cap by pollen tube is completed	New (current-year) growth completes elongation; new buds arise and scale differentiation begins	Quaking aspen vegetative growth nears completion; buds develop. Rocky Mountain ponderosa pine leaves extend about equal to length of basal sheath
10-20	New strobili become noticeable, but green	Cones double in length, and mature size is reached; fertilization occurs	New branchlets begin to show tan coloration; still quite succulent	
July 20-30		Cones retain reddish cast	Tan coloration continues; hardening begins	
August 1-10	Sporophylls begin to differentiate at base of strobili	Cones begin to harden	Coloration and hardening intensifies	
10-20	Sporophyll differentiation is essentially completed	Comes become very hard	Branchlets become tan and harden; new vegetative buds are still somewhat green	
20-30	Sporangia initiate	Cone scales show evidence of drying, becoming quite tan at tips		
September		Mature seeds are released; some cones fall from some trees, remain intact on others		Quaking aspen leaves color, but clonal variation is apparent. Wax currant fruit matures. Rocky Mountain ponderosa pine appears dormant
October[1]	Sporangial cell divisions very active early, differentiation completed by end of month; bud scales shiny, with very little reflexing		Buds show scale reflexing; this difference from male strobili persists throughout dormant period	Leaves of quaking aspen and other deciduous species have fallen

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[1] *Trees appear dormant from November through March.*

It is unlikely that heavy cone crops will occur in successive years on an individual tree, because the female strobili usually occupy terminal positions on lateral branchlets. Such terminal positions are at a minimum in the year following one of high seed production, because once differentiated from an apical meristem, only development of the strobilus occurs at that position during the following growing season. If a whorl of new axillary buds is produced on the branchlet at the base of the developing cone, these buds ordinarily will produce vegetative shoots for one season before female strobili are again differentiated. Thus, although blue spruce cones occasionally occupy sessile, axillary positions, the likelihood of heavy seed crops occurring more frequently than every 2 years is remote (Fechner 1964). Late spring freezing weather may also reduce cone production.

Heavy crops of cones were produced on blue spruce trees in the Fort Collins and Bennett Creek areas of northern Colorado in 1961 and 1964. Poor cone crops were produced in both locations in 1962 and 1963. Data obtained from the Colorado State University weather station show that the heavy cone crops were preceded by years during which the July was warmer and drier than normal.

Seedling Development

Seeds of blue spruce will germinate on a variety of media, although most natural reproduction takes place on exposed mineral soil with side shade and overhead light in the vicinity of seeding trees. Natural reproduction is probably scanty because the lightweight seeds are prevented from coming into contact with mineral soil by the dense herbaceous, grassy, and other groundcover vegetation that is usually abundant in the habitat of the species (Sudworth 1916).

Seeds of blue spruce were once thought to exhibit embryo dormancy. It is now known, however, that blue spruce seeds germinate in the laboratory promptly and completely without pretreatment, and under a wide range of temperatures, with or without light (Heit 1961).

Natural germination of blue spruce seed takes place the spring or summer following dispersal. In Arizona, where the spring and early summer is normally dry, blue spruce seeds germinate during the summer rainy season (early July); but if significant showers occur in June, some may start then (Jones 1974b). In most other parts of the blue spruce range, the spring and early summer months receive adequate moisture for seed germination.

In a spot seeding test in Arizona, soil in the seed spots was loosened with a mattock, and the seed was pressed in by foot June 27 to July 9. Germination was abundant; 36.6% of the seeds planted were known to have germinated, 64% of them within 3 to 4 weeks after planting. After 2 years, only two of the original 549 seedlings remained, and both of these were on one of the 300 seed spots planted (Jones 1974a). Some main known causes of mortality—frost heaving, predation, and burial from soil movement—could be identified; however, the causes of most mortality were unknown.

Although at the end of winter soils of the mixed conifer forest of the Southwest are wet, soil moisture deficits develop that are critical to initial seedling survival during spring and early summer drought periods of the southern part of the blue spruce range. Except on severe drought sites, these deficits usually do not kill seedlings established for two or more years. Within the blue spruce range, spring and early summer drought periods occur regularly only in the Southwest. Fall moisture deficits, which develop in most of the blue spruce range, are less detrimental to seedling establishment than spring and early summer deficits (Alexander 1974, Jones 1974b).

Blue spruce seedlings are more sensitive to day temperature between 55° and 88° F than to night temperature between 45° and 77° F (Tinus 1971). In one study, all trees died at 88° F within 20 weeks (Tinus 1974). In another study, under 24-hour light, seedlings grown at constant 54° and 64° F grew less than those at 77° F, and 88° F caused browning and death of many seedlings (Young and Hanover 1978).

The establishment of blue spruce seedlings under natural conditions is probably greatly affected by moisture availability and shading. Shading prolongs snow cover and soil moisture retention in late spring, thus providing improved conditions for seedling establishment (fig. 6).

Early growth of blue spruce seedlings is very slow. In a nursery study in Michigan, the tallest of 50 populations studied averaged 6.2 inches at 2 years (Hanover 1975). In another study in North Dakota, the tallest of seven sources was 23 inches, 5 years after outplanting at ages 3 to 5 years (Dawson and Rudolf 1966). Similarly, in a plantation in the southern part of the blue spruce range, trees were 19.1 to 23.3 inches tall after five growing seasons (Jones 1975).

Vegetative Reproduction

Natural vegetative reproduction of blue spruce has not been reported. The species does not sprout from the stump or root, but the development of epicormic branches on the trunk is common. However, grafting and air layering have been practiced successfully for many years to perpetuate desired horticultural varieties (Fröhlich 1957, Mergen 1958, Ravenstein 1957, Wells 1953). Similarly, success has also been achieved through the rooting of hardwood or greenwood stem cuttings, especially in sand-peat soil media, or hydroponically (Kirkpatrick 1940, Savella 1965, Sherwood 1968, White 1975).

Sapling and Pole Stage to Maturity

Growth and Yield

Blue spruce is a long-lived tree, living up to 600 years or more. Diameter growth is slow; trees 4 to 5 inches in diameter may be 125 to 135 years old, and trees 18 to 22 inches may be 275 to 350 years old (Sudworth 1916). The size-age relationship is dependent on site and stand density, however.

Few growth and yield data are available for blue spruce. In one study, in a mixed conifer forest in east-central Arizona, blue spruce was found to constitute a total of only 3.05 square feet per acre out of a total of 177.74 square feet. The 1,800-acre forest consisted of Douglas-fir (31.4%), quaking aspen (15.9%), white fir (14.5%), ponderosa pine (14.1%), Engelmann spruce (13.5%), southwestern white pine (5.6%), corkbark fir (*Abies lasiocarpa* var. *arizonica* (Merriam) Lemm.) (3.3%), and blue spruce (1.7%). In this study, the annual basal area growth for blue spruce was found to be 2.9% greater than that of any of the other species except corkbark fir, which was 3.7% per year (Embry and Gottfried 1971). The total basal area growth for blue spruce of 0.088 square feet per year was distributed as shown:

Size class *d.b.h.*	**Annual basal area increment** *square feet*	 *percent*
Sapling-small poles, 0.1 to 6.9 inches	0.45	48.8
Poles, 7.0 to 10.9 inches	0.63	18.3
Small sawtimber, 11.0 to 16.9 inches	1.03	18.3
Medium sawtimber, 17.0 to 22.9 inches	0.76	9.7
Large sawtimber, 23.0 inches and over	0.18	4.9
Total	3.05	100.0

Rooting Habit

Young seedlings of blue spruce are shallow-rooted, penetrating only about 2.5 inches during the first year (Jones 1973). Although blue spruce tissue is not damaged much by freezing (Pearson 1931), sequences of freezing and thawing, when the soil is wet and bare of protection from snow cover, often result in losses from frost-heaving (Alexander 1974).

Figure 6.—Blue spruce reproduction in north-central Colorado. Note coincidence of young trees and late spring snow pattern.

The root system of mature blue spruce trees is relatively shallow, compared with that of Douglas-fir and ponderosa pine, adapting it to the moist site on which it usually grows. In spite of the shallow root system, however, blue spruce is decidedly windfirm (Goor and Barney 1976, Preston 1940).

Reaction to Competition

Blue spruce is generally classed as intermediate in shade-tolerance, the middle of five tolerance categories for western conifers. It is less tolerant than subalpine fir, Engelmann spruce, and white fir; it is similar in tolerance to, or slightly more tolerant than, Douglas-fir; and it is more tolerant than southwestern white pine, ponderosa pine, lodgepole pine, Rocky Mountain juniper, quaking aspen, or its other moist-site hardwood associates (Baker 1949, Fechner 1980, Jones 1974b, Mauk and Henderson 1984).

The exact successional status of blue spruce depends upon the location within its geographic range and upon its immediate associates. For example, in the Southwest, blue spruce represents a topoedaphic climax, in which environmental factors compensate for one another (Daubenmire and Daubenmire 1968). Here blue spruce reproduces and is present in all sizes, along stream banks, in well-watered tributaries, on gentle lower slopes, and in forest borders of grassy meadows. On these sites, ponderosa pine and Douglas-fir may occur as a long-lived seral species, white fir and southwestern white pine may occur as minor seral species, and subalpine fir may be of accidental occurrence (Layser and Schubert 1979, Moir and Ludwig, 1979). Blue spruce appears to form climax stands with Engelmann spruce on slopes and in drainages at higher elevations and with Douglas-fir and white fir on lower slopes and north aspects at lower elevations (Alexander et al. 1984, Moir and Ludwig 1979). Blue spruce occurs occasionally as a minor seral species in white fir and subalpine fir-dominated forests on cooler sites (Layser and Schubert 1979), and it is a pioneer species on some wet sites (Dixon 1935).

On cool sites, a dense or moderately dense canopy favors regeneration of subalpine fir, blue spruce, white fir, and Engelmann spruce, to the exclusion of Douglas-fir. On warm sites, an open canopy favors ponderosa pine, whereas a moderate canopy favors Douglas-fir (Westveld 1939).

Blue spruce is most common on warm sites with abundant moisture. Yet, this species can withstand drought, growing on drier sites than any other spruces (Goor and Barney 1976). It can also withstand extremely low temperatures (−40° F), and it is more resistant to high insolation and frost damage than other associated species.

Damaging Agents

Windfall.—Blue spruce, though shallow-rooted, decidedly windfirm. Windfall is thus seldom a problem,

Insects.—Several insects are known to attack developing cones and seeds of blue spruce, but damage due to insects is not heavy. The spruce seed chalcid *Megastigmus piceae* Rohwer[4] is found throughout the range of the host (Furniss and Carolin 1977, Keen 1952, Keen 1958). Larvae of the spruce cone moth (*Laspeyresia youngana* (Kearf.)) bore food burrows through cone scales near the axis of the cones, destroying both scales and seeds. A single cone may contain one to five larvae. The growing larvae of the moth *Commophila fuscodorsama* (Kearf.) feed by boring irregular channels through cones, destroying scales and up to 10% of the seeds. Larvae of the spruce coneworm *Dioryctria reniculelloides* Mutuura and Munroe and the fir coneworm *Dioryctria abietvorella* (Groté)[5] mine young cones and feed on tender terminal growth and foliage (Hedlin et al. 1980; Keen 1952, 1958).

In addition to those attacking developing cones and seeds, other insects are occasionally damaging on blue spruce. The larvae of the western spruce budworm (*Choristoneura occidentalis* Freeman) feed on old needles in late April, and then enter the developing buds and defoliate new needles as they develop (Furniss and Carolin 1977, Leatherman 1979). Heavy, repeated attacks cause death of the tree.

The spruce needleminer (*Tanvia abolineana* Kearf.) is usually not a serious forest pest, although it may cause unsightly damage to ornamental spruce (Furniss and Carolin 1977, Hantsbarger and Brewer 1970, Keen 1952). Another needleminer (*Coleotechnites piceaella* (Kearf.)) is of less importance.

The Cooley spruce gall aphid (*Adelges cooleyi* (Gill.)) causes the formation of cone-shaped galls at the tips of the growing twigs, killing the current growth of the twigs. The attack is usually not severe enough to seriously affect large trees, but it may be of consequence on seedlings and saplings. Two other aphids, *Pineus pinifoliae* (Fitch) (pine leaf chermid) and *Pineus similis* (Gill.), also cause the formation of cone-shaped galls.

Other insects that attack blue spruce are the green spruce aphid (*Cinara fornacula* Hottes) and the related *Cinara coloradensis* (Gill.); these feed on terminal twigs, as does the white pine weevil (*Pissodes strobi* (Peck)). A twig beetle (*Pityophtorus* sp.) may attack injured trees, and the Engelmann spruce beetle (*Dendroctonus rufipennis* (Kirby)) also occurs on blue spruce. *Ips pilifrons* Swaine, which attacks recently downed trees, may deprive the Engelmann spruce beetle of favorable breeding places, thereby reducing the threat of a spruce beetle outbreak (Furniss and Carolin 1977). Secondary insects are *Dryocoetes affaber* Mannerheim and the four-eyed spruce bark beetle *Polygraphus rufipennis* (Kirby), ambrosia beetles *Gnathotrichus sulcatus* LeC. and *Trypodendron lineatum* (Olivier), and the golden buprested *Buprestis aurulenta* L., a flatheaded borer hat attacks the wood (Keen 1952).

Diseases.—The cone rust *Chrysomyxa pirolata* Wint.[6] infects the cones of blue spruce. However, it causes only minor reduction in seed produced, though malformation of the cones may interfere with seed dispersal. Seed viability in rust-infected cones may be reduced, but only a few seeds are totally destroyed (Hepting 1971, Nelson and Krebill 1970).

A variety of diseases also attack seedlings, leaves, stems, and roots of blue spruce. Damping-off, caused by *Phytophora cinnamomi* Rands, kills new seedlings, as does the cylindrocladium root rot, caused by *Cylindrocladium scoparium* Morgan (Cordell and Skilling 1975, Hepting 1971). Nematodes of at least seven different genera may cause reduced growth of blue spruce seedlings in nurseries (Ferris and Leiser 1965); they reduce root growth (Griffin and Epstein 1964). Low seedling vigor is also caused by the root lesion nematode *Pratylenchus penetrans* Cobb (Hepting 1971). Snow molds, which grow at low temperatures, may cause nursery losses during seasons of heavy snow (Skilling 1975).

Three species of *Chrysomyxa* cause needle rusts on blue spruce in the United States; they may cause moderate amounts of shedding of new needles (Hepting 1971). Another needle cast fungus, *Rhizosphaera kalkhoffii* Bub., was first reported as occurring on eastern species of spruce and in Christmas tree plantations of blue spruce in the Middle West and the East (Nicholls et al. 1974, Waterman 1947). This disease was first reported on blue spruce in its native range in Arizona (Hawksworth and Staley 1968). In natural stands, this needle cast is not associated with the serious damage that it inflicts when the species is grown far from its native habitat, however.

Chrysomyxa arctostaphyli Diet. causes the perennial yellow witches'-broom on blue spruce branches. Abundant pycnia, produced on the needles of the broom in late spring, give off a distinctive, strong, foul odor. Spikelike tops and dead branches are commonly associated with this disease. Seldom, however, do more than 25% of the trees bear brooms. *Arctostaphylos uva-ursi* (L.) Spreng, the common bearberry or kinnikinnick, is the host of Stage III of the fungus causing yellow witches'-broom (Peterson 1969).

Armillaria mellea Vahl. ex Fr. and *Polyporus tomentosus* Fr. cause root rot in blue spruce. However, although both fungi are common, damage is slight. *Fomes pini* (Thore) Lloyd, which causes red heart, is the principal heartrot fungus on blue spruce. It is not serious, however, because the trees are usually old before the rot becomes a factor. Other heartrots, including *Fomes pinicola* (Schwartz ex Fr.) Cke., *Polyporus borealis* Fr., and *Polyporus caesius* Schrad. also attack blue spruce (Hepting 1971).

SPECIAL USES

Shortly after the species was first discovered in 1861, early writers described blue spruce as "a finely-shaped

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[4] Scientific and common names of insects used in this report are in accord with Furniss and Carolin (1977).

[5] During a 1984 controlled pollination study on the Colorado State University campus, approximately 10% of young cones were infested with larvae of the fir coneworm. The larvae destroyed ovules in approximately the lower one-half of the infested cones.

[6] Scientific and common names of diseases used in this report are in accord with Hepting (1971).

tree" (Parry and Engelmann 1862) and "the most beautiful species of conifer" (André 1876), alluding to the symmetrical, pyramidal form and the glaucous, bluish or silvery-gray foliage that some trees display. The needle coloration, caused by the presence of surface waxes (Reicosky and Hanover 1976), apparently intensifies with tree age (Cram 1983b, 1984a). These traits of symmetry and blue or silver-gray cast, so common in horticultural plantings, are only occasionally found in nature. In natural stands, trees with similar color tend to occur in small, local populations, a situation that suggests genetic control of the color trait.

When young, blue spruce trees usually exhibit a pronounced layering of stiff branches, which gives it the distinct pyramidal form; when the trees become older, the branches begin to droop and the crown becomes open and irregular. Boles of blue spruce are usually highly tapered, and the epicormic shoots, which commonly develop, may give the tree a ragged appearance.

At least 38 cultivars of blue spruce have been named, based primarily on leaf coloration and crown form. Some of the more common cultivars are listed in table 2. Its leaf coloration, coupled with symmetrical crown form, makes blue spruce an exceptionally attractive Christmas tree. Christmas tree plantations of this species have been established in many eastern states (Goodno and Quink 1975, Nicholls et al. 1974).

Because of its pyramidal forms, its resistance to winter temperatures, and its relative resistance to drought stress, blue spruce is often used as a windbreak tree. It is especially popular for this use in Canada (Cram 1966), and it has been widely planted in Russia.

Blue spruce, primarily a streambottom tree, provides streambank protection. Furthermore, it enhances the esthetic value of the streambottom landscape, where it is frequently in sight of travelers on highways that follow the streamcourses. Conversely, the streambottom habitats often support a lush herbaceous vegetation and are often disturbed by grazing and fire (Alexander et al. 1984, Hoffman and Alexander 1983).

GENETICS

Population Differences

In a study of seven provenances from Arizona, Colorado, Utah, and Wyoming, grown in North Dakota, 5-year survival varied from 22% for the Targhee National Forest, Idaho, source to 96% for an Ashley National Forest, Utah, source (Dawson and Rudolph 1966). In the same study, height differed significantly among the sources; interestingly, one of the two sources from Ashley National Forest was the tallest (1.88 feet) and the other, the shortest (1.23 feet). No latitudinal nor altitudinal pattern of survival, growth, or frost resistance seemed apparent.

In an East Lansing, Mich., nursery study of progenies from 50 populations of blue spruce throughout the native range of the species, from Montana to Arizona,

Table 2.—Some cultivated varieties of blue spruce (*Picea pungens* Engelm.).

Cultivar	Characteristics	Authorities[1]
'Argentea' Rosenthal	Silvery white	B & B, dO & B, W
'Aurea' Niemitz	Golden yellow	B & B, dO & B, W
'Bakeri' Bailey	Deep bluish white, long-leaved	B & B, dO & B, W
'Caerulea' Beissner	Bluish white	B & B, W
'Compacta' Rehder	Dwarf, compact, densely flat-topped	B, dO & B, W
'Glauca' Beissner	Bluish green; collective name for all glaucous-leaved cultivars	B & B, dO & B, W
'Glauca Pendula' Koster ex Beissner	Pendulous, bluish leaves, strongly sickle-shaped	B, dO & B
'Hoopsii' Hoops ex F. J. Grootend.	Dense, pyramidal; leaves very silvery	B & B, dO & B
'Hunnewelliana' Hornibr.	Dwarf, dense, pyramidal; leaves pale green	B & B, dO & B, W
'Koster' Boom	Pyramidal, pendulous-branched, with main branches almost horizontal; leaves bluish white to silvery white	B & B, dO & B, W
'Moerheimi' Ruys	Pyramidal, slender, dense, compact; leaves deep blue	B & B, dO & B, W
'Thomsen' Thomsen	Pyramidal; leaves whitish blue to silvery blue; long	B & B, dO & B
'Viridis' Regel	Dull green	B, dO & B, W

[1] *B = Bailey (1929–1930).*
B & B = Bailey and Bailey (1976).
dO & B = den Ouden and Boom (1965).
W = Wyman (1961).

year-old seedlings from Colorado, New Mexico, and rizona grew more rapidly than those from Utah, yoming, or Montana. The average heights of the 10 llest populations ranged from 7.4 to 6.3 inches; all ere either from Colorado, New Mexico, or Arizona anover 1975).

Variation in foliage color is apparently under strong enetic control, although the mechanism of inheritance not yet known. Because some inconsistency in blue olor from any one geographic source exists, some ariation in the blue color characteristic is to be ex-ected from seed-produced trees (Heit 1968). However, year-old progenies from Arizona and New Mexico ed sources showed a much higher incidence of "blue-ess" than those from other areas, when grown in a ichigan nursery (Hanover 1975).

Significant variation exists between populations in e terpene concentration derived from cortical tissue. ive populations, each consisting of ten selected seed ees, differed significantly in the concentration of each eight monoterpenes in a Michigan study. Although the tal percentages of the eight monoterpenes were milar among the populations, the Utah, Colorado, and yoming populations were distinct from the New Mex-o and Arizona populations, because of similarity in ercentages of specific monoterpenes. For example, the erage percentage of α-pinene was 14.3 for the three orthern populations and 8.5 for the two southern ones, hereas β-phellandrene averaged 0.58% for the north-n populations and 0.89% for the southern populations anover 1974).

These studies suggest that genetic variation in tural populations of blue spruce does not conform to a inal pattern. Rather, the pattern appears to be eco-pic, and considerable stand-to-stand variation and dividual-tree variation also exists.

Hybrids

From studies of morphological features in 21 natural pulations of blue spruce, Engelmann spruce, and ixed populations of the two species, it was concluded at blue spruce and Engelmann spruce do not hybridize nature, although no morphological character ab-lutely separating the two species was found (Dauben-ire 1972). Considerable overlap in cone size between ese two species has also been found; Engelmann ruce varied from 1.1 to 2.3 inches and blue spruce ried from 1.8 to 4.2 inches in 11 populations growing thin a radius of about 15 miles in northern Colorado unsch 1975). In a study of cone and seed characters in populations of blue spruce and Engelmann spruce, e two species were often indistinguishable (Hanover 75).

n an earlier study of controlled crosses between blue ruce and Engelmann spruce, up to 1% to 2% sound ed set was obtained, when Engelmann spruce was the nale parent (Fechner and Clark 1969). In another idy, the reciprocal cross was also successful. Only oc-sional embryos developed following crosses between the two species, but, more frequently, reproductive failure occurred prior to embryo formation (Kossuth and Fechner 1973).

Reciprocal, controlled pollinations between blue spruce and white spruce (*Picea glauca* (Moench) Voss) have also been successful, as verified by measurement of germination rate, needle length, and concentration of 3-carene in the hybrid progeny (Hanover and Wilkinson 1969).

These research results suggest that although hybridization between blue spruce and Engelmann spruce is not common in nature, barriers between the two species are not absolute. Furthermore, in a report of the occurrence of blue spruce in northern Montana, various intergrades between blue spruce, white spruce, and Engelmann spruce were reported for that area (Strong 1978). That, in addition to the work of Hanover and Wilkinson (1969), indicates that hybridization barriers also are not absolute between blue spruce and white spruce.

Information on inheritance patterns for some characteristics of blue spruce, though somewhat inconclusive, is provided by the results of half-sib and full-sib progeny studies involving that species. For example, Cram (1983b, 1984a) studied inheritance of needle coloration, using a qualitative rating scale of one (green) to four (silvery blue) for comparison. He found that although the proportion of blue seedlings was not significantly related to the blue color ratings of their open-pollinated parents, the needle-color ratings of 10-year-old progeny were related to those of their self-pollinated parents ($r = 0.83$). One selfed tree produced 94% blue progeny.

As is true for certain other coniferous species, albinism in blue spruce is apparently controlled by a single gene. Cram (1983a) found that the proportion of normal (green) to albino seedlings derived from self-pollinated seeds of two different trees produced a good fit to a 3:1 ratio, suggesting heterozygosity for a simple lethal factor.

In Michigan studies, hybrid progeny from crosses between white spruce and blue spruce showed a slight, but nonsignificant, increase in germination rate over the parental half-sib progeny, and at 42 weeks needle length was intermediate between those of the parental progeny. Although the hybrid progeny as a group displayed intermediacy in 3-carene biosynthesis ability between the two parents, individual-tree values showed genetic segregation in the open-pollinated (half-sib) blue spruce progeny and uniformity in the open-pollinated (half-sib) white spruce progeny (Hanover and Wilkinson 1969). Yet, the range of values for 3-carene concentration in these hybrid progeny conformed to frequencies expected from a mating of a homozygous recessive white spruce parent to a heterozygous blue spruce parent, suggesting that inheritance of 3-carene biosynthesis ability is controlled by a single pair of alleles, as had been shown for western white pine (*Pinus monticola* Dougl. ex D. Don) (Hanover 1966). However, when natural populations of blue spruce were studied for this characteristic, allele frequencies for the 3-carene gene did not conform to expected values in Colorado and New

Mexico populations, although they did conform to expected single-gene frequencies in the Utah, Arizona, and Wyoming populations (Hanover 1974). These apparent discrepancies could be artifacts of sample size or other unknown factors.

Fechner and Clark (1969) found that whereas the initiation date of germination of hybrid seed was intermediate between parental (half-sib) seed of blue spruce and Engelmann spruce, cotyledon number, mean day of total germination, and hypocotyl color were similar to those of the female parent. From their studies of controlled crosses among white spruce, blue spruce, and red spruce (*Picea rubens* Sarg.), Bongarten and Hanover (1982) reported that F_2 progeny of white spruce x blue spruce crosses were much stunted in height and in needle length. Further results of their findings are summarized in table 3.

In summary, it would appear that for most needle, chemical synthesis, and germination characteristics that have been studied in blue spruce, the gene action is quantitative. Exceptions to this seem manifest in the biosynthetic ability of 3-carene and in the production of albino seedlings, which may be single-gene controlled, and cotyledon number, hypocotyl color, and mean germination date, which may be under strong maternal influence in that species.

Table 3.—Summary of inheritance of various traits from crosses among red, white, and blue spruces. Adapted from Bongarten and Hanover 1982.

Spruce combination	Character response
(White x blue) x white (backcross)	- Similar to white spruce in all measured characters.
(White x blue) x blue (backcross)	- Similar to blue in 6-month height, needle curvature, and 3-carene concentration. - Similar to white in needle serrations. - Intermediate in β-pinene concentration.
(White x blue) x red (trihybrid)	- Similar to red in needle serrations, limonene concentration, and needle curvature. - Similar to white x red in needle color. - Similar to white x blue in 3-carene and β-pinene concentrations.

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APPENDIX

Habitat types in which *Picea pungens* is a major climax, co-climax, minor climax, or major seral species

Habitat type	Location	Site	Successional status *P. pungens*	Principal tree associates	Principal understory species	Authority
			Picea pungens series			
Picea pungens/ *Amelanchier alnifolia* H.T.	Mountains of west-central Colorado	Warm moist	Climax	*Abies lasiocarpa* *Pseudotsuga menziesii* *Populus angustifolia*	*A. alnifolia* *Cornus stolonifera* *Carex geyeri* *Swida servicea*	Hess and Wasser[1] 1982 Komarkova 1984[2]
Picea pungens/ *Arctostaphylos uva-ursi* H.T. [*P. pungens-Pseudotsuga menziesii*/*A. uva-ursi* H.T.]	San Juan Mountains, Colorado	Warm dry	Co-climax with *P. menziesii* *A. concolor*	*Abies concolor* *P. menziesii* *Pinus ponderosa* *Populus tremuloides* *Pinus flexilis*	*A. uva-ursi* *Juniperus communis* *Festuca arizonica* *Fragaria ovalis*	DeVelice et al. 1984[3] Moir and Ludwig 1979
Picea pungens/ *Berberis repens* H.T.	Mountains of Utah	Cool dry	Climax	*P. menziesii* (minor climax) *P. tremuloides* *Pinus contorta* *P. ponderosa* *Juniperus scopulorum* *P. flexilis*	*B. repens* *J. communis* *Pachistima myrsinites* *Aquilegia coerulea* *Pyrola secunda* *Ribes montigenum* *Symphoricarpos oreophilus*	Mauk and Henderson 1984 Pfister 1972 Youngblood 1984[4]
Picea pungens/ *Cornus stolinifera* H.T.	Mountains of north-central and northwestern New Mexico	Warm moist	Co-climax with *P. menziesii*	*P. menziesii* *P. tremuloides* *Juniperus* spp.	*C. stolinifera* *B. repens* *P. myrsinites* *Carex foenea*	Alexander et al. 1984b[5]
Picea pungens/ *Juniperus communis* H.T.	Mountains of central Utah	Cool dry	Climax	*P. menziesii* *P. tremuloides* *P. ponderosa* *P. flexilis* *J. scopulorum*	*J. communis* *A. uva-ursi* *S. oreophilus* *B. repens* *P. myrsinites*	Youngblood 1984[4]
Picea pungens/ *Linnaea borealis* H.T. [*P. pungens-Pseudotsuga menziesii*/*L. borealis* H.T.]	Mountains of southern Colorado and northern New Mexico	Cool well-drained	Co-climax with *P. menziesii*	*P. menziesii* *A. concolor* *P. tremuloides* *P. flexilis* *A. lasiocarpa* *Picea engelmannii*	*L. borealis* *P. myrsinites* *Vaccinium myrtillus* *Rubus parviflorus* *A. uva-ursi*	DeVelice et al. 1984[3] Moir and Ludwig 1979
Picea pungens/ *Agropyron spicatum* H.T.	Uinta Mountains, Utah	Warm dry	Climax	*P. menziesii* (minor climax) *P. tremuloides* *P. ponderosa* *P. contorta* *P. flexilis* *J. scopulorum*	*A. spicatum* *B. repens* *J. communis* *P. myrsinites*	Mauk and Henderson 1984
Picea pungens/ *Festuca arizonica* H.T.	Mountains of northern New Mexico and southern and western Colorado	Warm dry	Co-climax with *P. menziesii*	*A. concolor* *P. menziesii* *P. ponderosa* *P. tremuloides*	*F. arizonica* *C. foenea* *Erigeron* spp. *Fragaria* spp.	DeVelice et al. 1984[3] Fitzhugh, et al. 1984[6] Komarkova 1984[2]
Picea pungens/ *Poa pratensis* H.T.	Mountains of New Mexico	Warm to cool moist	Climax	*P. menziesii* *P. ponderosa* *P. tremuloides* *A. concolor* *Pinus strobiformis*	*P. pratensis* *Erigeron superbus* *E. eximius*) *Geranium richardsonii* *Fragaria virginiana*	Fitzhugh et al. 1984[6] Moir and Ludwig 1979
Picea pungens/ *Poa* sp. H.T.	Streambanks and foothills of north-central Colorado	Warm moist	Climax	Usually pure stands; occasionally contains *P. menziesii* *P. tremuloides*	*Poa* spp. *A. alnifolia* *Rosa* spp. *Salix* spp.	Hoffman and Alexander 1983
Picea pungens/ *Carex foenea* H.T.	White Mountains and Kaibab Plateau, Arizona; mountains of northern New Mexico	Warm to cool moist	Co-climax with *P. menziesii*	*P. menziesii* *P. ponderosa* *A. concolor* *P. tremuloides* *P. strobiformis* *P. engelmannii*	*C. foenea* *F. arizonica* *Muhlenbergia montana* *Bromus ciliatus* *Fragaria* spp. *Festuca* spp. *B. repens*	Alexander et al. 1984b[5] DeVelice et al. 1984[3] Fitzhugh et al. 1984[6] Moir and Ludwig 1979

APPENDIX—Continued

Habitat type	Location	Site	Successional status *P. pungens*	Principal tree associates	Principal understory species	Authority
Picea pungens/ *Arnica cordifolia* H.T.	Front Range, north-central Colorado	Cool moist	Climax	*P. menziesii* *P. tremuloides*	*A. cordifolia* *Smilacina stellata* *J. communis* *Calamagrostis canadensis*	Hess 1981
Picea pungens/ *Equisetum arvense* H.T.	Mountains of southern Utah	Warm to cool wet	Climax	*P. engelmannii* *P. tremuloides* *P. menziesii*	*E. arvense* *G. richardsonii* *Thalictrum fendleri* *Osmorphiza chilensis*	Youngblood 1984[4]
Picea pungens/ *Erigeron eximus* H.T. [*P. pungens-Picea engelmannii*/ *E. superbus* H.T.]	Mountains of northern New Mexico and southern Colorado	Cool dry	Co-climax with *A. concolor* *P. menziesii* *P. engelmannii*	*A. concolor* *P. menziesii* *P. engelmannii* *P. flexilis* *P. tremuloides* *A. lasiocarpa* *P. ponderosa* *P. strobiformis*	*E. superbus* (*E. eximius*) *C. foenea* *G. richardsonii* *T. fendleri* *F. arizonica* *F. virginiana*	DeVelice et al. 1984[3] Fitzhugh et al. 1984[6] Moir and Ludwig 1979
Picea pungens/ *Fragaria ovalis* H.T. [*P. pungens-Pseudotsuga menziesii*/*Valeriana acutiloba* H.T.]	Mountains of New Mexico and eastern Arizona	Cool moist	Co-climax with *P. menziesii*	*P. menziesii* *A. concolor* *P. strobiformis* *P. ponderosa* *P. tremuloides* *P. engelmannii* *A. lasiocarpa*	*F. ovalis* *V. acutiloba* *C. foenea* *F. arizonica* *Erodium circutarium* *E. superbus* *Artemisia dracunculus*	Alexander et al. 1984a Fitzhugh et al. 1984[6] Moir and Ludwig 1979
Picea pungens/*Senecio cardamine* H.T. [*P. pungens-Picea engelmannii*/*S. cardamine* H.T.]	White Mountains, Arizona	Cool moist	Co-climax with *P. engelmannii* *A. lasiocarpa*	*P. engelmannii* *A. lasiocarpa* *A. concolor* *P. ponderosa* *P. menziesii* *P. tremuloides* *P. strobiformis*	*S. cardamine* *Pteridium aquilinum* *Helenium hoopesii* *Viola canadensis*	Fitzhugh et al. 1984[6] Moir and Ludwig 1979
***Pseudotsuga menziesii* series**						
Pseudotsuga menziesii/ *Muhlenbergia virescens* H.T.	Mountains of southwestern New Mexico	Warm dry	Minor climax to *P. menziesii* *P. ponderosa*	*P. menziesii* *P. ponderosa* *P. strobiformis* *P. tremuloides*	*M. virescens* *Quercus gambelii*	Fitzhugh et al. 1984[6]
Pseudotsuga menziesii/ Scree H.T. [*P. menziesii*/ *Physocarpus monogynus* H.T.]	Mountains of New Mexico	Warm well-drained	Minor climax to *P. menziesii*	*P. menziesii* *P. tremuloides* *A. concolor*	*P. monogynus* *B. repens* *P. pratensis*	Moir and Ludwig 1979
***Abies concolor* series**						
Abies concolor/ *Acer glabrum* H.T.	Mountains of northern New Mexico and southern Colorado	Warm moist to well-drained	Minor climax to *A. concolor* *P. menziesii*	*A. concolor* *P. menziesii* *P. engelmannii* *P. tremuloides*	*A. glabrum* *A. alnifolia* *B. repens* *P. myrsinites*	DeVelice et al. 1984[3]
Abies concolor/ *Arctosaphylos uva-ursi* H.T.	Mountains of southern Utah	Warm dry	Seral to *A. concolor*	*A. concolor* *P. menziesii* *P. flexilis* *P. ponderosa* *J. scopulorum*	*A. patula* *S. oreophilus* *J. communis* *B. repens*	Youngblood 1984[4]
Abies concolor/ *Berberis repens* H.T.	Mountains of central and southern Utah	Warm dry	Seral to *A. concolor*	*A. concolor* *P. menziesii* *P. ponderosa* *P. tremuloides* *P. flexilis*	*B. repens* *J. communis* *S. oreophilus* *Rosa woodsii* *P. myrsinites*	Youngblood 1984[4]
Abies concolor/ *Juniperus communis* H.T.	Mountains of southern Utah	Warm dry	Seral to *A. concolor*	*A. concolor* *P. menziesii* *P. tremuloides* *P. flexilis*	*J. communis* *R. woodsii* *S. oreophilus* *B. repens*	Youngblood 1984[4]
Abies concolor/ *Vaccinium myrtillus* H.T.	Mountains of northern New Mexico and southern Colorado	Cool dry	Minor climax to *A. concolor* *P. menziesii*	*A. concolor* *P. menziesii* *A. lasiocarpa* *P. engelmannii* *P. tremuloides*	*V. myrtillus* *A. glabrum* *A. uva-ursi* *P. myrsinites* *R. parviflorus*	DeVelice et al. 1984[3]

APPENDIX—Continued

Habitat type	Location	Site	Successional status *P. pungens*	Principal tree associates	Principal understory species	Authority
Abies concolor/ Erigeron eximius H.T.	Mountains of northern New Mexico	Cool moist	Minor climax to *A. concolor* *P. menziesii*	*A. concolor* *P. menziesii* *P. engelmannii* *P. tremuloides* *P. ponderosa*	*E. eximius* (*E. superbus*) *C. foenea* *Lathyrus* sp. *Fragaria* sp.	DeVelice et al. 1984[3]
Abies concolor/ Sparse H.T.	Mountains of northern New Mexico and southern Colorado	Warm dry	Minor climax to *A. concolor* *P. menziesii*	*A. concolor* *P. menziesii* *P. tremuloides* *P. ponderosa* *P. strobiformis*	*S. oreophilus* *Q. gambelii* *B. repens* *Robinia neomexicana*	DeVelice et al. 1984[3] Moir and Ludwig 1979
			***Picea engelmannii* series**			
Picea engelmannii/ Carex disperma H.T.	Mountains of northwestern Wyoming and east-central Idaho	Cool moist	Occasional co-climax with *P. engelmannii*	*P. engelmannii* *P. contorta* *A. lasiocarpa*	*C. disperma*	Steele et al. 1983
Picea engelmannii/ Equisetum arvense H.T.	Mountains of northwestern Wyoming and east-central Idaho	Warm wet	Occasional co-climax with *P. engelmannii*	*P. engelmannii* *P. contorta* *A. lasiocarpa*	*E. arvense* *Streptopus amplexifolius* *Senecio triangularis* *Luzula parviflora*	Steele et al. 1983
Picea engelmannii/ Galium triflorum H.T.	Mountains of northwestern Wyoming	Cool moist	Occasional co-climax with *P. engelmannii*	*P. engelmannii* *P. contorta* *P. menziesii*	*G. triflorum* *Actaea rubra* *S. stellata*	Steele et al. 1983
Picea engelmannii/ Senecio cardamine H.T.	Blue Mountains, Arizona	Cool moist	Seral to *P. engelmannii*	*P. engelmannii* *P. menziesii* *A. lasiocarpa* *A. concolor* *P. ponderosa* *P. strobiformis* *P. tremuloides*	*S. cardamine* *F. ovalis* *G. richardsonii* *V. canadensis*	Fitzhugh et al. 1984[6]
			***Abies lasiocarpa* series**			
Abies lasiocarpa/ Acer glabrum H.T.	Mountains of central and southern Utah	Warm moist	Seral to *A. lasiocarpa*	*A. lasiocarpa* *A. concolor* *A. menziesii* *P. engelmannii* *P. flexilis* *P. tremuloides*	*A. glabrum* *A. alnifolia* *B. repens* *S. oreophilus* *O. chinensis* *T. fendleri*	Youngblood 1984
Abies lasiocarpa/ Berberis repens H.T.	Mountains of northern Utah	Warm well-drained	Seral to *A. lasiocarpa*	*A. lasiocarpa* *P. engelmannii* *P. contorta* *P. menziesii* *A. concolor* *P. flexilis* *P. tremuloides*	*B. repens* *R. montigenum* *J. communis* *C. geyeri* *S. oreophilus* *R. woodsii* *P. myrsinites*	Mauk and Henderson 1984 Youngblood 1984
Abies lasiocarpa/ Juniperus communis H.T.	Mountains of southern Utah	Warm dry Cool dry	Seral to *A. lasiocarpa*	*A. lasiocarpa* *P. engelmannii* *P. tremuloides* *P. menziesii* *P. ponderosa* *A. conolor*	*J. communis* *R. woodsii* *S. oreophilus* *B. repens*	Youngblood 1984
Abies lasiocarpa/ Vaccinium myrtillus H.T. [*A. lasiocarpa/V. myrtillus- Linnea borealis* H.T.] [*A. lasiocarpa/Vaccinium scoparium-L. borealis* H.T.]	Mountains of northern New Mexico and southern Colorado	Cool moist well-drained	Seral to *A. lasiocarpa* *P. engelmannii*	*A. lasiocarpa* *P. engelmannii* *A. concolor* *P. tremuloides* *P. menziesii*	*V. myrtillus* *V. scoparium* *L. borealis* *E. superbus* (*E. eximius*) *F. virginiana* *P. myrsinites* *V. candensis*	DeVelice et al. 1984[3] Moir and Ludwig 1979
A. lasiocarpa/ Calamagrostis canadensis H.T.	Mountains of northern Utah	Warm wet	Seral to *A. lasiocarpa*	*A. lasiocarpa* *P. engelmannii* *P. contorta* *P. tremuloides*	*C. canadensis* *L. borealis* *E. arvense* *G. trifolium*	Mauk and Henderson 1984
Abies lasiocarpa/ Actaea rubra H.T.	Mountains of northwestern Wyoming, and southern Idaho	Warm moist	Seral to *A. lasiocarpa*	*A. lasiocarpa* *P. engelmannii* *P. menziesii* *P. contorta*	*A. rubra* *Lonicera utahensis* *Vaccinium globulare* *A. glabrum*	Steele et al. 1983

APPENDIX—Continued

Habitat type	**Location**	**Site**	**Successional status *P. pungens***	**Principal tree associates**	**Principal understory species**	**Authority**
Abies lasiocarpa/ Erigeron eximius H.T. [*A. lasiocarpa/ E. superbus* H.T.]	Mountains of Arizona and New Mexico; southern Colorado	Cool dry	Seral to *A. lasiocarpa* *P. engelmannii*	*A. lasiocarpa* *P. engelmannii* *A. concolor* *P. tremuloides* *P. menziesii* *P. strobiformis*	*E. superbus* (*E. eximius*) *B. ciliatus* *F. virginiana* *Lonicera involucrata* *A. cordifolia*	DeVelice et al. 1984[3] Moir and Ludwig 1979
			Riparian series			
Alnus tenuifolia/ Equisetum arvense H.T.	Streambanks, montane zone, north-central Colorado	Warm moist to wet	Minor climax to *A. tenuifolia*	*A. tenuifolia* *Betula occidentalis* *P. ponderosa* *P. tremuloides*	*Salix* spp. *Rosa woodsii* *E. arvense* *A. glabrum*	Hess 1981
Populus angustifolia/ Salix exigua H.T.	Streambanks and foothills of north-central Colorado	Warm moist to wet	Minor climax to *P. angustifolia*	*P. tremuloides* *P. angustifolia* *P. ponderosa* *P. menziesii* *J. scopulorium*	*Salix* spp. *A. glabrum*	Hess 1981

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[4] *Youngblood, Andrew P. 1984. Coniferous forest habitat types of central and southern Utah. USDA Forest Service. Draft of manuscript in preparation. Intermountain Forest and Range Experiment Station, Ogden, Utah.*

[5] *Alexander, Billy G., Jr., E. Lee Fitzhugh, Frank Ronco, Jr., and John A. Ludwig. 1984. A classification of forest habitat types on the Cibola National Forest, New Mexico. USDA Forest Service. Draft of manuscript in preparation. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo.*

[6] *Fitzhugh, E. Lee, William H. Moir, John A. Ludwig, and Frank Ronco, Jr. 1984. Forest habitat types in the Apache, Gila, and part of the Cibola National Forests. USDA Forest Service. Draft of manuscript in preparation. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo.*

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U.S. Department of Agriculture
Forest Service

Rocky Mountain Forest and Range Experiment Station

Rocky Mountains

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The Rocky Mountain Station is one of eight regional experiment stations, plus the Forest Products Laboratory and the Washington Office Staff, that make up the Forest Service research organization.

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Research programs at the Rocky Mountain Station are coordinated with area universities and with other institutions. Many studies are conducted on a cooperative basis to accelerate solutions to problems involving range, water, wildlife and fish habitat, human and community development, timber, recreation, protection, and multiresource evaluation.

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United States
Department of
Agriculture

Forest Service

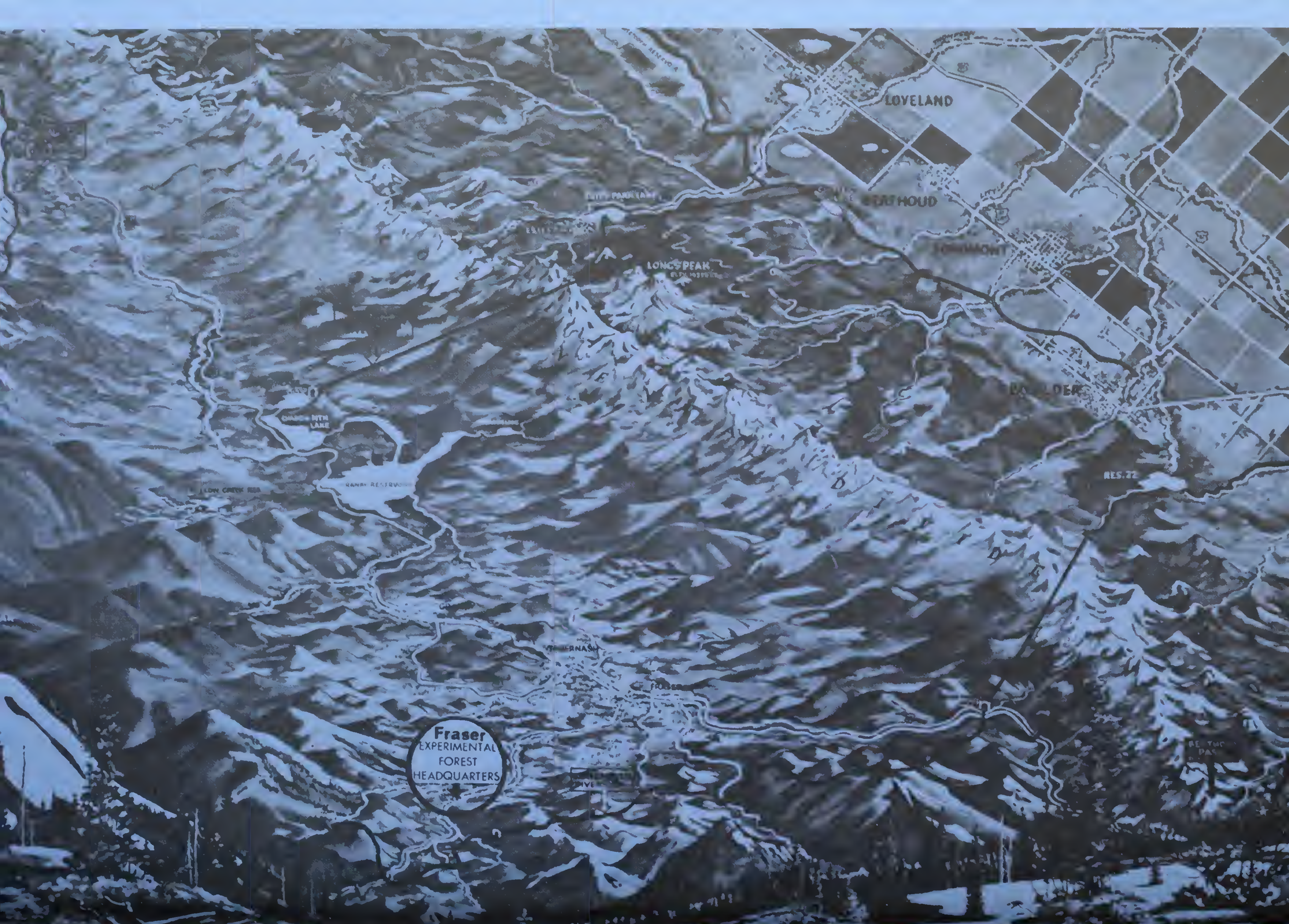
**Rocky Mountain
Forest and Range
Experiment Station**

Fort Collins,
Colorado 80526

**General Technical
Report RM-118**

The Fraser Experimental Forest, Colorado: Research Program and Published Research 1937–1985

Robert R. Alexander, Charles A. Troendle, Merrill R. Kaufmann,
Wayne D. Shepperd, Glenn L. Crouch, and Ross K. Watkins


LOVELAND
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HEADQUARTERS

Abstract

This report provides an overview of the research done on the Fraser Experimental Forest. It replaces GTR's RM–40 and RM–40A by Robert R. Alexander and Ross K. Watkins, published in 1977 and 1978. Included are descriptions of physical features and resources, highlights of past and current research, and the publications derived from that research.

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The Fraser Experimental Forest, Colorado: Research Program and Published Research 1937–1985

Robert R. Alexander, Chief Silviculturist and Project Leader
Charles A. Troendle, Principal Hydrologist
Merrill R. Kaufmann, Principal Plant Physiologist
Wayne D. Shepperd, Silviculturist
Glenn L. Crouch, Principal Wildlife Biologist
and
Ross K. Watkins, Forestry Research Technician
Rocky Mountain Forest and Range Experiment Station[1]

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[1] *Headquarters is in Fort Collins, in cooperation with Colorado State University.*

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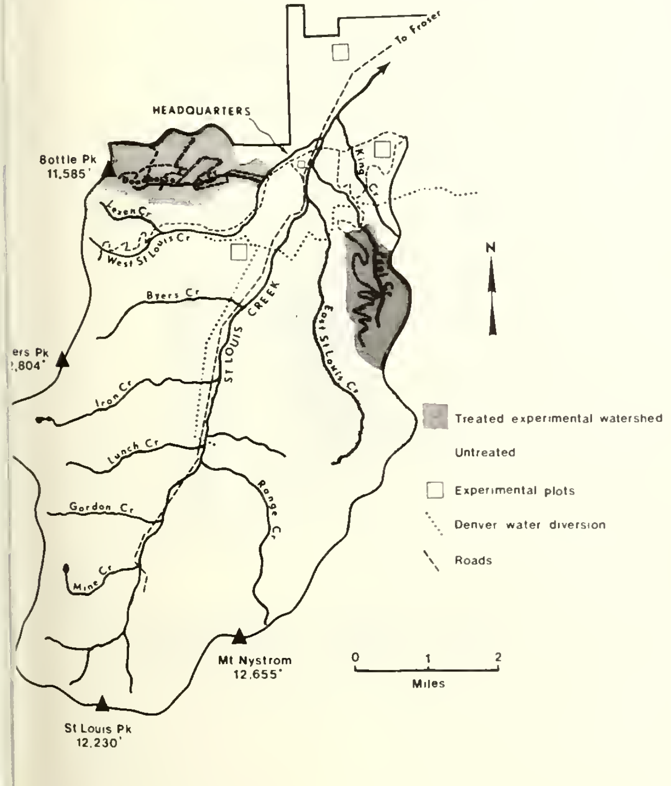
The Fraser Experimental Forest, Colorado: Research Program and Published Research 1937–1985

Robert R. Alexander, Charles A. Troendle, Merrill R. Kaufmann,
Wayne D. Shepperd, Glenn L. Crouch, and Ross K. Watkins

The Fraser Experimental Forest was established in 937 in the heart of the central Rocky Mountains. This 6-square-mile outdoor research laboratory maintained y the Rocky Mountain Forest and Range Experiment tation is located 50 air miles west of Denver, Colo. The ocation is well suited to the study of timber, water, and ildlife management, and their integration in high levation subalpine coniferous forests.

In the West, water is vital to life and development. St. ouis Creek, the main drainage on the Fraser Experiental Forest, is typical of headwater streams that are e source of 85% of the annual yield of about 20 million cre-feet of water from the Colorado Rockies.



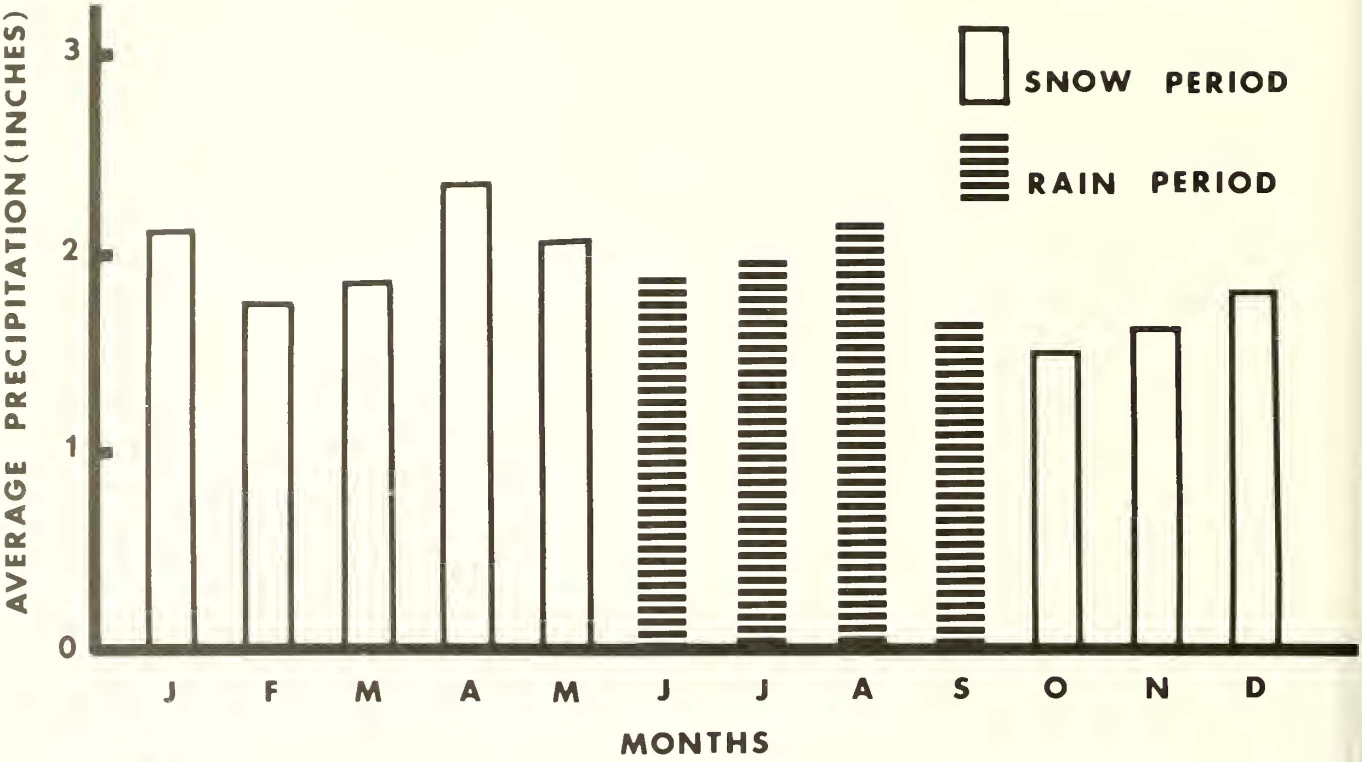
The relationship between water sources in high elevation forests, extensive transmountain diversion, and domestic, industrial, and agricultural users is shown in the schematic view of the Fraser Experimental Forest and its surrounding country on the inside front cover. The Colorado-Big Thompson transmountain diversion taps the headwaters of the Colorado River and brings water through the 13-mile-long Alva Adams Tunnel to users on the east side of the Continental Divide. The Fraser River transmountain diversion, constructed by the City of Denver to bring water from St. Louis and Vasquez Creeks, crosses the Continental Divide through the pioneer bore of the 6-mile-long Moffat Tunnel.

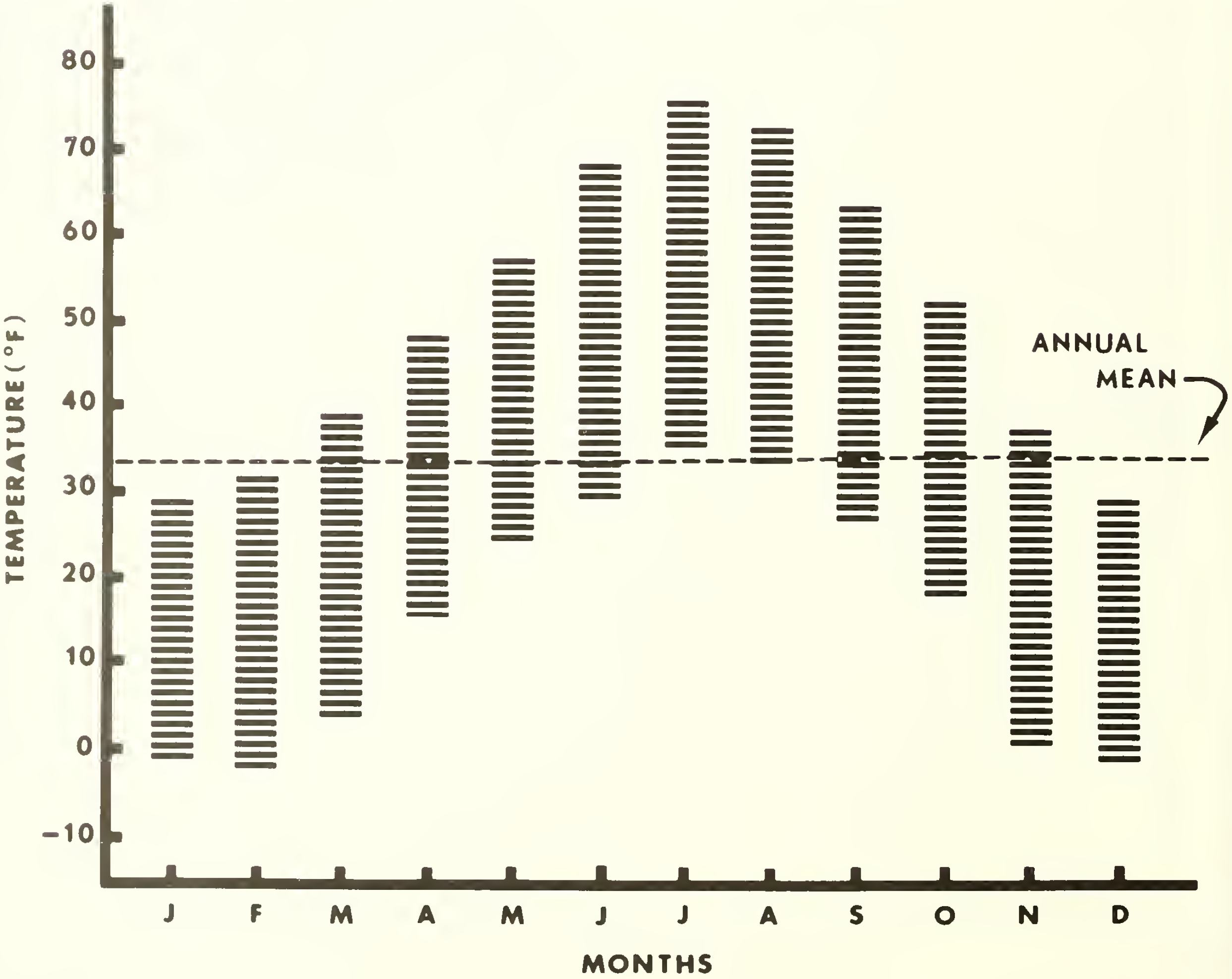
THE FOREST

Elevation of the Experimental Forest ranges from 8,800 feet at the main entrance along the road from the town of Fraser, to 12,804 feet at the summit of Byers Peak. About three-fourths of the Forest lies above 10,000 feet, and about one-third is above timberline.

Climate

Climate is cool and humid with long, cold winters and short, cool summers. Average yearly temperature at Forest headquarters (9,000 feet elevation) is 33° F, and frost can occur any month of the year. Mean monthly temperature for January is 14° F, for July 55° F, with an observed range of about –40 F° to 90° F. Annual precipitation measured at the headquarters area varies from about 17 to 28 inches, with an average of nearly 23 inches. Precipitation over the entire Experimental Forest averages about 28 to 30 inches, with nearly two-thirds falling as snow from October through May.


AVERAGE PRECIPITATION (INCHES)
3
2
1
0
SNOW PERIOD
RAIN PERIOD
J
F
M
A
M
J
J
A
S
O
N
D
MONTHS


TEMPERATURE (°F)
80
70
60
50
40
30
20
10
0
−10
ANNUAL MEAN
J
F
M
A
M
J
J
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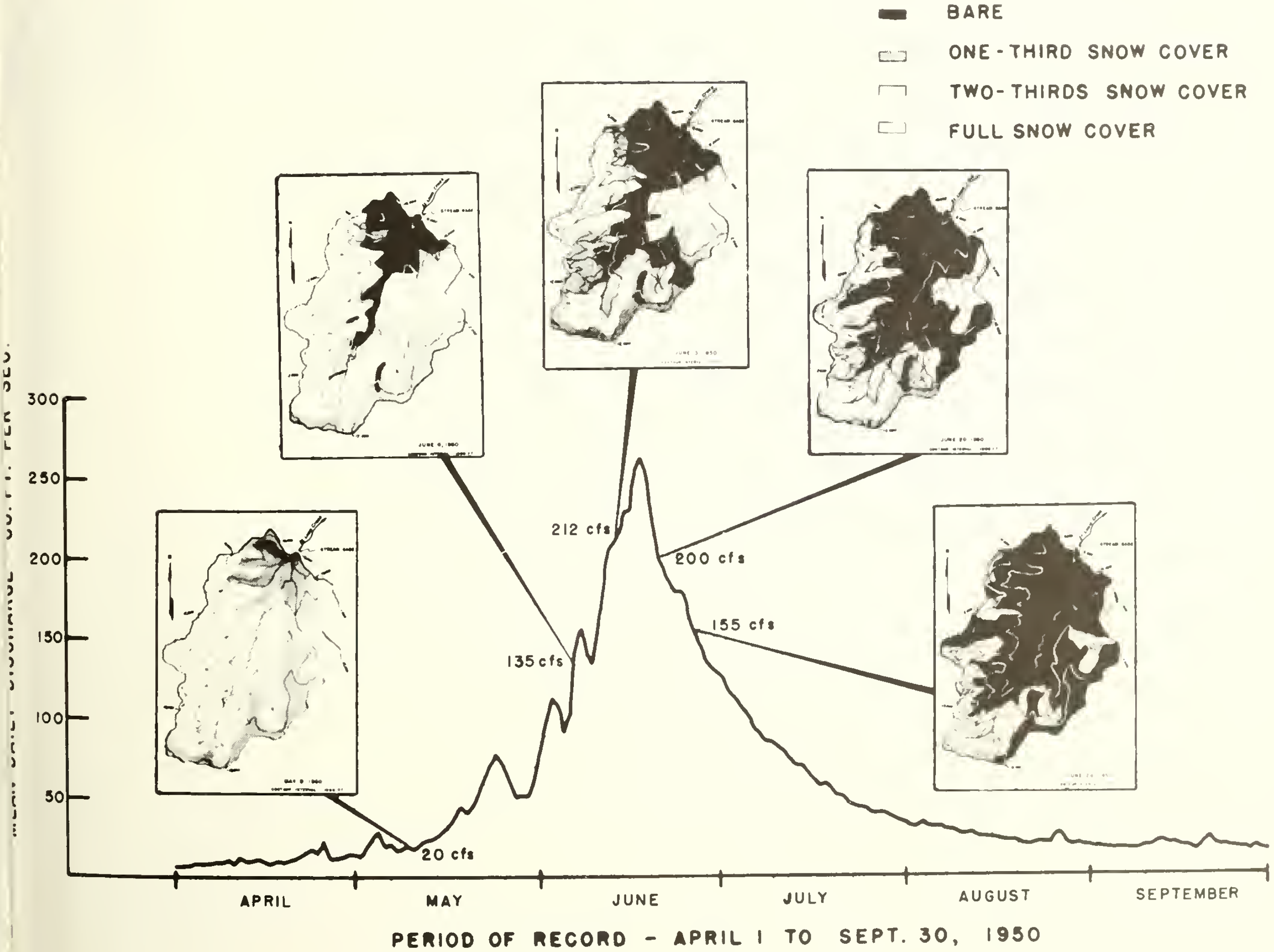
S
O
N
D
MONTHS

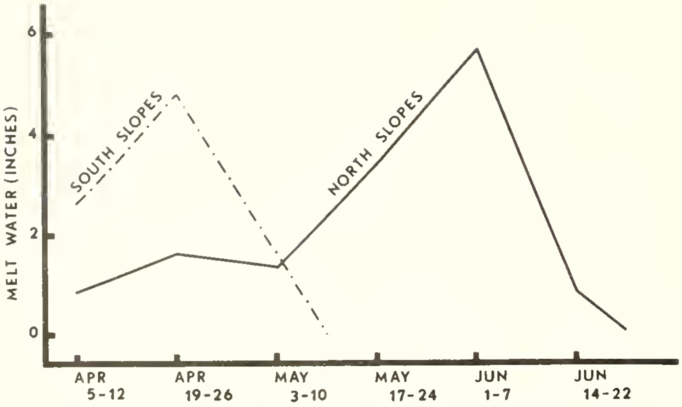
Water Yield

Snowfall is the key to water yield. On the Experimental Forest, the first snow is deposited in early fall, and the pack gradually accumulates to its peak water equivalent in early spring. Long, cold winters keep temperatures within the snowpack well below freezing until late March or April. Peak seasonal snow accumulation averages about 15 inches water equivalent, and during melt season, the depleting snowpack is augmented by 5 inches or more of additional precipitation. Rainfall during summer and early fall averages 8 to 10 inches. Of the total 28 to 30 inch input, about 12 to 15 inches becomes streamflow. Streams begin to rise from minimum flows in April, reaching peak levels in June. Streamflow then rapidly recedes, nearing baseline flows again in late summer.

Snow Cover Disappearance

The entire Forest is covered with snow by the end of winter. As spring advances, snow disappears progressively from lower to higher elevations. Snow melts and disappears from south slopes first. Maximum melt rate is about 0.75 inches per day on south slopes and 0.5 inches on north slopes. When 50% of the snow has disappeared, spring streamflow peaks on the main drainage; when 80% of the snow is gone, streamflow is declining. Temperature, humidity, and wind also influence the daily rate of snowmelt which, in turn, governs streamflow. Continuous records of these factors have been useful in calculating rates of streamflow on the St. Louis Creek drainage, and in forecasting daily streamflow.





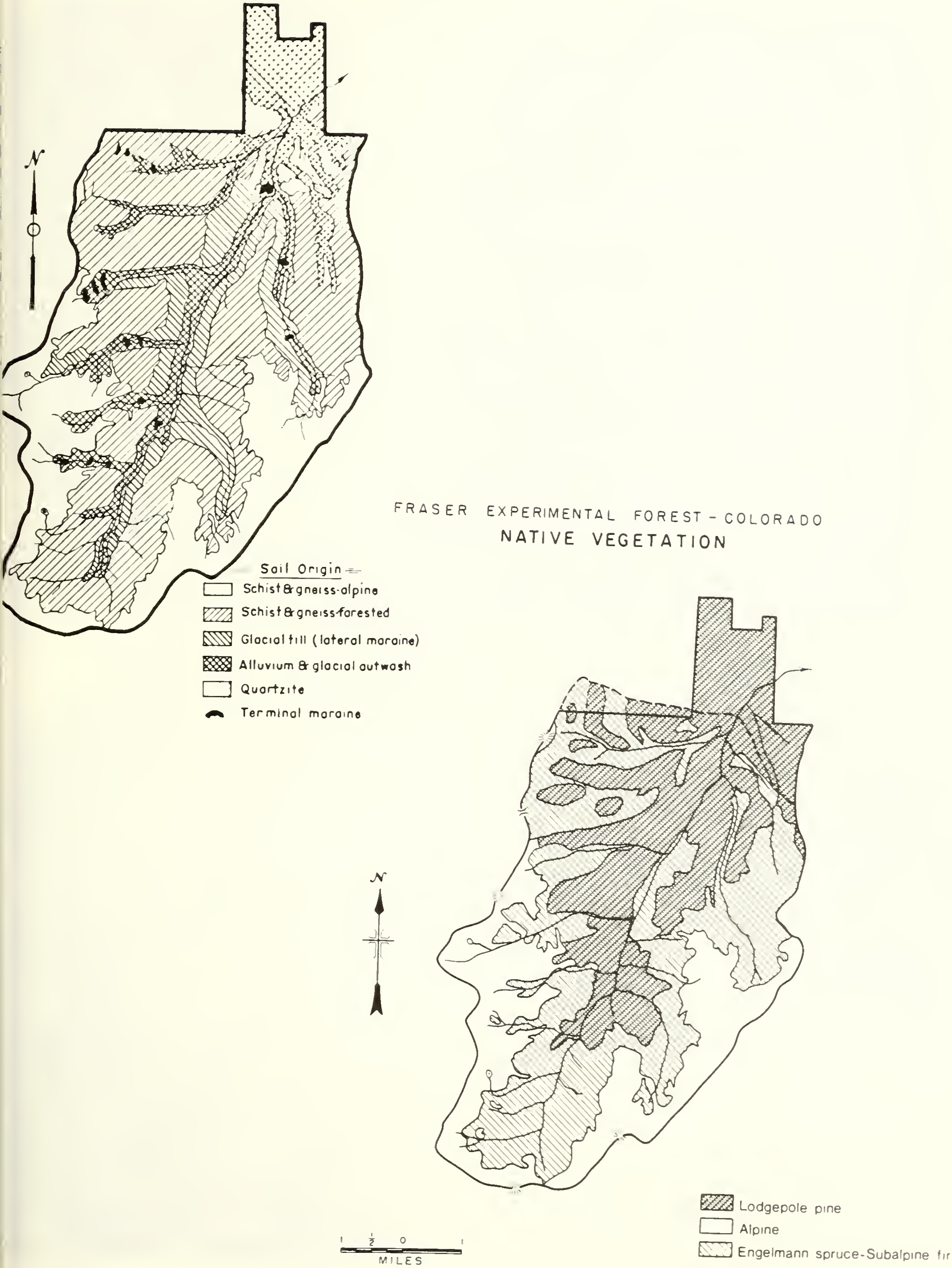
Geology, Landforms, and Soils

Topography of the Experimental Forest is typical of the Southern Rocky Mountain Province. The west side of the Forest is characterized by rugged mountains and narrow, steep-sided valleys filled with alluvium and glacial outwash. South and east sides of the Forest are remnants of an old peneplain, dissected by mountain glaciers and characterized by long, gentle, relatively uniform slopes. The north side is a nearly level, broad valley dissected by St. Louis Creek and surrounded by rolling hills.

Parent material of soils on the Forest generally is derived from gneiss and schist rocks. Occasionally, there are small outcroppings of granitic rock, which weathers more slowly than schists. Typical soils from schistic and granitic rock contain angular gravel and stone, with very little silt and clay. They are very permeable and capable of storing considerable amounts of water during snowmelt. At high elevations, especially on the west side of the Forest, soils have developed in material weathered from sandstones. These soils are shallow, have large amounts of stone, and have fine sand or sand textures. Alluvial soils occur along main streams, with parent material a mixture of glacial till, glacial outwash, and recent valley fill. Bogs originating from seeps or springs that emerge on slopes are scattered throughout the Forest.

Vegetation

Native vegetation is typical of the subalpine forest zone of the central Rocky Mountains. Engelmann spruce and subalpine fir are predominant trees at higher elevations, on north slopes, and along streams; lodgepole pine is the predominant tree at lower elevations and on drier upper slopes. In virgin stands, trees range from 200 to 400 years old. Second-growth lodgepole pine on the north end of the Forest originated after fires, and is about 60 years old. Scattered patches of aspen occur in areas opened up by logging or fire. Occasionally, a large, old (450 to 500 years) Douglas-fir can be found The forest floor generally is covered with a layer of duf and litter and often a dense mat of whortleberry. Herbaceous vegetation is generally sparse except along streams, and in openings resulting from disturbance Barren rocks intermix with alpine tundra, meadows and bogs above timberline.



FRASER EXPERIMENTAL FOREST – COLORADO
NATIVE VEGETATION

Wildlife

Many kinds of wildlife live on the Forest, but no one species is abundant. Trout occur in some streams, beaver ponds, and lakes. Elk, deer, black bear, and mountain lion are the Forest's big game animals. Moose have occasionally been sighted but are not considered part of the Forest's resident big game population. Elk are found in alpine grasslands and high cirque basins in summer, but do not winter in any part of the Forest. Mule deer are more common than elk. In summer, they graze in timbered areas and openings intermixed with timber. In winter, they move to lower areas off the Forest. Black bears are shy and rarely seen. Mountain lions are only occasional visitors. Small, fur-bearing mammals include marten, weasel, mink, badger, muskrat, red and gray foxes, coyote, bobcat, and beaver along some watercourses. Snowshoe hares, pine squirrels, porcupines, marmots, chipmunks, ground squirrels, mice, gophers, shrews, and voles also are present. Numerous game and nongame birds occur on the Forest. Some are residents, others are seasonal, and still others are migratory.

Recreation

The Forest provides a variety of recreational opportunities, with two developed campgrounds, 20 miles of specified roads, and many trails. In summer, users camp, hike, fish, backpack, and view and photograph scenery. In fall, hunters seek blue grouse, elk, and deer. Snowmobiling and ski-touring are popular in winter.

RESEARCH PROGRAM

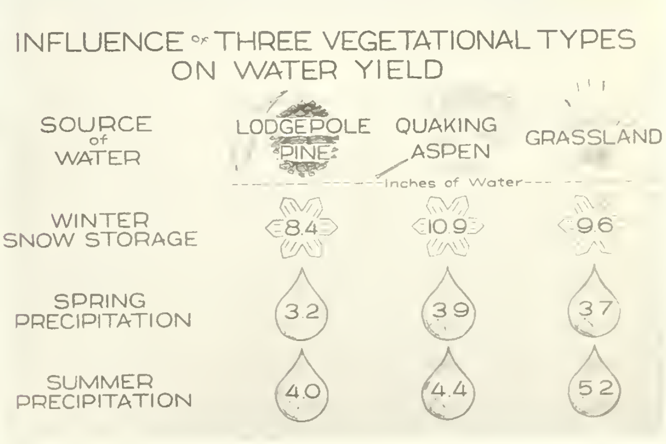
The research program at the Fraser Experimental Forest is concerned with regenerating new forest stands, increasing growth and yield of trees, increasing water supplies and maintaining water quality, determining water use and availability, improving wildlife habitat for game and nongame animals, and determining the integrated effects of timber harvesting on these resources. Specifically, research objectives are:

1. Understanding how trees grow, reproduce, and interact; how the hydrologic system operates on headwater streams, and what the food and cover requirements of wildlife are.
2. Learning how natural forest cover influences the tree, water, and wildlife systems.
3. Observing how harvesting timber changes the influence of the forest on these systems; and
4. Devising timber harvesting systems to achieve the desired changes in forest cover that will provide the best mix of timber, water and wildlife benefits.

Publications derived from research at the Fraser Experimental Forest are listed by subject matter categories at the end of the text

RESEARCH HIGHLIGHTS

Early studies included observations in natural plant communities or environments to determine their effects on snow accumulation. Results showed more precipitation reached the ground under aspen and in grasslands than under dense lodgepole pine stands. These studies provided clues to the effect on water yield when forest stands were harvested for timber or thinned to improve growth.



INFLUENCE OF THREE VEGETATIONAL TYPES ON WATER YIELD

SOURCE of WATER	LODGEPOLE PINE	QUAKING ASPEN	GRASSLAND
	Inches of Water		
WINTER SNOW STORAGE	8.4	10.9	9.6
SPRING PRECIPITATION	3.2	3.9	3.7
SUMMER PRECIPITATION	4.0	4.4	5.2

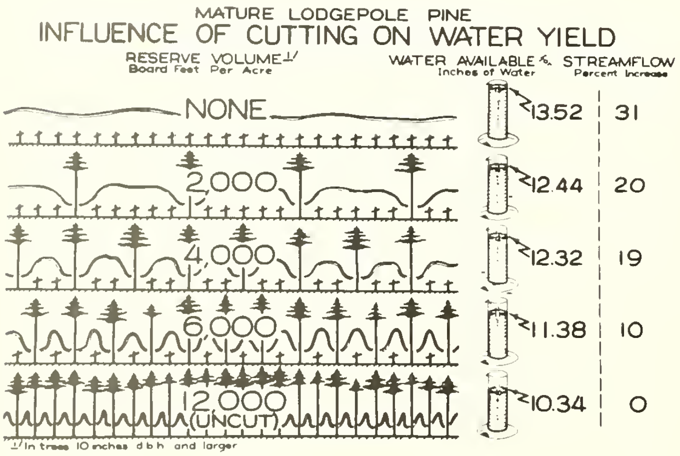
Plot studies of harvest cuttings and thinnings followed. Their purpose was to determine how different methods and intensities of tree removal affected the snowpack and tree reproduction, growth, and mortality. A third research phase applied a timber harvesting system to an entire watershed to measure its effects on (1) streamflow and snow accumulation and melt; (2) sedimentation; (3) tree regeneration, growth, and mortality; and (4) big game use, forage availability, and preference. This included basic hydrologic studies aimed at measuring water loss from both vegetation and the overwinter snowpack. The present phase involves pilot testing of timber, water, and wildlife systems and their interactions in relation to timber harvesting on other watersheds; and basic studies of water use by trees and stands and the movement of meltwater through the soil profile.

Harvest Cutting in Lodgepole Pine

Twenty 5-acre plots were established in 1938 on the King Creek drainage in mature lodgepole pine. After snowpack, regeneration, and stand inventory measurements had been recorded, plots were logged in 1940, with treatments ranging from clearcutting to no cutting. Residual volumes in trees 9.5 inches in diameter and larger on logged plots were 0, 2,000, 4,000, and 6,000 board feet (fbm) per acre. Uncut plots averaged about 12,000 fbm per acre.

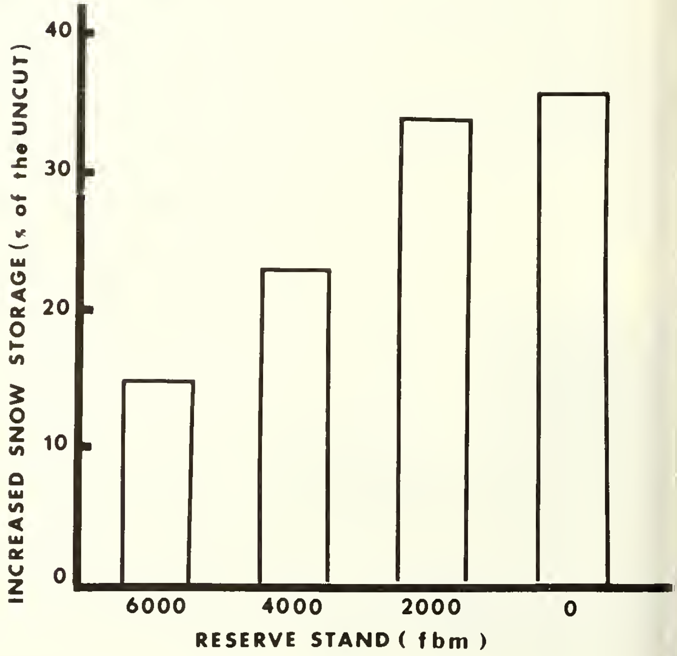
Water Available for Streamflow

After winter snowpack accumulation, net summer precipitation input, and growing season soil moisture depletion following timber harvest were monitored, an estimate was made of the effect that different cutting intensities have on water available for streamflow. The estimate was based largely on changes in net precipitation and only superficially addressed other E.T. changes known to have occurred. The largest increase was on clearcut plots; the smallest was on 6,000 fbm reserve plots.



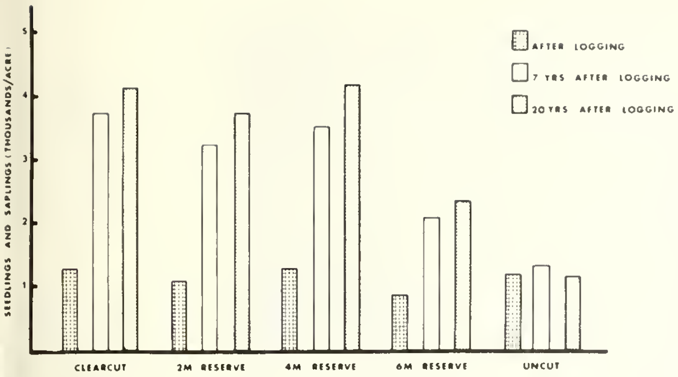
Snow Accumulation

Most of the increase in water available for streamflow came from increased snow storage on cutover plots. Although young trees developed rapidly on cutover plots, snow storage amounts have changed little in the years since cutting, especially on the clearcut plots. The increased snow on clearcut plots is primarily due to the aerodynamic effect of the openings on the snow deposition pattern rather than solely due to reduced interception loss. More snow is deposited in the openings and less in the downwind forest during the storm. The smaller increases observed under partial cutting were largely a reflection of interception saving rather than changes in the deposition pattern. This increased accumulation in the open will persist until new trees, established after logging, are tall enough to change the aerodynamic effect on snow accumulation. To increase snow accumulation, clearcutting of mature lodgepole pine in small patches is the most desirable method of harvesting.



Regeneration

Enough new trees were established on all cutover plots. Before cutting, plots contained 1,978 seedlings and saplings per acre. Logging, where skidding was done with horses, destroyed 44% of the advance growth, but new seedlings came in rapidly after logging. In only 7 years, new seedlings increased total reproduction twofold to threefold on all cutover plots. The increase was greatest on clearcut plots and least on 6,000 fbm reserve plots. Reproduction continued after 1947, but at a much slower rate, and the increase was not directly related to cutting method.

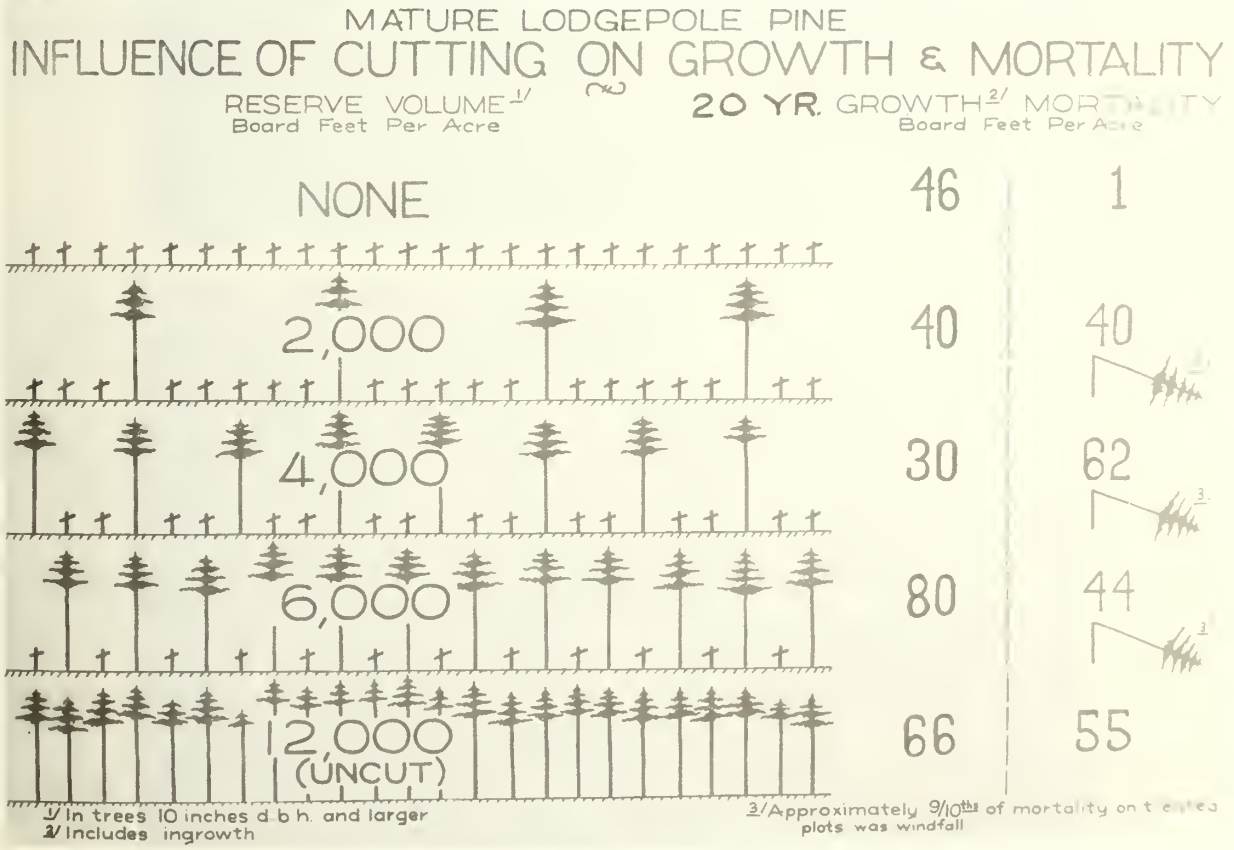


Growth and Mortality

Heavy mortality during the first 7 years after cutting resulted in little new growth on 6,000 fbm reserve and uncut plots, and an actual loss of volume on 2,000 and 4,000 fbm reserve plots. No measurable volume losses occurred on clearcut plots because no merchantable-sized trees were left. After 1947, mortality declined, and net growth increased on all plots. After 20 years, however, only the 6,000 fbm reserve plots grew more than uncut plots. Windfall was responsible for nearly all mortality on partially cut plots and about half the mortality on uncut plots. Because of heavy mortality, clearcutting and replacement of the old stand with a vigorous new one is recommended as the most desirable method for harvesting old-growth lodgepole pine. Partial cutting requires leaving large reserve volumes of low vigor trees, increasing the risk of future mortality.

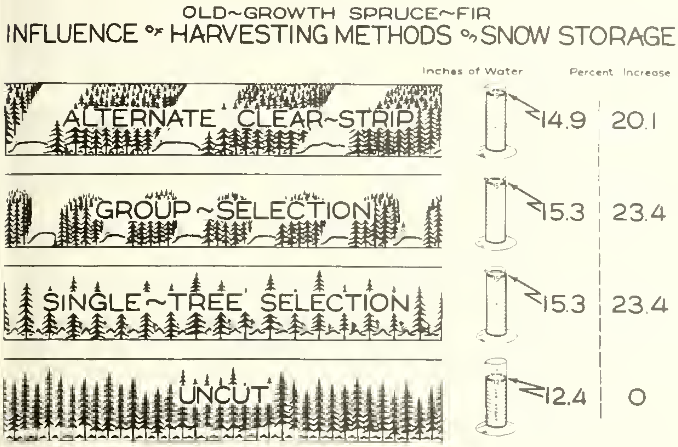
Harvest Cutting in Spruce-Fir

In 1944, four 8-acre plots were established on the West St. Louis Creek drainage to evaluate methods of cutting in old-growth spruce-fir forests. Treatments tested were alternate-strip clearcutting, group selection cutting, and individual tree selection cutting. Each treatment removed 60% of the volume in trees 9.5 inches diameter at breast height (d.b.h.) and larger. Alternate-strip clearcutting removed 50% of the volume in alternate strips 1 chain wide; an additional 10% was removed from the leave strips by cutting overmature trees. Group selection cutting was used to remove 50% of the volume in small circular openings about 1 chain in diameter; an additional 10% was removed by cutting trees in the between-groups stand. Individual tree selection cutting removed 60% of the volume uniformly over the entire plot. Residual volume on cutover plots averaged 6,460 fbm per acre. The original volume of 17,745 fbm per acre remained on the uncut plot.



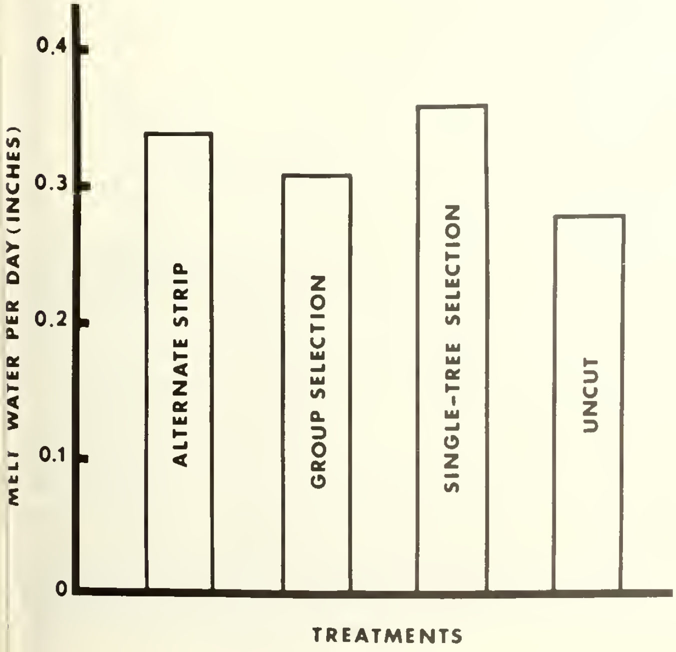
Snow Accumulation

Snowfall reaching the ground increased on all cutover plots after logging. Measurements in four of the years after logging showed an average accumulation of 22% more water equivalent on cutover plots than on the uncut plot, but there were no differences in snow storage between treatments.



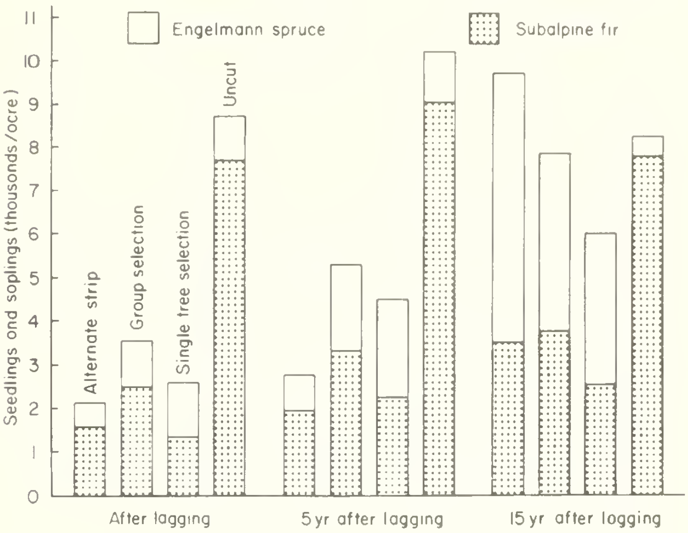
Snowmelt

Weekly measurements of rates of snowmelt during the spring showed only slight differences between treatments. Snow melted fastest (0.36 inch per day) after individual tree selection cutting and slowest (0.28 inch per day) in the uncut plot.



Regeneration

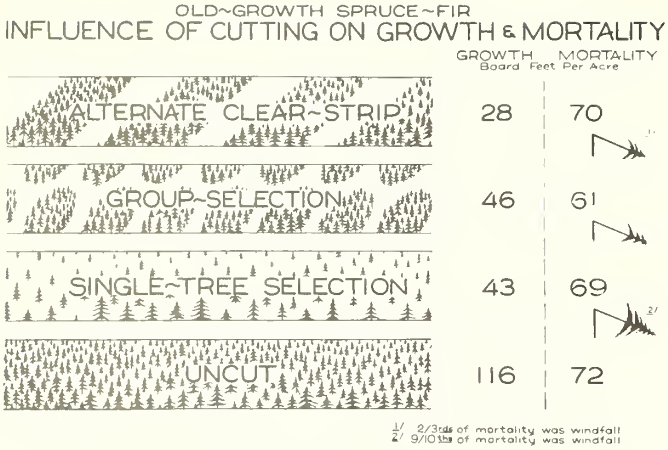
Reproduction was adequate under any cutting method tested. Before logging, plots averaged 6,344 seedlings and saplings per acre, with the ratio of fir to spruce ranging from 5 to 1 on the alternate strip clearcut plot to about 1 to 1 on the individual tree selection plot. Logging—where skidding was done with horses—destroyed 52% of the advanced reproduction. Damage among the three cut plots was heaviest on the individual tree selection plot where the entire area was disturbed, and was least on the group selection plot where about one-third of the area was disturbed. Subsequent reproduction established at only a moderate rate during the first 5 years after logging. Initial recovery was poorest on the alternate strip clearcut plot, where only about half as many trees established as on other cutover plots. The rate new reproduction established accelerated after 1949. The largest increase was on the alternate strip clearcut plot where new reproduction outnumbered the increase on group and individual tree selection cutting plots by three and four times, respectively. The number of new spruces was three to five times greater than new firs on all cutover plots.



Growth and Mortality

Growth of residual stands was not stimulated by the cutting methods tested. Furthermore, differences in board foot volume growth between cutting treatments were unimportant. Mean annual growth on all plots was proportional to reserve volume.

Mortality was not materially different between plots. Windfall caused at least two-thirds of the mortality on cutover plots, with the heaviest losses on the individual tree selection plot. Disease and insects were responsible for most of the mortality on the uncut plot. Because of more abundant and better distributed spruce reproduction, and less susceptibility of residual stands to windthrow, alternate strip clearcutting and group selection cutting were the most desirable harvesting method tested for old-growth spruce-fir stands.

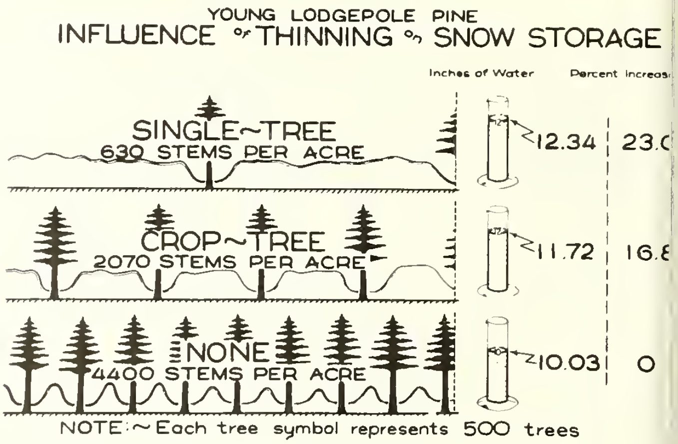


Thinning Young Lodgepole Pine

Eighteen 1/4-acre plots were established in 1944 in young (35-year-old) lodgepole pine stands in the main St. Louis Creek drainage to test thinning methods. Original stand density varied from 2,100 to 8,576 stems per acre. After snowpack and stand inventory measurements were made, six plots—designated single tree—were thinned uniformly from below in 1945, reserving 630 trees per acre. On six other plots—designated crop tree—all trees within a 16-foot-diameter circle around each of 100 crop trees per acre were cut. The remaining six plots were left unthinned as a control.

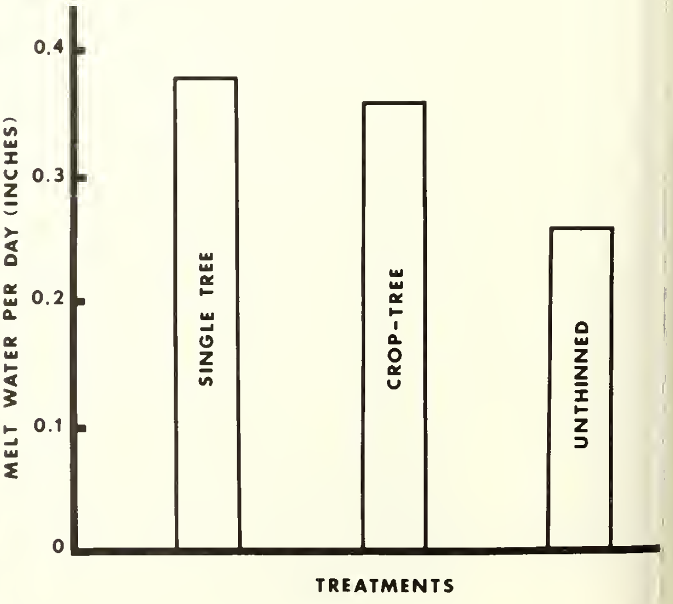
Snow Accumulation

Cutting resulted in more snow reaching the ground on thinned plots than in natural stands. The highest snow accumulation observed during a 3-year period was on single-tree plots where the largest number of trees had been removed.



Snowmelt

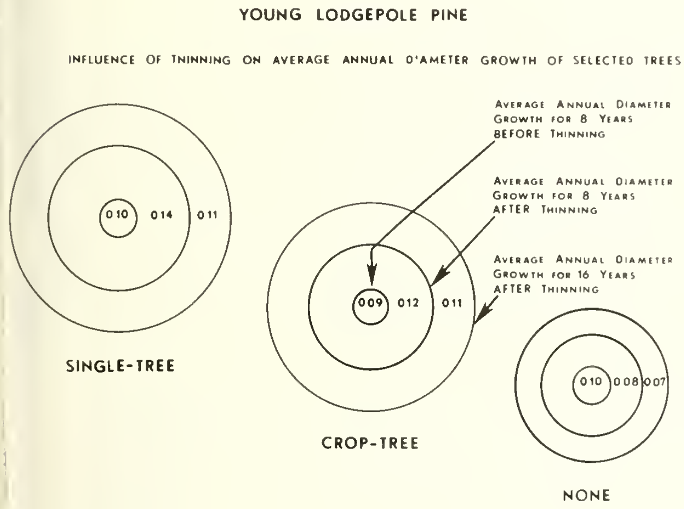
The rate of snowmelt during spring was greater on thinned than unthinned plots, but there was little difference in melt between single-tree and crop-tree thinning.



Growth

Diameter growth of the best 100 trees per acre was increased about 1–1/2 times by both thinning methods during the 16 years of observation, but diameter growth of all trees on plots was increased only by single-tree thinning. Basal area increment of the total stand was not affected by thinning. Cubic volume growth during the first 8 years of observation was greater in unthinned than thinned stands, but during the last 8 years of observation, there was no difference in cubic volume growth between thinned and unthinned plots.

Because of larger increases in water available for streamflow and concentration of total stand growth on fewer stems, single-tree thinning was recommended, but not necessarily at the spacing tested.


YOUNG LODGEPOLE PINE

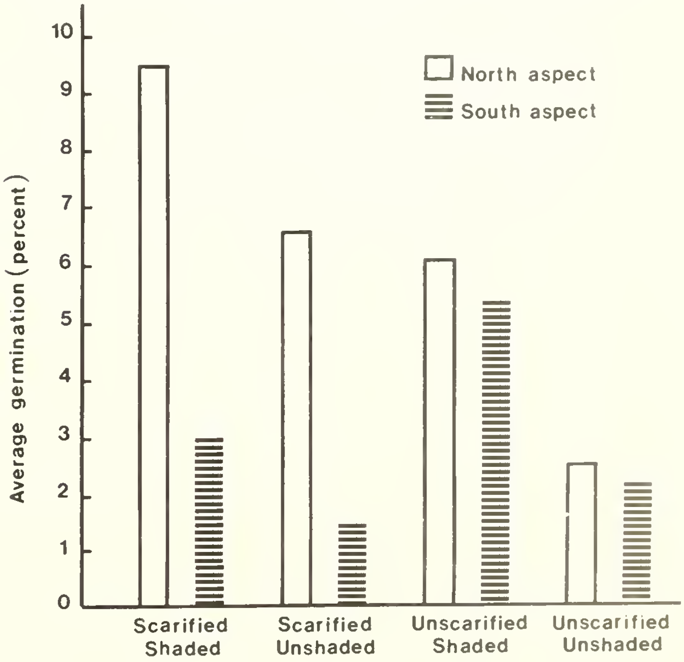
INFLUENCE OF THINNING ON AVERAGE ANNUAL O'AMETER GROWTH OF SELECTED TREES

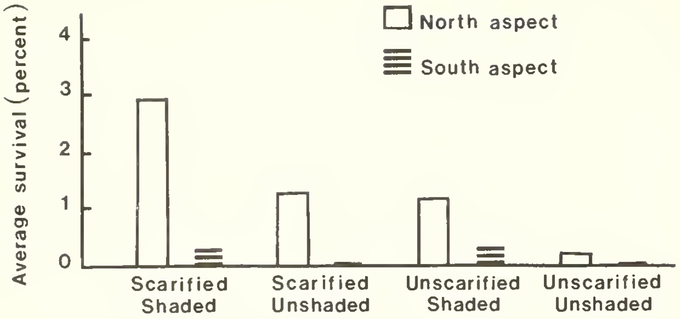
Environmental Factors Affecting Engelmann Spruce Regeneration

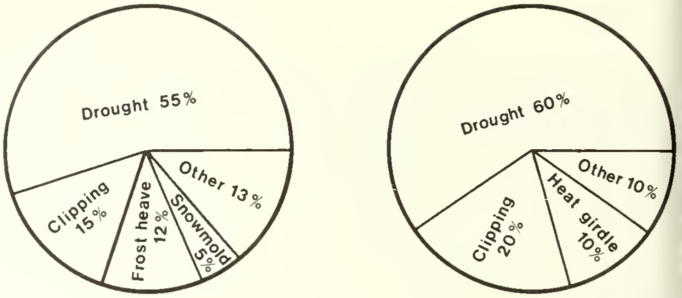
Two study areas were established in 1968 to identify factors limiting spruce regeneration success, and determine cultural practices needed to provide an environment suitable for spruce regeneration. Study plots were located in two 3.5-acre clearcut openings at 10,500 feet elevation, one on a north aspect of the Fool Creek drainage, the other on a south aspect of the West St. Louis Creek drainage.

Each year for 10 years, twelve 1/4 milacre seedbeds were prepared at each study site. Each set was composed of four seedbed treatments—scarified-shaded, scarified-unshaded, unscarified-shaded, and unscarified-unshaded—replicated three times each. Seed from local sources was sown each fall on the current set of seedbeds to simulate natural seedfall.

Germination and survival observed from 1969 to 1982, was considerably better on the north aspect than the south aspect. However, total germination on the north aspect was only 6.1%, and only 2.9% of the seeds sown survived to the end of the study. Both germination and survival on the north aspect was best on scarified-shaded seedbeds and poorest on unscarified-unshaded seedbeds. Nearly 76% of the germinating seedlings died, with about 66% of the mortality occurring the first year. Nearly all the mortality was caused by drought, clipping by birds, frost heave and snowmold. Total germination of the south aspect was only 1.4%, and only 0.2% of the seeds sown survived to the end of the study. Germination was best on the unscarified-shaded seedbeds and poorest on the scarified-unshaded seedbeds. Survival was about the same on the scarified-shaded and unscarified-shaded seedbeds, but no seedlings survived on the scarified-unshaded and unscarified-unshaded seedbeds. About 95% of the germinating seedlings died on the south aspect, with 90% of the mortality occurring the first year. Most mortality was caused by drought, clipping by birds, and heat girdle.







North aspect

South aspect

Conditions favorable and unfavorable to Engelmann spruce regeneration are summarized below.

REGENERATION CONDITIONS

	FAVORABLE		UNFAVORABLE
a	>250,000 seed/acre	SEED CROP	<50,000 seed/acre
b	North and East	ASPECT	South and West
c	Ambient air >32° F night and <78° F day; maximum surface <90° F	TEMPERATURES	Ambient air <32° F night and >78° F day; maximum surface >90° F
d	>0.50 in./week	PRECIPITATION	<0.40 in./week
e	Light-textured, sandy-loam	SOIL	Heavy-textured, clay-loam
f	>40% exposed mineral soil	SEEDBED	<20% exposed mineral soil
g	50–70% dead shade		<30% dead shade
h	<2 in. duff and litter		>4 in. duff and litter
i	Light vegetative cover <30% non sod-forming		Heavy vegetative cover >60% sod-forming
j	Seedlings >12 weeks old by mid-Sept.	SURVIVAL	Seedlings <12 weeks old by mid-Sept.
k	Low population of birds and small mammals that eat tree seed and young seedlings		High population of birds and small mammals that eat tree seed and young seedlings
l	Protection from trampling		No protection from trampling
m	Fall snow cover when frost heaving conditions exist		No fall snow cover when frost heaving conditions exist
n	No late lying spring snowfields when conditions favorable to snowmold exist		Late lying spring snowfields when conditions favorable to snowmold exist

Watershed Studies: Fool Creek-East St. Louis Creek

Because more snow accumulated on experimental plots after timber harvest, it was assumed that more water was available for streamflow.[2] It was only an assumption, however, until similar cutting was done on a forested watershed where streamflow was measured and the assumption verified. Paired watersheds, one treated (Fool Creek) and one a control (East St. Louis Creek), were monitored as part of the experiment to determine the effect of timber harvest on streamflow.

Fool Creek.—This is a 714-acre watershed at elevations ranging from 9,500 to 11,500 feet. Streamflow, precipitation, and snowpack accumulation have been measured since 1940. The original gaging station at Fool Creek, a combination San Dimas flume and two broad-crested weirs, was replaced with a 120° V-notch weir in 1980. The main channel flows north, with generally east and west aspects comprising 70% of the watershed area.

East St. Louis Creek.—This is a 1,984-acre watershed with elevation varying from 9,500 to 12,200 feet. It lies adjacent to Fool Creek, and is the untreated control. Major vegetation consists of lodgepole pine, Engelmann spruce and subalpine fir, with alpine tundra above timberline. Streamflow, precipitation, and snowpack accumulation have been measured since 1943. The original gaging station was a trapezoidal flume that was replaced in 1963 with a Cipolletti weir. Flow from the two watersheds correlated well during the pretreatment years, and changes in streamflow on Fool Creek resulting from timber harvest can be estimated using the flow of East St. Louis Creek.

Alternate Strip Clearcutting

Fool Creek originally supported 6 million fbm of merchantable timber on 550 acres. About 55% was in the lodgepole pine type and 45% in the spruce-fir type.

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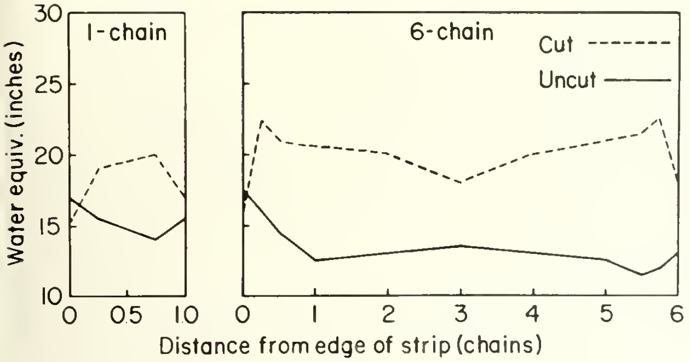
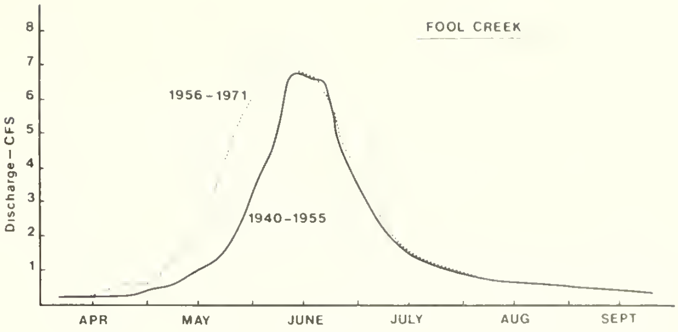
[2] Streamflow is the quantity of surface water flowing past a given point in a stream channel. It is measured by flumes, weirs, or water control structures. Streamflow generally is expressed as a rate in cubic feet per second, or as an amount in acre-feet, or inches depth over a known area.

These stands were overmature—250 to 350 years old. To harvest timber on Fool Creek, 3.3 miles of main access road and 8.8 miles of spur roads were constructed between 1950 and 1952. Spur roads were about 600 feet apart, located on the contour. Timber harvest, beginning in 1954 and ending in 1956, removed trees in alternate cleared strips at right angles to the contour. Four clearing widths—1, 2, 3, and 6 chains—were used. No timber was cut within 90 feet of the stream to minimize damage to the channel. On strips designated for cutting, all live trees 4 inches in diameter and larger were felled, and tops were lopped and scattered. In all, 278 acres of watershed were cleared, including 35 acres of roads. A total of 3.5 million fbm of timber was removed.





Snow Accumulation

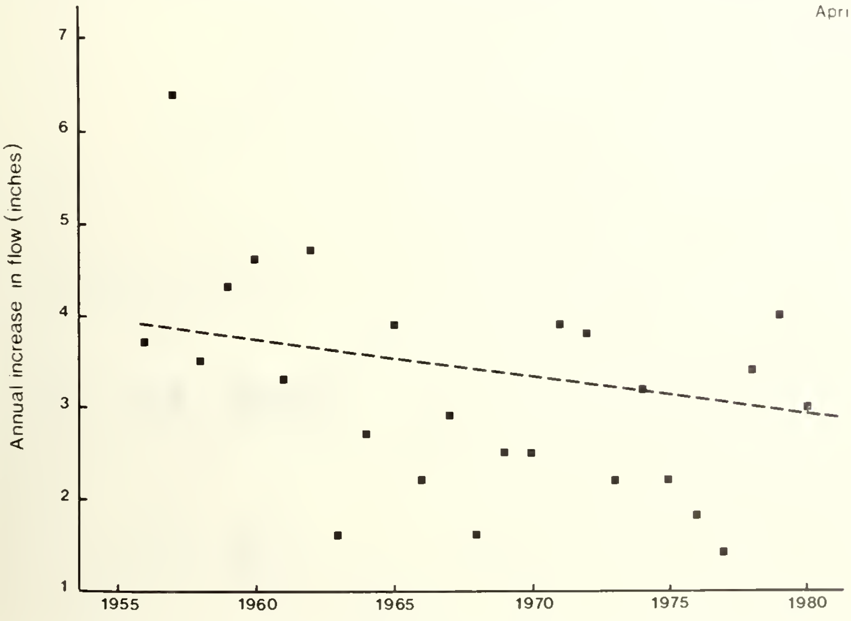
Comparisons of snowpack accumulation in alternate forested and clearcut strips indicate a large increase in water equivalent in open areas, with a small net increase in total snow accumulation on the watershed. There is a pronounced redistribution of snow as a result of cutting; more snow accumulates in cut strips than in the uncut forest. Before cutting, wind distributed snow rather evenly within the forest. Afterwards, the aerodynamics of the canopy were changed and the openings in the canopy efficiently trapped snow that formerly settled in adjacent forested strips. Thirty percent more water equivalent is deposited in the openings, largely the result of redistribution. However, the long-term record now available indicates that reduction in interception loss has resulted in a 10% increase in the peak snow water accumulation on Fool Creek.

Snowmelt and Water Yield

Removing timber from Fool Creek accelerated snowmelt rates and increased water yield by almost 40%. Most of the increase occurs as a substantially enlarged spring runoff. Peak flows, although increased, are not affected appreciably, and there is no detectable change in streamflow during midsummer and early fall. Twenty years passed before there was any strong indication that the effect of cutting timber on streamflow had diminished. Today, analyses indicate that the average effect of the timber harvesting treatment is being diminished by about 0.04 inches per year and that 70 to 80 years will be required for full return to pretreatment conditions.

Cutting trees and resultant redistribution of seasonal snowpack substantially increased runoff because some water formerly used during the melt period to replace soil moisture consumed by vegetation is now available for streamflow. Because more snow is deposited in openings where soil moisture deficits are lowest, and higher melt rates in openings make meltwater available earlier before evapotranspiration can deplete it, the efficiency of the treatment is enhanced.

After nearly 30 years the increase in streamflow is still 25% above pretreatment flow. This change is due largely to increased consumptive use by vegetative regrowth rather than any change in snowpack deposition pattern.



April to September runoff increase since harvest

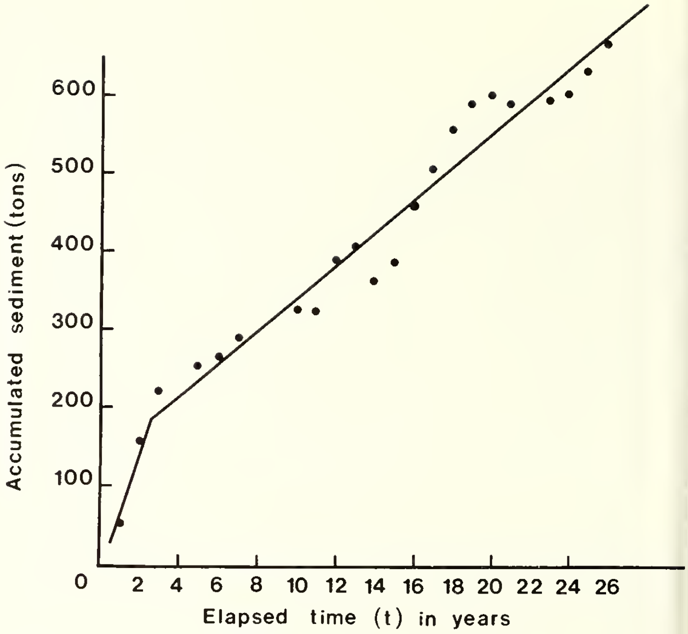
1956	3.7
57	6.4
58	3.5
59	4.3
60	4.6
61	3.3
62	4.7
63	1.6
64	2.7
65	3.9
66	2.2
67	2.9
68	1.6
69	2.5
70	2.5
71	3.9
72	3.8
73	2.2
74	3.2
75	2.2
76	1.8
77	1.4
78	3.4
79	4.0
80	3.0
81	1.7
82	4.5
83	4.0
$\bar{x}$	3.2 (inches)

Increase in annual flow from Fool Creek since harvest in 1955

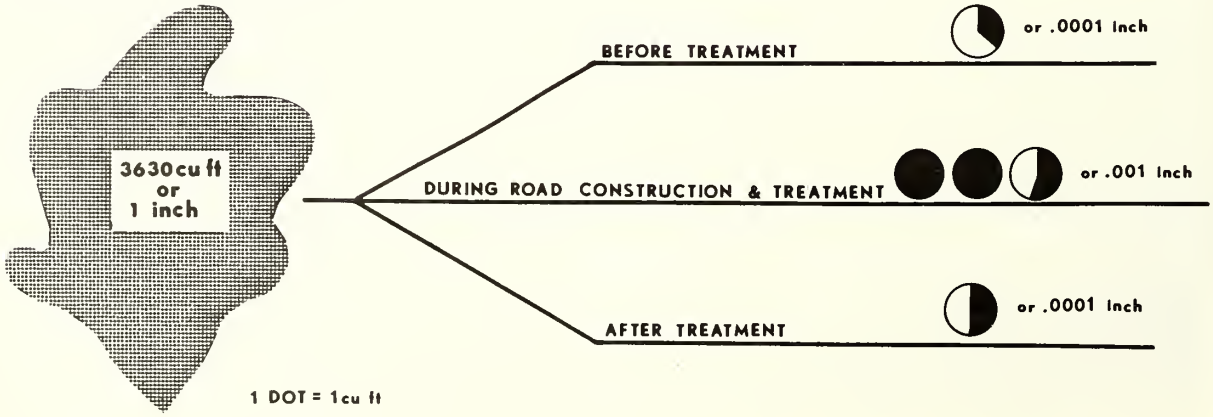
Sediment Yields

Construction of the road system on Fool Creek and associated timber harvesting caused little erosion, with no apparent reduction in water quality. The main access road was located to avoid damage to the stream channel, and spur roads were provided with surface drainage and culverts at stream crossings. After logging, spur roads were seeded to grass, and culverts were removed from alternate spur roads to reduce traffic. The main haul road is still routinely maintained.

Sediment yield during road construction and subsequent logging averaged about 200 pounds per acre, but decreased rapidly after logging despite continuing increase in runoff after timber harvest. Since logging, sediment yields have averaged 43 pounds per acre, compared with yields of 11 to 21 pounds per acre from undisturbed watersheds. The continuing increase in sediment yield may come from the 3.3 miles of main access road that are still being maintained. Suspended sediment was less than 5 parts per million during high flow periods in 1964 and 1965.

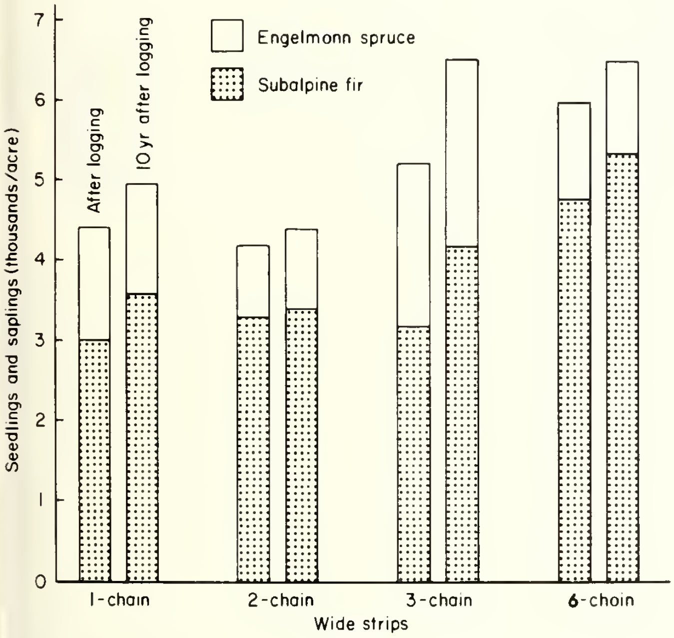


INCREASES IN SEDIMENT YIELD FROM **FOOL CREEK WATERSHED**
(714 ACRES)



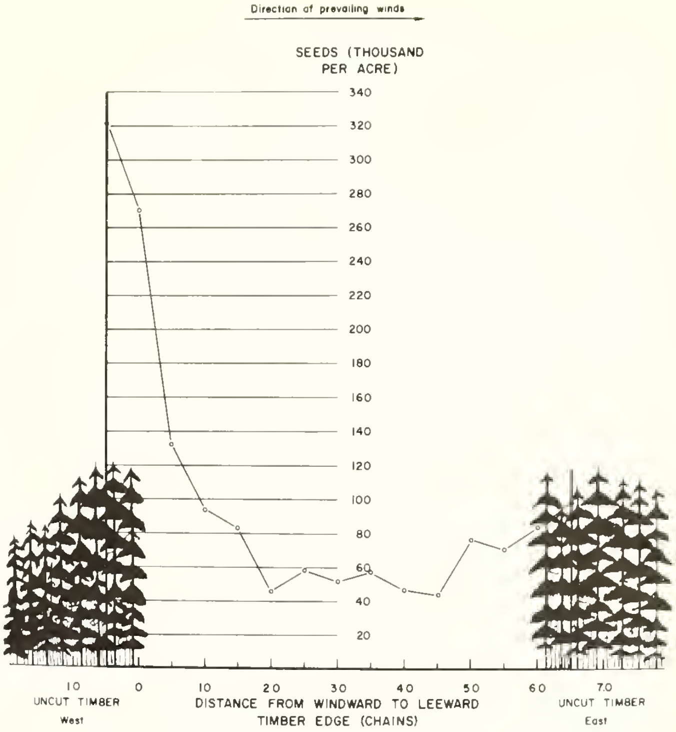
Regeneration: Spruce-Fir Type

In the spruce-fir type on Fool Creek where logs were skidded with horses, enough advanced reproduction survived logging to restock all cutover strips. The number of seedlings and saplings left after logging ranged from 4,183 per acre on 2-chain-wide strips to 5,957 per acre on 6-chain-wide strips. Firs outnumbered the more valuable spruces on all strip widths. Subsequent reproduction was not abundant on any strips 10 years after cutting. Recovery was best on 3-chain-wide strips, and poorest on 2-chain-wide strips. More new firs than spruces were established on all but 2-chain-wide strips.



Seed Dispersal: Engelmann Spruce

An adequate supply of viable seed is necessary for natural reproduction. During a 10-year period, 1956 through 1965, Engelmann spruce seed production in uncut strips on Fool Creek was 321,000 sound seeds per acre, but annual seedfall varied considerably. The 1961 crop contributed about 40% of the total seedfall. Moderate crops were produced in 1959 and 1963, but seed crops were rated poor to complete failure in the other seven years of observation. The number of seeds dispersed from standing trees into the cleared strips was greater in years of heaviest seed production, but seedfall was not uniformly distributed over the openings. In the 6-chain-wide strips, about half the seed dispersed fell within 1.5 chains of timber edge, with only about 10% falling near the center of the openings.



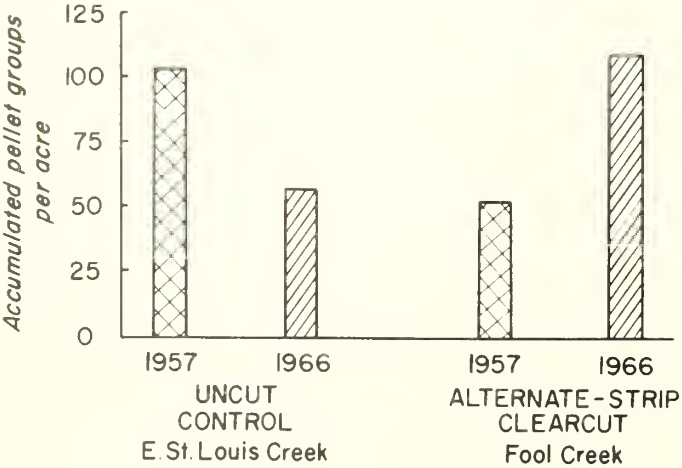
Windfall

Windfall after clearcutting on Fool Creek was observed for 10 years after cutting was completed. Blowdown was related to exposure to wind, cutting unit characteristics, and tree characteristics in the following ways:

1. Approximately 70% of 2,844 windthrown trees were felled by stormwinds from the west and the southwest.
2. About two-thirds of the trees blew down along the N, NE, E, and SE (leeward) cutting boundaries.
3. More trees were windthrown on downwind than on upwind aspects.
4. Cutting boundaries on ridgetops suffered heavy damage. Fewer, and about equal, numbers of trees blew down on upper, middle, and lower slopes.
5. Windfall was not directly related to width of opening.
6. Cutting boundaries oriented parallel to the direction of prevailing windstorms suffered more damage than those oriented at right angles to windstorms.
7. About two-thirds of the blowdown occurred within the first 2 years after logging.
8. Trees growing on soils where average depth of solum exceeded 12 inches were more windfirm than trees growing on shallower soils.
9. Trees growing in situations with rapid drainage were more windfirm than trees growing where drainage was slow.
10. All species and size classes were predisposed to windthrow in the same proportion in which they occurred in uncut stands.
11. Defect was associated with one-third or less of windthrow trees.

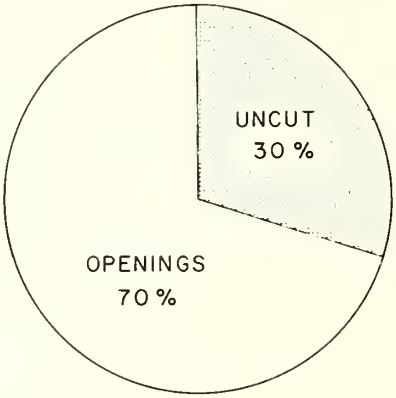
Mule Deer Use and Forage Values

Immediately after logging, mule deer summer use on Fool Creek was less than on the adjacent unlogged watershed. Comparatively low use on Fool Creek may have been due to logging slash and to other disturbance associated with timber harvest. Ten years after logging, deer use was substantially higher on Fool Creek than on the control watershed, with most of the increase on cut strips. Comparisons among cut strips indicated 3-chain-wide strips were used most heavily on both spruce-fir and lodgepole pine forests. The 1-chain-wide strips were used least in lodgepole pine, while 6-chain-wide strips were used least in spruce-fir.



Tame mule deer observed in food habit studies spent about 70% of their time and obtained about 70% of their food on cut strips. Since there were no differences between cut and uncut areas with respect to digestibility, crude protein content, or moisture content of forage species, deer preference for open areas was attributed to the increased amounts and variety of forage in cut strips. Although logging stimulated habitat changes beneficial to deer, enough forage was produced in unlogged areas to carry more deer than currently occupy the summer range. Deer populations in this area are limited by availability of winter range at elevations lower than on the Forest.

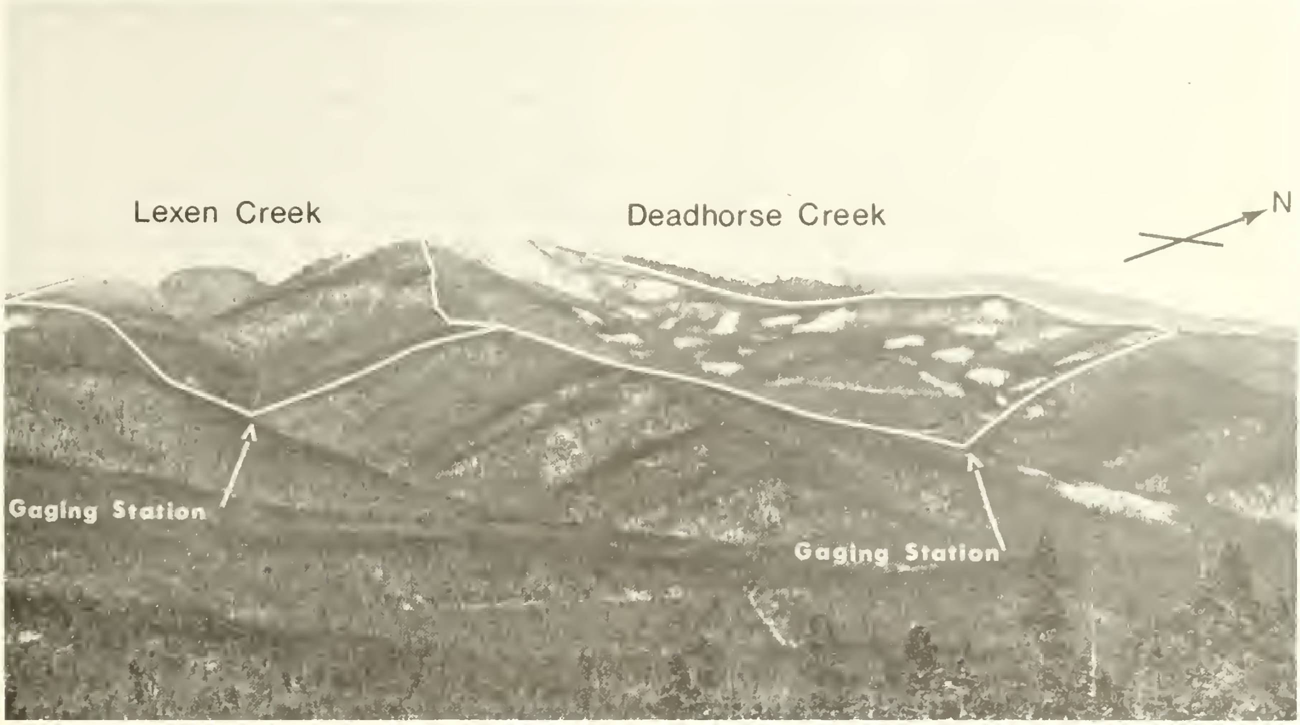
DEER USE OF OPENINGS AND UNCUT TIMBER



CURRENT RESEARCH

Watershed Studies: Deadhorse Creek—Lexen Creek

The hydrology of Deadhorse and Lexen Creeks has been studied since 1955. Long-term records of streamflow, snow accumulation and depletion, precipitation, sediment yield, and water quality are available. A comprehensive study of the snowmelt regime on these and other watersheds on the Fraser Experimental Forest resulted in development of the Subalpine Hydrologic Water Balance Model, a simulation model capable of predicting short- and long-term hydrologic impacts of a broad range of land-use alternatives. This model represents the state of the art after more than 30 years of watershed management research in subalpine coniferous forests. Any tool of this complexity and scope requires pilot testing before routine operational application. Pilot testing is being accomplished on Deadhorse Creek by (1) simulating several timber harvesting options on various subunits, (2) selecting and applying one of these alternatives on the ground in each subunit, and (3) comparing the runoff response predicted by the model with actual streamflow.

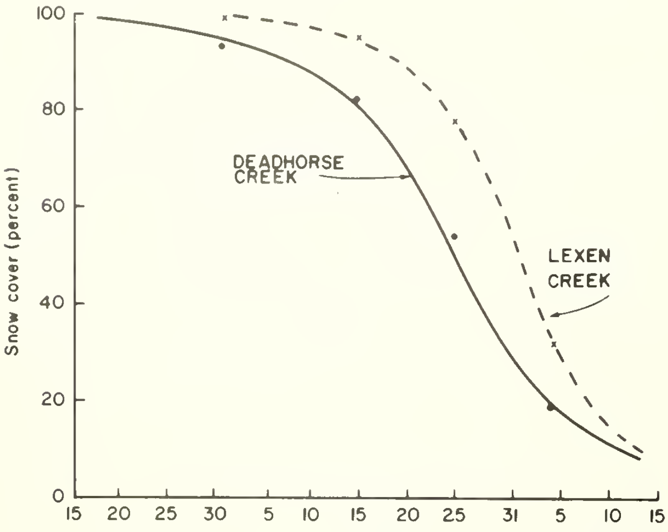


Deadhorse Creek.—This 667-acre watershed, which generally drains from west to east, was selected for treatment. Elevations vary from 9,450 feet at the main gaging station to 11,600 feet at the summit of Bottle Mountain. Major vegetation is spruce-fir along stream bottoms and all north and upper slopes, lodgepole pine on all lower and mid-south slopes, and alpine tundra above timberline. Deadhorse Creek is steeper than Fool Creek, with side slopes averaging almost 40%. The north and south exposures receive unequal amounts of energy in contrast to nearly equal radiant energy load on the east and west slopes of Fool Creek. There are hree stream gaging stations on Deadhorse Creek. The main stream gage is a 120° V-notch weir, and gaging stations on the 100-acre North Fork and the 200-acre Upper Basin are 90° V-notch weirs. The main stream gage was constructed in 1955, the North Fork in 1970, and the Upper Basin in 1975.

Lexen Creek.—This is a 306-acre watershed at elevations ranging from 9,850 feet at the stream gaging station to 11,600 feet. It lies adjacent to Deadhorse Creek and is the untreated control. Vegetation, soils, and topography are similar to Deadhorse Creek. The stream gaging station is a 120° V-notch weir constructed in 1955. Flows from the two watersheds are well correlated, and Lexen Creek also can be used to estimate changes in streamflow on Deadhorse Creek caused by timber harvesting.

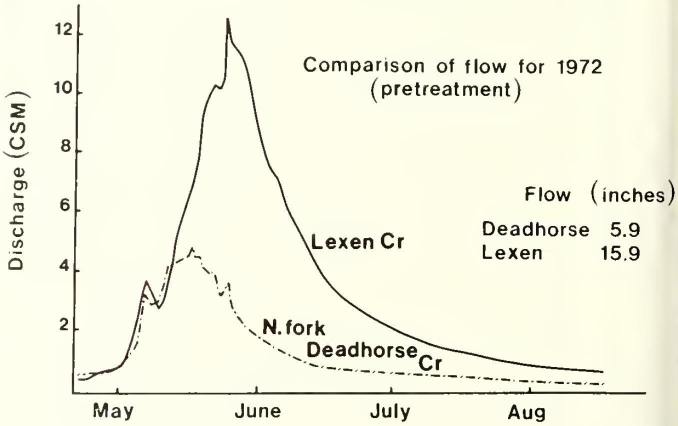
Pretreatment Hydrology

Snow Cover Depletion.—Depletion of the snowpack on Deadhorse Creek starts earlier than on Lexen Creek because of advanced snowmelt on the low-elevation south slopes. The rate of depletion on the Upper Basin of Deadhorse Creek was similar to Lexen Creek.



Snowmelt.—Snowpack melt rates differed considerably between low elevation north and south slopes on Deadhorse Creek. Time of maximum snowmelt on the Upper Basin of Deadhorse Creek and on Lexen Creek varied considerably less between north and south slopes. As a result, nearly 90% of seasonal runoff volume from the entire basin is generated before 60% of the area is bare of snow in either the Upper Basin of Deadhorse Creek or Lexen Creek. Also, more than 80% of these watersheds are still covered with snow when seasonal peak snowmelt runoff rates are reached.

Water Yields.—Streamflow from Deadhorse Creek varied from 60% of that of Lexen Creek in high runoff years to nearly 90% in low runoff years. The difference results from the variation in contribution to streamflow from the Upper Basin, North Fork, and lower Deadhorse Creek subdrainages. Streamflow from lower Deadhorse Creek averages less than 50% of that generated from the Upper Basin, even though precipitation at lower elevations is 80% of that at higher elevations. The North Fork, before treatment, yielded only about one-third as much streamflow as the Upper Basin.

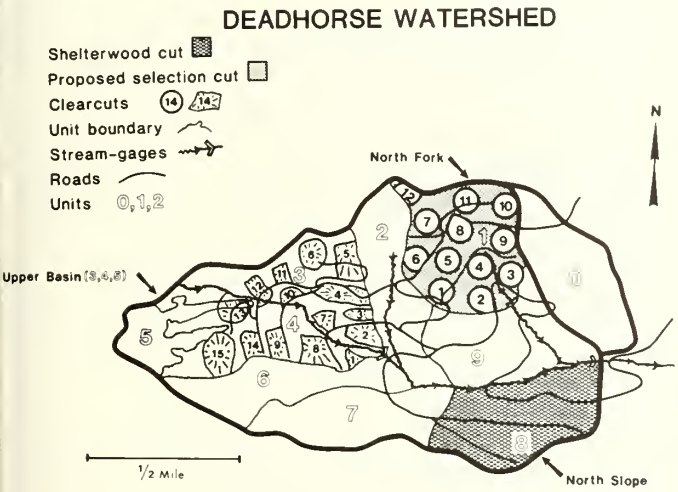


Sediment Yields.—Yields averaged 11 to 21 pounds per acre before road building and logging. These watersheds are very stable, characterized by coarse drainage structure and mature topography. Sediment yields were correlated with both peak and annual flows. In the undisturbed state, most total sediment load came from stream bank erosion and channel degradation. Trapped sediment particles ranged from well-graded gravel to fine sand.

Water Quality.—Natural flows from Deadhorse and Lexen Creeks were generally pure. Concentrations of all chemical components were low, pH values near neutral, and temperatures very cold (32° to 44° F).

Timber Harvest

In contrast to the roads in Fool Creek, which were constructed over a 2-year period, the approximately 9 miles of roads constructed in Deadhorse Creek have been constructed over a 26-year period. One mile of main access road was built in 1955 to harvest timber and construct stream gaging stations on Deadhorse Creek. Another 2.5 miles of main access road was constructed in 1970–1971. About 1 mile of main access road and about 0.75 mile of spur road were built in the North Fork unit in 1976. Approximately 1 mile of main access road and 0.5 mile of spur road were built in 1977–1978 in the North Slope unit, and about 2 miles of main access and spur roads were built in the Upper Basin unit in 1981.



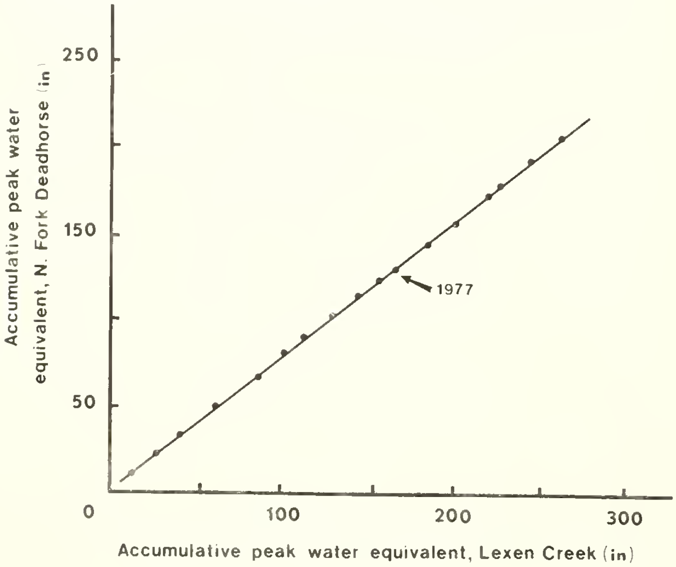
North Fork (Response Unit 1).—Timber harvest on 11 subunits of this 100-acre unit was started and completed in 1977. The twelfth subunit was cut in 1978. Approximately one-third of the old-growth timber—principally lodgepole pine—was clearcut in 3-acre circular patches, spaced so that about equal areas of uncut timber were left between each opening. All live trees 4 inches d.b.h. and larger on the cut patches were felled. Logs were removed by skidding them downhill with wheeled skidders and small crawler tractors. Slash was lopped and scattered. Skid roads were water-barred, brushed in, and seeded. A total of 360,000 fbm of timber was removed. Water yields from this lower south slope have increased about 2 inches annually since cutting was completed, which is in agreement with the long-term simulation of the hydrologic impact of this option. Present plans call for recutting the patches in about 30 years to maintain the increase in streamflow. A series of light partial cuts will be started in the between-patch stand with the ultimate goal of converting the old-growth stands to a managed broad-aged stand while maintaining the height of the present canopy.

North Slope (Response Unit 8).—Timber harvest on this 100-acre unit was started in 1980 and completed in 1981. Approximately 35% of the mixed spruce-fir—lodgepole pine timber in trees 7 inches d.b.h. and larger were removed on an individual tree basis over the entire area in the preparatory cut of a 3-cut shelterwood. Logging was by conventional downhill machine skidding. Slash was lopped and scattered. Skid roads were water-barred, brushed in, and seeded. A total of 600,000 fbm of timber was removed. Water yields from the North Slope have increased less than on the North Fork, which is in agreement with the long-term simulation of the hydrologic impact of this option. Present plans call for harvesting an additional 30% of the old-growth timber with the seed cut of a 3-cut shelterwood 20 years after the first cut, with the remainder of the timber removed 40 years after the first cut.

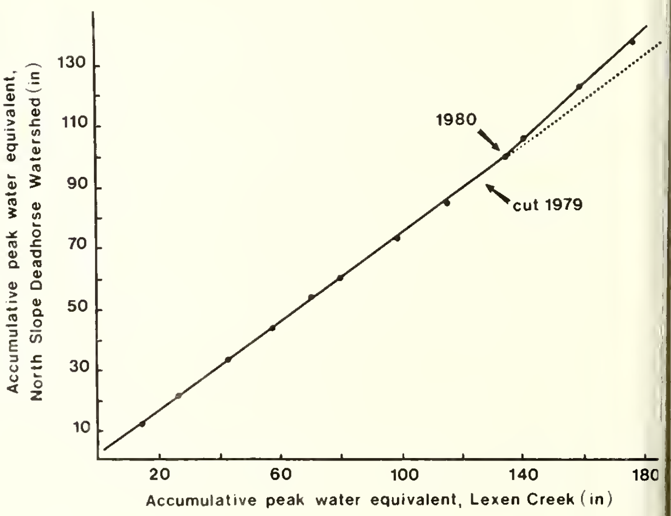
Upper Basin (Response Units 3 and 4).—Timber harvest on the 150 operable acres of this 200-acre unit was started in 1982 and completed in 1984. Approximately one-third of the old-growth mixed pine—spruce-fir was clearcut in 15 irregular-shaped patches that ranged in size from 1 to 5 acres. The openings were spaced so that about equal areas of uncut timber were left between each opening. All live trees 7 inches d.b.h. and larger on the cut patches were felled, and tops were lopped and scattered. Logging was by conventional downhill machine skidding. Skid roads were water-barred, brushed in, and seeded. A total of about 750,000 fbm of timber was removed. Long-term simulation of the hydrologic impacts of this option indicates an initial increase in streamflow of about 2+ inches. This option differs from the North Fork in that plans call for allowing the initial openings to regenerate and grow to maturity. An additional one-third of the area will be cut in new openings approximately 30 years after the first cut, with the last of the old-growth removed approximately 60 years after the initial cutting.

Posttreatment Hydrology

Snowpack Accumulation.—Unlike results on Fool Creek, clearcutting small openings on the North Fork (Response Unit 1) of Deadhorse Creek has not increased total snowfall accumulation. Although 22% more water occurs in the opening than in the surrounding forest, this accumulation pattern is primarily due to differences in snow deposition and redistribution rather than a reduction in interception loss. Because of its southerly exposure, any reductions in interception loss on the North Fork are assumed to be offset by increased ablation of the exposed snowpack in the openings where the snowpack melts earlier in the year.

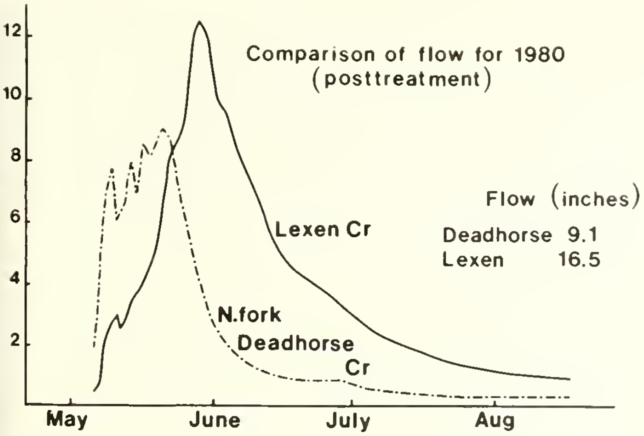


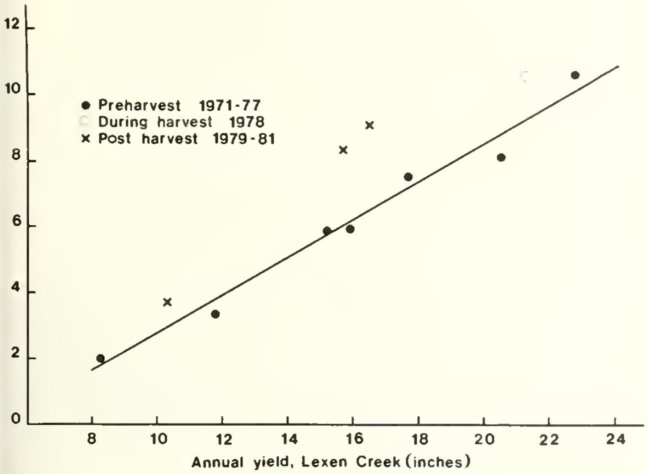
Harvesting timber by removing individual trees under a 3-cut shelterwood on the North Slope (Response Unit 8) significantly reduced evaporative loss of snow that otherwise would have been intercepted by the canopy. Long-term snow measurements on the North Slope and Lexen Creek show that the removal of about one-third of the basal area resulted in an increase in water in the snowpack by an average of 1.5 inches. This increase probably reflects a reduction in interception loss by the canopy that is not offset by increases in ablation loss from the snowpack below. The North Slope has a north exposure where shading of the snowpack is more effective in reducing evaporative loss than a south exposure In normal water years, most of the increase in water in the snowpack can show up as increased streamflow.



Streamflow.—For the first 4 years after timbe harvest, flow from the North Fork (Response Unit increased 1.8 inches. Most of this increase came in Ma because of early melt and reduced recharge requir ments, with no detectable effect from July to Septembe The magnitude of change is correlated with precipit tion—the wetter the year, the larger the increase—a with Fool Creek. Peak discharges occur earlier than o Fool Creek but do not appear to be significantly i creased. It is too soon to determine if the shelterwoo cutting on the North Slope (Response Unit 8) has a signi icant effect, but an increase in streamflow is apparer It is expected that the patch clearcutting in the Upp Basin (Response Units 3 and 4) will result in increases streamflow comparable to the North Fork (Respon Unit 1).

Water Quality.—Estimates of sediment production weir ponds are the only observation of water quali made on Deadhorse and Lexen Creeks. Sediment expo from the North Fork (Response Unit 1) of Deadhor Creek more than doubled following road constructi





nd timber harvest, but recovery appears to have ocurred in 4 to 6 years after harvest:

Year	Sediment		Change
	Expected	Observed	
	lb/acre		
1978	19	52	33
1979	13	26	13
1980	16	23	7
1981	12	2	−10

he significant increase in accumulated sediment was etected at the North Fork weir, but no impact was deected downstream at the main Deadhorse Creek weir.

perational Watershed Management

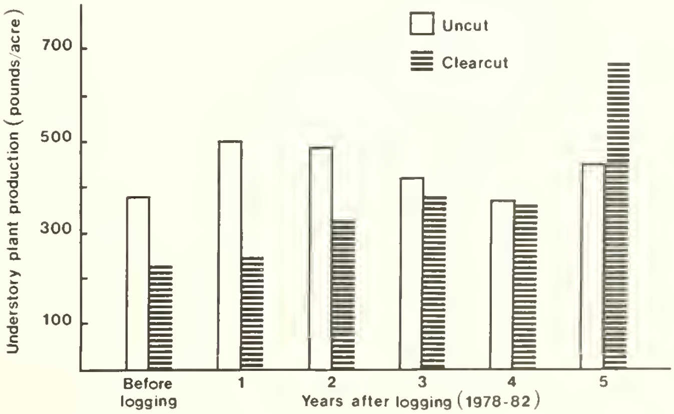
One of the objectives of the Deadhorse Creek study is evaluate and verify the capability to simulate in adance the effect on streamflow of different timber arvesting options. Using the Subalpine Water Balance lodel and a procedure using nomographic simplificaons of the model (WRENSS), predictions were made efore harvesting on the North Fork (Response Unit 1) of e average response expected after timber harvest:

Year	Observed increase	Simulated increase	
		Subalpine Hydrologic Model	WRENSS
	inches		
1978	1.4	1.5	0.9
1979	2.3	1.8	1.8
1980	2.6	1.8	2.0
1981	0.8	1.8	1.6
$\bar{x}$	1.8	1.7	1.6

In general both simulators performed well. Technologies and models developed at the Fraser Experiment Forest are currently being studied in a large-scale pilot program on the East Fork Encampment River in Wyoming that will test water yield augmentation practices developed at Fraser under operational management conditions and evaluate the state-of-art hydrologic model.

Game Animal and Forage Response

Overall plant production was greater during the initial 5 years after clearcutting than before logging on the North Fork of Deadhorse Creek (Response Unit 1). Before harvest, most of the understory vegetation was *Vaccinium* spp. and a few woody plants, and this pattern continued after cutting. Graminoids (mostly sedges) and forbs, scarce in the uncut stand, increased somewhat after clearcutting but remained a lesser understory component. As indicated by percentages of crude protein and digestibility, the relative quality of understory as forage increased during the postlogging period. Pellet counts showed that big game use was low in the Deadhorse Creek watershed and continued so after logging, although a trend toward increased use by both elk and deer was evident on the clearcut areas of the North Fork.



Studies of understory vegetation and big game responses to the first entry shelterwood harvest on the North Slope (Response Unit 8) in 1979–1980 continue. Results will be summarized after the initial 5 years of postharvest observations have been completed.

Nongame Bird and Small Mammal Response

Compared with the uncut controls, clearcutting of small circular patches had little adverse effect on small mammal and songbird populations during the initial 2 years after cutting on the North Fork of Deadhorse Creek (Response Unit 1). Numbers of chipmunks increased, but changes in populations of other small mammals could not be attributed to clearcutting. After logging, bird species density increased in the North Fork, but bird numbers were slightly lower. Most of the decline was to species in picking and gleaning feeding and foliage nesting guilds.

There were about 18 Engelmann spruce, subalpine fir, and lodgepole pine snags 4 inches d.b.h. and larger per acre left on the North Fork after cutting, but less than one-half percent had cavity-nesting holes. Cavity-nesting birds used few of those available, selecting mainly trees larger than 8 inches d.b.h., with broken tops. No other characteristics examined seemed important in nest site selection.

Temperature and Humidity in Subalpine Watersheds

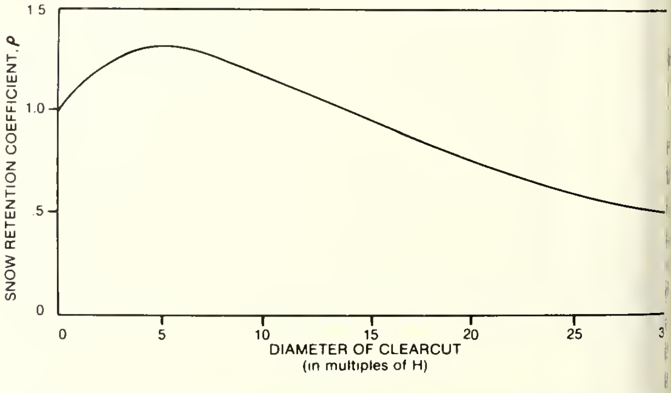
Studies were conducted to determine how air and canopy temperature and ambient absolute humidity could be predicted for subalpine watersheds, using weather data collected at a central weather station near the lower end of the watersheds. Direct beam irradiance had very little effect on air or canopy temperature, but temperatures within watersheds were influenced strongly by elevation. During most of the daylight hours, temperatures in watersheds could be estimated from central weather station temperatures adjusted with a standard adiabatic lapse rate effect of −5.4° F per 1,000-foot increase in elevation.

Cold air drainage reduced air temperatures at the central weather station by nearly 13° F during most of the night and early morning hours. Cold air drainage must be taken into account in estimating watershed temperatures from lower-elevation weather records. The cold air drainage provides a daily sample of upper-elevation air masses at the lower-elevation weather station. Thus humidity measurements made at lower elevations during cold air drainage can be used to estimate upper-level ambient absolute humidities or vapor pressures. However, localized thunderstorm activity causes variation in temperature and humidity during the storm period.

Water Transport and Use

Timber Harvesting Options and Snowpack Accumulation

Timber harvesting effects on snowpack accumulation have been a common objective of most watershed studies on the Experimental Forest. Clearcutting has had the most significant impact. Accumulated knowledge from numerous studies led to the development of a relationship between opening size, expressed in average tree heights, and the increase in snowpack accumulation. Openings trap more snow at the expense of the downwind forest because of changes in the aerodynamics of the forest canopy. Circular plots, 5 tree heights (5H) in diameter, were used on the North Fork of Deadhorse Creek because they are the optimal size for maximum snowpack accumulation. Irregular-shaped openings, 2H to 8H wide, are also considered practical, but large openings in excess of 15H in diameter have been considered detrimental to snowpack accumulation and water yield because wind scour reduces net precipitation. Partial cutting and/or thinning have not been considered as snowpack management alternatives because there is little or no opportunity for the redistribution of snow associated with clearcutting.



However, recent studies of thinning in young lodgepole pine and partial cutting in mature pine and spruce fir indicate that these practices may result in a ne increase in peak water equivalent. Preliminary results indicate that canopy reduction from removal of trees on an individual basis results in less interception of snow and subsequent evaporation from the canopy, resulting in a net increase in the snowpack on the ground. This increased snowpack will result in an increase in streamflow in all but the driest years.

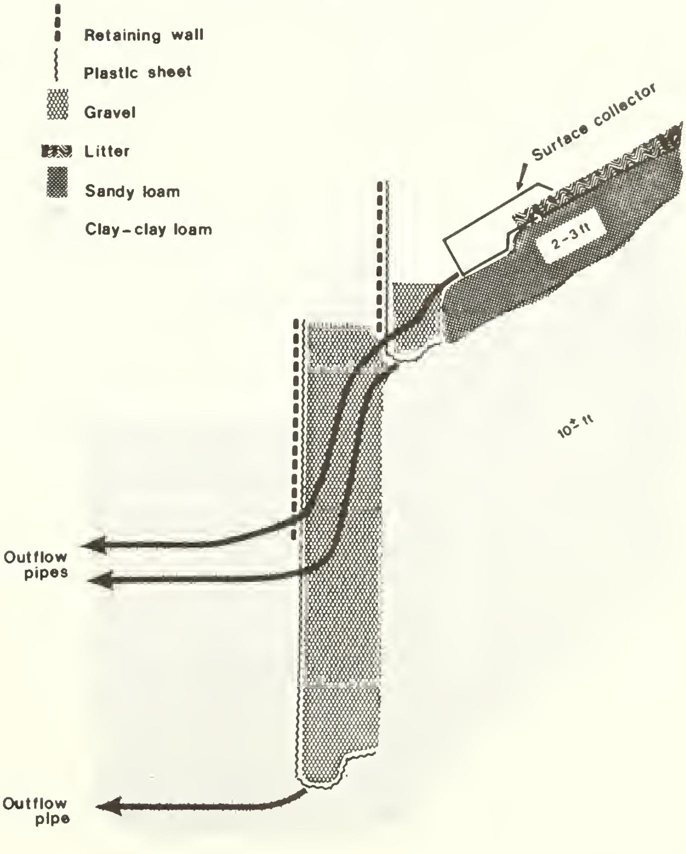
Research is also continuing on how large clearcuts—n excess of 15H—can be managed to minimize wind cour and maintain the snowpack on site. In a 22H openng where there were numerous residual stems and oderately heavy slash was left in place to provide oughness to retain snow, 20% to 30% more water acumulated in the snowpack than in the uncut forest. fter the residual standing stems were removed, the emaining 18 to 24 inches of slash retained 10 inches of ater in the snowpack, but wind scour removed about 0% to 80% of the additional snow after the slash was lled with snow. How long the slash will be effective is ot known. Other alternatives, such as windrowing rge material to maintain roughness until new regenerion can provide it naturally, need to be examined. esearch will continue on how to describe the nature of e required surface roughness in large openings and on ow to provide it.

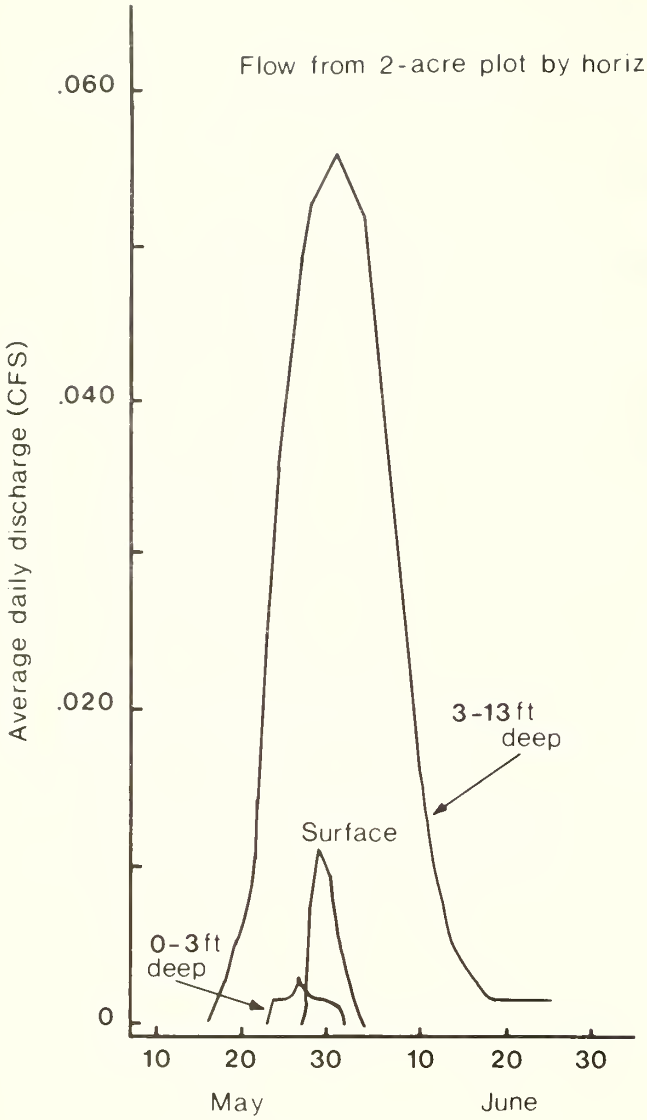
echanics of Meltwater Movement

The pathway that meltwater takes as it moves rough the soil to the stream channel greatly affects its ltimate disposition—whether the water is stored in lace, lost to vapor through evapotranspiration, ecomes streamflow, or enters the groundwater eserve. The significance of snow redistribution in the ydrologic cycle depends upon what happens to meltater, as do increases in water following partial cutting ecause the increase in water equivalent must reach e stream channel to affect water yield. Timber harvest at reduces vegetation also reduces transpirational epletion of soil water, thereby making more on-site ater available for streamflow. The mechanism by hich water is routed through the soil controls the effiency by which different timber harvesting practices d/or locations influence streamflow.

How water moves through the soil and the effects of nber harvesting on soil water content have been udied for several years. Study plots 50 to 100 feet wide d 600 feet long were installed to intercept and measure water moving laterally down forested hillsides on the surface and from two subsurface layers (0–3 feet and 3–13 feet below the surface). Observations from these plots indicate that meltwater generally infiltrates the soil mantle and percolates into less permeable layers; this results in a buildup of a temporary water table, causing the meltwater to move laterally downslope toward the stream. On the study sites, a restricting layer occurs 7 to 10 feet below the surface, and under continuous melt the soil mantle above this layer saturates and a perched water table develops resulting in significant lateral or downslope subsurface water movement. Most flow occurs in the deeper soil layers, with successively more occurring in shallower layers as the perched water table builds toward the surface. Little surface water flow has been observed. In most years, 6 to 8 inches of water equivalent has been lost from the snowpack before significant lateral subsurface flow occurred. For the study site, this represents an estimate of the recharge requirements under fully forested conditions. This information will assist in improving the Subalpine Hydrologic Model by providing a more site-specific simulation of impacts on water yield following timber harvest or other management activities that manipulate vegetation.

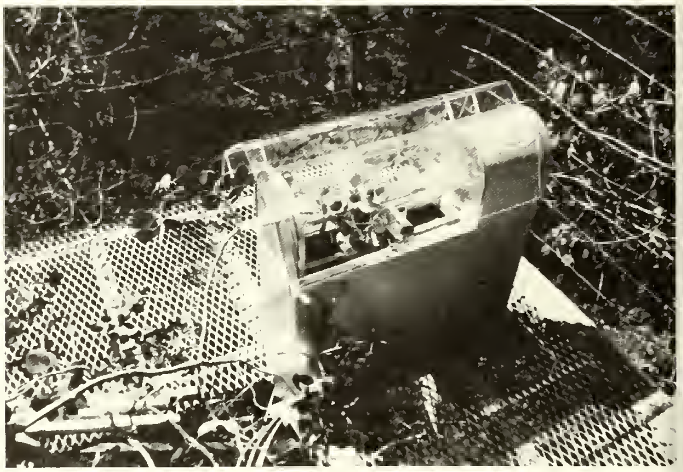
Surface/Subsurface Flow Collection System

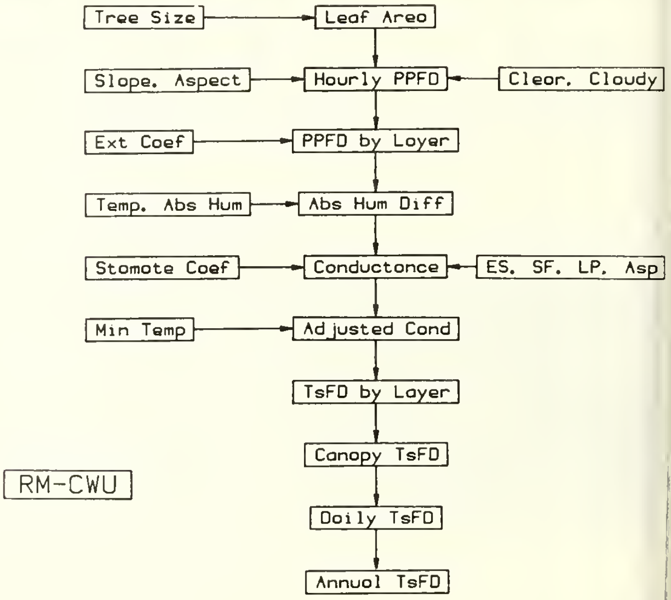




Tree Stomatal Behavior and Transpiration

About half of the precipitation falling on the Fraser Experimental Forest as either snow or rain is lost by evapotranspiration before it reaches the stream channel. Most of this loss is transpiration of water vapor from forest tree canopies. Stomatal regulation of gas exchange between air and plant is the key to transpiration. Using chambers to measure transpiration, it has been determined that the stomata of different tree species on the Fraser Experimental Forest respond primarily to visible irradiance and the humidity difference from leaf to air, with secondary responses to plant water stress and low temperature. Knowledge of stomatal behavior of forest trees has been used to develop a canopy layer model (RM–CWU) that estimates annual transpiration of subalpine forest canopies and stands for a wide range of stand and physiographic conditions.

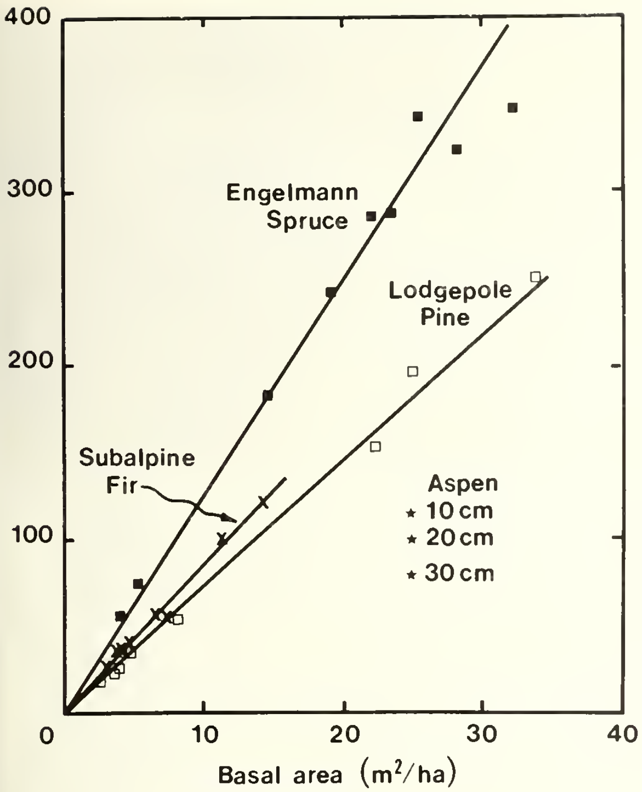




Tree Species Differences in Transpiration and Water-Use Efficiency

Differences in rates of transpiration among tre species in subalpine forests means that some specie utilize less water and leave more available fo streamflow. Data collected on the East St. Louis an Lexen Creek drainages show that in comparable stand Engelmann spruce transpires 72% and subalpine f 17% more water than lodgepole pine:

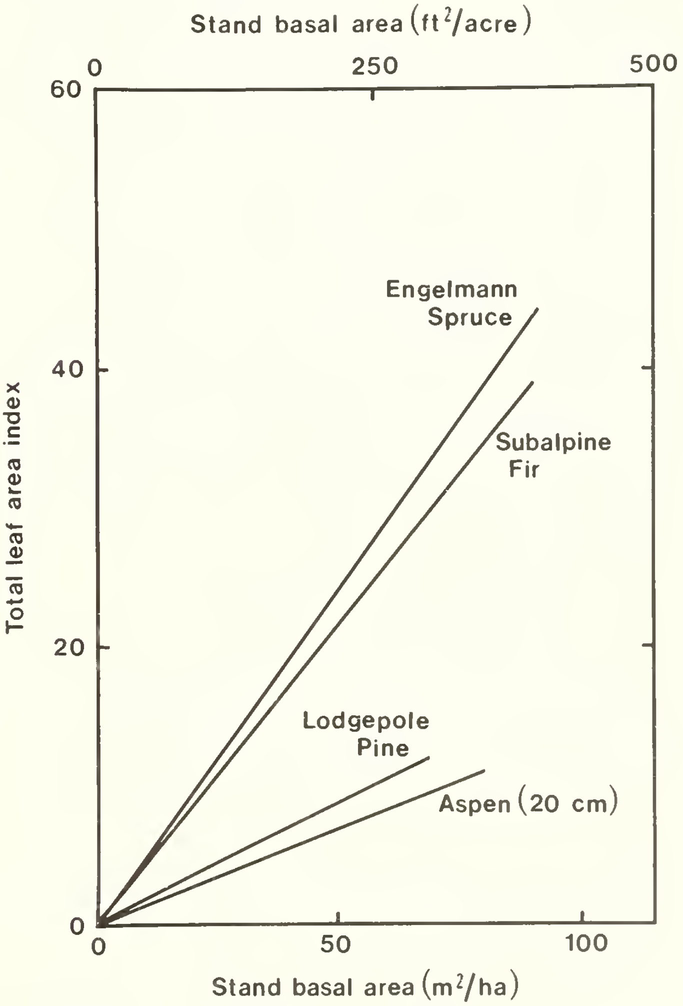
Rotation period	Timber volume	Transpiration	Water-us efficienc
	m³/ha		m³/m³
Lodgepole pine			
120 years	505	205,000	0.0025
Engelmann spruce			
120 years	448	323,000	0.0014
180 years	762	602,000	0.0013



While these watersheds do not contain aspen, estimates of the annual transpiration of aspen indicate less water used than by conifers. Under similar condition, sites where aspen stands occur are in part more moist because aspen uses less water. Large differences in transpiration between forest tree species suggests that total runoff from a watershed may be influenced by regulating species composition. Lodgepole pine has a much higher water-use efficiency because less water is used by pine to produce the same volume of wood as spruce-fir forests under the same site and stand conditions.

Foliage Area of Forest Tree Species

Surface area of tree foliage is an important factor in many forest processes and conditions such as transpiration, photosynthesis, interception of precipitation, environmental conditions on the forest floor, and wildlife habitat conditions within and beneath the forest canopy. Engelmann spruce, subalpine-fir, lodgepole pine, and aspen show a good relationship between leaf area and cross-section area of sapwood conducting tissue, and between leaf area index and basal area of each species in a stand. These relationships resulted in the development of predictive tools for estimating leaf area index from routine stand measurements that is a significant improvement over earlier estimates from crown closure and crown cover density.

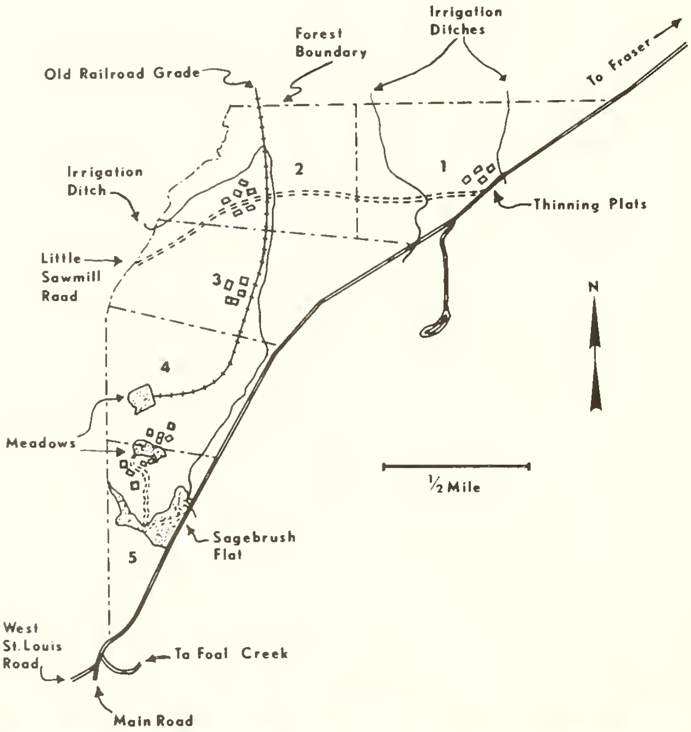


Factor	Engelmann spruce	Subalpine fir	Lodgepole pine	Aspen
Midday leaf conductance (cm/sec)				
Full sunlight	0.06	0.04	0.012	0.20
10% full sunlight	0.02	0.01	0.04	0.07
Leaf-air temperature difference (°C)	0	0	0	−1 to −5
Leaf area index (m^2/m^2)	15	5	6	5
Length of transpiration season (days)	210–245	210–245	210–245	105–115

Levels of Growing Stock—Young Lodgepole Pine

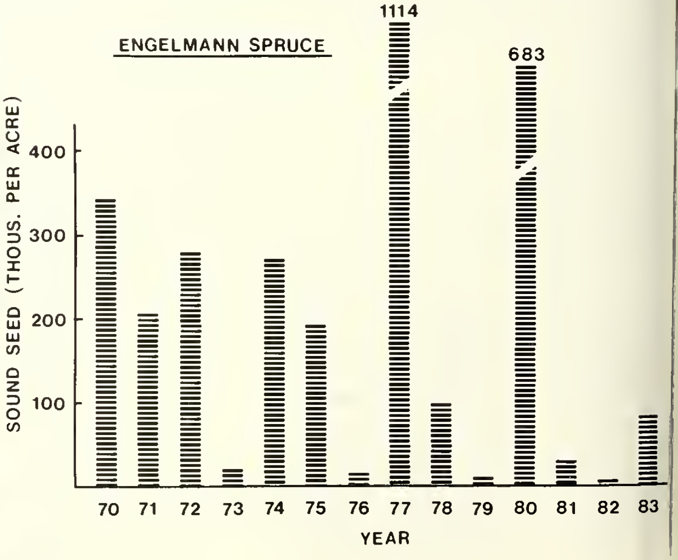
In 1975, a study was started in 60- to 70-year-old second-growth lodgepole pine stands on St. Louis Creek drainage to test different thinning levels. The study area was divided into five units, with one unit thinned each year for 5 years. Within each unit, four 0.4-acre plots were thinned from below, each to a different growing stock level (GSL's 40, 80, 100, 120). The first series of plots in Unit 1 were thinned in 1976, the last series of plots in Unit 5 were thinned in 1980. Additional plots thinned to a growing stock level of GSL 160 were added in 1981 in Units 2, 3, and 4. Suitable stands were not available in Units 1 and 5.

Periodic remeasurement will provide information on stand growth at different stocking levels, rate of spread and intensification of dwarf mistletoe infection, relative herbage production in relation to basal area of residual overstory, soil moisture withdrawal in relation to overstory density and depth below the soil surface, and seasonal progress of soil moisture depletion. Present plans call for rethinning every 20 years to maintain stocking levels.



Engelmann Spruce Seed Production

A long-term study of Engelmann spruce seed production was started in 1968 on the Forest. By 1970, thirteen 0.4-acre plots had been established in stands with different age-classes and site characteristics. Good-to-heavy seed crops were produced during 7 of the first 14 years of observation, with some locations occasionally producing bumper crops. A higher proportion of sound seeds were produced in years with good-to-bumper crops than in years of poor-to-fair crops. Seed production was related to the number per acre and height of dominant and codominant spruces. This study will be continued to provide data needed to refine estimates of the frequency of good seed crops and the proportion of sound seeds produced in relation to total seedfall, and to identify the kinds of stands that produce good seed crops.



Aspen Thinning

An aspen thinning study was established in 1981 to determine the growth response of a 65-year-old aspen stand to treatments that remove 0%, 25%, 50%, 75%, and 100% of the original stand basal area. Half of each treatment area was fenced to exclude domestic livestock and big game. In addition to growth response, the effects of thinning on sucker response, production of understory vegetation, soil moisture, occurrence of disease, and use by large animals are monitored annually or throughout the growing season.

Expansion of Aspen in Conifer-Dominated Stands

Small patches of aspen, or widely spaced individual trees, grow in extensive conifer-dominated stands throughout the Rocky Mountains. Aspen provides prime habitat for many wildlife species, and its expansion into existing coniferous stands could improve habitat for current users and provide habitats for some species that conifers do not provide. Studies are currently underway in small circular openings with differing amounts of aspen and conifers, to determine how much residual aspen is required to insure that aspen is the dominant species after clearcutting. Concurrent studies are comparing species of nongame birds and mammals in small aspen patches growing as inclusions in extensive stands of 70-year-old lodgepole pine.

Initial Spacing of Lodgepole Pine

In 1984, a study was started to test the effects of initial spacing (500, 1,000, 1,500, and 2,000 stems per acre) on the diameter and height growth of lodgepole pine from the time of establishment until trees reach age 20 years.

Cutting Methods Demonstration Plots

Twelve cutting methods demonstration plots were installed on the Fraser Experimental Forest in 1983. Six cutting methods representing both even- and uneven-aged silviculture are duplicated in spruce-fir and lodgepole pine stands. Even-aged silviculture is represented by clearcutting and three shelterwood options. Clearcutting removed all growing stock regardless of size. Twoand three-step shelterwood removed trees from below, leaving the larger trees to provide a seed source and overstory shelter to new reproduction. Simulated shelterwood removed the overstory from a established stand of advanced reproduction.

Uneven-aged silviculture is represented by individua tree and group selection cutting methods. Individua tree selection removed trees in all diameter classes from multistoried stands. Group selection in lodgepole pin removed trees in groups in a stand composed of severa age classes. Group selection in spruce-fir stands removed groups of trees in a stand where trees were naturally clustered in groups separated by small openings.

SIDELIGHTS

Facilities of the Fraser Experimental Forest are used ccasionally for graduate training, undergraduate field ork, field meetings of forestry and conservation ocieties, and Foreign Agriculture Service programs in orestry. Excellent examples nearby serve as on-the-round illustrations of both beneficial and harmful anagement practices in mountain ecosystems.

Opportunities for graduate students to undertake funamental research in conservation and use of natural sources are excellent. Arrangements may be made on cooperative basis with the USDA Forest Service rough colleges, universities, foundations, or other terested groups.

The Fraser Experimental Forest is also a Biosphere eserve (MAB–8) in the Man in Biosphere (MAB) proam, which is designed with full recognition that ooperative interdisciplinary research at all levels is eeded if pressing global environmental problems are to solved. It is an intergovernmental effort to focus search, education, and technical training on filling is need.

Visitors are always welcome. To obtain more detailed published information about the experimental work, ask the resident scientists or send a request to Director, Rocky Mountain Forest and Range Experiment Station, 240 West Prospect, Fort Collins, Colo. 80526.

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APPENDIX 1

List of Ph.D. Dissertations and Masters' Theses

Timber Management

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Tree Physiology

onco, Frank. 1967. The influence of high light intensity on the survival of planted Engelmann spruce. D.F. dissertation, 128 p. Duke University, Durham, N.C. [Diss. Abstr. 29(2B):0429].

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Fire and Atmospheric Sciences

ergen, James D. 1964. Some aspects of cold air drainage on a forested mountain slope. Ph.D. dissertation, 188 p. Colorado State University, Fort Collins. [Diss. Abstr. 28(5B):2077].

cCammon, Bruce P. 1974. Snowpack influences on dead fuel moisture. M.S. thesis, 47 p. Colorado State University, Fort Collins.

Watershed Management and Soils

Meteorology

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Water Yield

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Measurement Techniques and Instrumentation

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Multiple Use

Black, Peter Elliott. 1961. Timber and water resource management. A physical and economic approach to multiple-use on Denver's municipal watershed. Ph.D. dissertation, 130 p. Colorado State University, Fort Collins. [Diss. Abstr. 22(5):1335].

Wildlife Habitat Management

Milchunas, Daniel G. 1977. In vivo-in vitro relationships of Colorado mule deer forage. M.S. thesis, 133 p. Colorado State University, Fort Collins.

Porter, Kenneth A. 1959. Effects of sub-alpine timber cutting on wildlife in Colorado. M.S. thesis, 92 p. Colorado State University, Fort Collins.

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APPENDIX 2

Species List of Birds

Common Name	**Scientific Name**
MIGRATORY BIRDS	
Mallard	*Anas platyrhynchos*
Teal	*Anas* spp.
Golden eagle	*Aquila chrysaetos*
American kestrel	*Falco sparverius*
Spotted sandpiper	*Actitis macularia*
Mourning dove	*Zenaida macroura*
Rufous hummingbird	*Selasphorus rufus*
Black-billed magpie	*Pica pica*
Clark's nutcracker	*Nucifraga columbiana*
Black-capped chickadee	*Parus atricapillus*
Mountain bluebird	*Sialia currucoides*
Red-winged blackbird	*Agelaius phoeniceus*
Western flycatcher	*Empidonax difficils*
Western wood pewee	*Contopus sordidulus*
Olive-sided flycatcher	*Nuttallornis borealis*
Horned lark	*Eremophilia alpestris*
Steller's jay	*Cyanocitta stelleri*
Common crow	*Corvus brachyrhynchos*
Dipper	*Cinclus mexicanus*
Red-breasted nuthatch	*Sitta canadensis*
White-breasted huthatch	*S. carolinesis*
Brown creeper	*Certhia familaris*
American robin	*Turdus migratorius*
Townsend's solitaire	*Myadestes townsendi*
Hermit thrush	*Catharus guttatus*
Gold-crowned kinglet	*Regulus satrapa*
Ruby-crowned kinglet	*R. calendula*
Yellow-rumped warbler	*Dendroica coronata*
Song sparrow	*Melospiza melodia*
Lincoln's sparrow	*M. lincolnii*
Wilson's warbler	*Wilsonia pusilla*

Common Name	**Scientific Name**
SEASONAL NESTING BIRDS	
Goshawk	*Accipiter gentilis*
Sharp-skinned hawk	*A. striatus*
Marsh hawk	*Circus cyaneus*
Red-tailed hawk	*Buteo jamaicensis*
Screech owl	*Otus asio*
Great horned owl	*Bubo virginianus*
Common nighthawk	*Chordeiles minor*
Broad-tailed hummingbird	*Selasphorus platycercus*
Northern flicker	*Colaptes auratus*
Yellow-bellied sapsucker	*Sphyrapicus varius*
Williamson's sapsucker	*S. thyroideus*
Hammond's flycatcher	*Empidonax hammondii*
House finch	*Carpodacus mexicanus*
Pine grosbeak	*Pinicola enucleator*
Pine siskin	*Carduelis pinus*
Red crossbill	*Loxia curvirostra*
Dark-eyed junco	*Junco hyemalis*
White-crowned sparrow	*Zonotrichia leucophrys*
YEARLY RESIDENT BIRDS	
Blue grouse	*Dendragapus obscurus*
White-tailed ptarmigan	*Lagopus leucurus*
Hairy woodpecker	*Picoides villosus*
Downy woodpecker	*P. pubescens*
Three-toed woodpecker	*P. tridactylus*
Gray jay	*Perisoreus canadensis*
Common raven	*Corvus corax*
Mountain chickadee	*Parus gambeli*

APPENDIX 3

Species List of Mammals

Common Name	Scientific Name
Vagrant shrew	*Sorex vagrans*
Northern watershrew	*S. monticolus*
Masked shrew	*S. cinereus*
Little brown myotis (bat)	*Myotis lucifugus*
Black bear	*Ursus americanus*
Marten	*Martes americana*
Longtail weasel	*Mustela frenata*
Shorttail weasel (rare)	*M. erminea*
Mink (rare)	*M. vison*
Striped skunk	*Mephitis mephitis*
Badger (occasional)	*Taxidea taxus*
Red fox	*Vulpes vulpes*
Gray fox	*Urocyon cenereoargenteus*
Coyote	*Canis latrans*
Mountain lion (rare)	*Felis concolor*
Bobcat	*Lynx rufus*
Yellowbelly marmot	*Marmota flaviventris*
Golden mantled squirrel	*Spermophilus lateralis*
Least chipmunk	*Eutamias minimus*
Colorado chipmunk (questionable)	E. quandrivittatus
Uinta chipmunk	*E. umbrinus*
Red squirrel	*Tamiasciurus hudsonicus*
Northern pocket gopher	*Thomomys talpoides*
Deer mouse	*Peromyscus maniculatus*
Bushytail woodrat	*Neotoma cinerea*
Mountain phenacomys (Heather vole)	*Phenacomys intermedius*
Boreal roadback vole	*Clethrionomys gapperi*
Montane vole	*Microtus montanus*
Long-tailed vole	*M. longicaudus*
Western jumping mouse	*Zapus princeps*
Muskrat	*Onadatra zibethica*
Beaver	*Castor canadensis*
Porcupine	*Erethizon dorsatum*
Pika	*Ochotona princeps*
Snowshoe hare	*Lepus americanus*
Elk	*Cervus elaphus*
Mule deer	*Odocoileus hemionus*
Moose	*Alces alces*

Alexander, Robert R., Charles A. Troendle, Merrill R. Kaufmann, Wayne D. Shepperd, Glenn L. Crouch, and Ross K. Watkins. 1985. The Fraser Experimental Forest, Colorado: Research program and published research 1937–1985. USDA Forest Service General Technical Report RM-118, 46 p. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo.

This report provides an overview of the research done on the Fraser Experimental Forest. It replaces GTR's no. 40 and 40A by Robert R. Alexander and Ross K. Watkins in 1977. Included are descriptions of physical features and resources, highlights of past and current research, and the publications derived from that research

Keywords: Cutting methods, forest regeneration, water yield, water-use, wildlife habitat

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U.S. Department of Agriculture
Forest Service

Rocky Mountain Forest and Range Experiment Station

Rocky Mountains

Southwest

Great Plains

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Department of
Agriculture

Forest Service

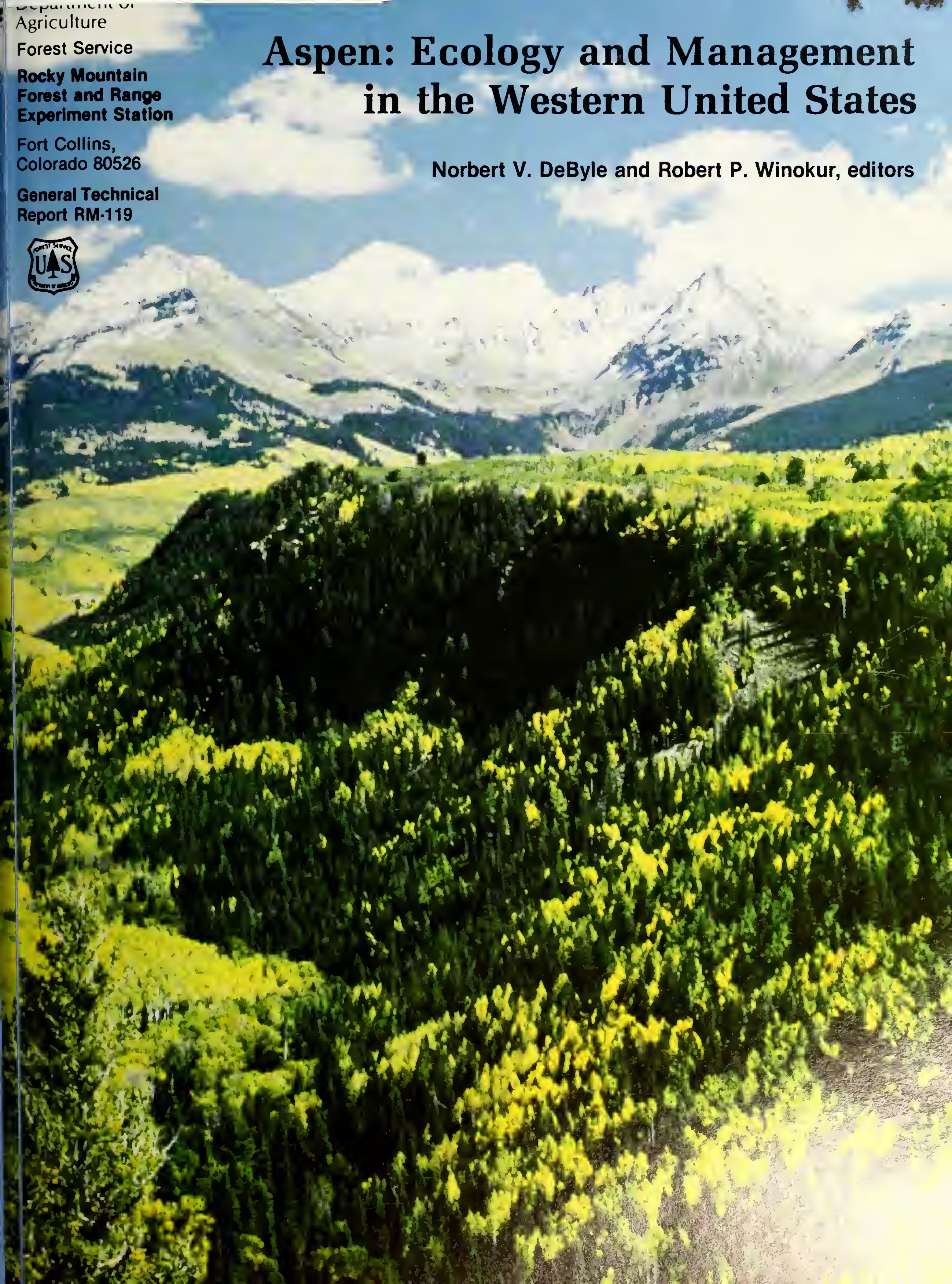
**Rocky Mountain
Forest and Range
Experiment Station**

Fort Collins,
Colorado 80526

**General Technical
Report RM-119**

Aspen: Ecology and Management in the Western United States

Norbert V. DeByle and Robert P. Winokur, editors



Abstract

Information about the biology, ecology, and management of quaking aspen on the mountains and plateaus of the interior western United States, and to a lesser extent, Canada, is summarized and discussed. The biology of aspen as a tree species, community relationships in the aspen ecosystem, environments, and factors affecting aspen forests are reviewed. The resources available within and from the aspen forest type, and their past and potential uses are examined. Silvicultural methods and other approaches to managing aspen for various resources and uses are presented.

For sale by the Superintendent of Documents, U.S. Government Printing Office, Washington, D.C. 20402

FOREWORD

This book reviews the body of knowledge applicable to ecology and management of aspen on the mountains and plateaus of the interior western United States and, to a lesser extent, Canada. Alaska and Canada farther north and east are only incidentally considered. Much of the information on aspen is from other parts of North America. If something was pertinent to aspen in the West, it was included. The large volume of knowledge about aspen in the Lake States and eastern Canada is included only when it applies to the West.

This book is organized in four parts: PART I. THE TREE, reviews the biology of aspen as a species. PART II. ECOLOGY, reviews environments and community relationships. PART III. RESOURCES AND USES, considers the resources available in and from the aspen forest type. All of these provide the background for PART IV. MANAGEMENT, which discusses silvicultural methods and management approaches.

This is a reference and source book—a structured compilation and review of information. The authors have attempted to resolve contradictions in the literature, and have summarized each subject area to the best of their understanding. Gaps in knowledge are apparent as voids in this compilation; pure speculation is avoided. Because this publication will be used as a reference, each chapter is fairly self-contained. As a result, there is some repetition among chapters, with a different content and focus in each.

The latest available information has been included wherever feasible. However, as aspen research continues, new findings may differ from those presented here. Nevertheless, this book should provide a foundation upon which new research can build.

A compilation of this nature and size would not be possible without the able assistance of many people. Each of the authors deserves a special thanks for searching the literature, interpreting and summarizing it, and then writing chapter(s) that fit the style and objectives of this volume.

John R. Jones began this work several years ago, and developed the basic organization of this publication. He amassed a wealth of aspen literature and wrote the first drafts of all chapters that bear his name as an author. Later revisions, updates, and sometimes extensive rewriting of these chapters by others, as well as preparation of new chapters resulted in additional authorship credit. Thanks John, for getting us started on this needed publication!

More than 40 people technically reviewed chapters of this volume. George Schier of the Intermountain Forest and Range Experiment Station, and Burton Barnes of the University of Michigan, provided especially detailed and useful critiques of several chapters. Wayne Shepperd of the Rocky Mountain Forest and Range Experiment Station provided valuable review and revision of most of the chapters in PART IV. MANAGEMENT, consistent with the latest available information. Dean Einspahr at the Institute of Paper Chemistry also was very helpful. Revision of each chapter after high-quality technical review markedly improved this work. We greatly appreciate the contribution of all reviewers, whether or not their names are mentioned.

Special thanks go to Delloris M. Cade, Editorial Assistant at the Rocky Mountain Forest and Range Experiment Station, who spent countless hours reviewing and researching the hundreds of literature citations, and cross-checking them with each chapter, and copy editing and proofreading the typeset galley proofs. Her diligent efforts greatly improved the quality of this book, and speeded its publication.

The authors contributing to this volume are:

Diane M. Bowers, Graduate Student, Department of Biology, Utah State University, Logan, 84322.
Thomas C. Brown, Economist, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo. 80526.
Robert B. Campbell, Botanist, Intermountain Forest and Range Experiment Station, Forestry Sciences Laboratory, Missoula, Mont. 59806.
Norbert V. DeByle, Principal Plant Ecologist, Intermountain Forest and Range Experiment Station, Forestry Sciences Laboratory, Logan, Utah 84321.
Dennis M. Donnelly, Research Forester, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo. 80526.
Kimball T. Harper, Professor, Botany and Range Science Department, Brigham Young University, Provo, Utah 84601.
Thoms E. Hinds, now retired, formerly Research Plant Pathologist, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo. 80526.
Craig W. Johnson, Professor, Landscape Architecture and Environmental Planning Department, Utah State University, Logan, Utah 84322.
John R. Jones, novelist (pen name John Dalmas), formerly Principal Plant Ecologist, Rocky Mountain Forest and Range Experiment Station, Forestry Sciences Laboratory, Flagstaff, Ariz. 86001.
Merrill R. Kaufmann, Principal Plant Physiologist, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo. 80526.
Donald C. Markstrom, Research Wood Technologist, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo. 80526.
Walter T. McDonough, now retired, formerly Principal Plant Physiologist, Intermountain Forest and Range Experiment Station, Forestry Sciences Laboratory, Logan, Utah 84321.

Walter F. Mueggler, Principal Plant Ecologist, Intermountain Forest and Range Experiment Station, Forestry Sciences Laboratory, Logan, Utah 84321.

E. Arlo Richardson, Associate Professor Emeritus and former State Climatologist, Soil Science and Biometeorology Department, Utah State University, Logan, 84322.

George A. Schier, Principal Plant Physiologist, Northeastern Forest Experiment Station, Forestry Sciences Laboratory, Delaware, Ohio 43015.

John D. Shane, Senior Geologist, Exxon Company USA, Houston, Tex. 77001. Formerly a graduate student in the Botany and Range Science Department, Brigham Young University, Provo, Utah.

Wayne D. Shepperd, Silviculturist, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo. 80526.

Michael L. Timmons, Associate Professor, Landscape Architecture and Environmental Planning Department, Utah State University, Logan, 84322.

Eugene M. Wengert, Extension Specialist, Department of Forest Products, Virginia Polytechnic Institute and State University, Blacksburg, Va. 24061. Formerly Research Wood Technologist at the USDA Forest Products Laboratory, Madison, Wisc., on assignment to the Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo.

Robert P. Winokur, Supervisory Technical Publications Editor, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo. 80526.

Harold E. Worth, now retired, formerly Principal Market Analyst, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo. 80526.

Aspen: Ecology and Management in the Western United States

Norbert V. DeByle and Robert P. Winokur, editors[1]

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[1] *DeByle is Principal Plant Ecologist, Intermountain Forest and Range Experiment Station, at the Station's Forestry Sciences Laboratory in Logan, Utah. Station headquarters is in Ogden, Utah. Winokur is Supervisory Technical Publications Editor, Rocky Mountain Forest and Range Experiment Station. Station headquarters is in Fort Collins, in cooperation with Colorado State University.*

Aspen: Ecology and Management in the Western United States

Norbert V. DeByle and Robert P. Winokur, editors

INTRODUCTION

Norbert V. DeByle and Robert P. Winokur

Quaking or trembling aspen (*Populus tremuloides* Michx.) is the only aspen in western North America. Therefore, in this part of the continent, it is commonly and correctly referred to simply as "aspen". Throughout much of the interior West, it is the only upland hardwood. Aspen occupies millions of acres, and, in some states, it is the most widespread forest type.

This review begins with the description by Charles Sprague Sargent (1890):

> "In the West and Southwest, Aspen grows on the high slopes of mountains and along the banks of streams, and is usually not large, although individuals a hundred feet tall sometimes occur.... A graceful tree with its slender pendulous branches, shimmering leaves, and pale bark, the aspen enlivens the spruce forests of the north, and marks steep mountain slopes with broad bands of color, light green during the summer and in autumn glowing like gold against backgrounds of dark cliffs and stunted pines."

Several major publications about aspen ecology and management predate this one. Most notable are: "Aspens: Phoenix Trees of the Great Lakes Region" by Graham et al. (1963), "Aspen: Symposium Proceedings" published by the USDA Forest Service (1972), and "Quaking Aspen: Silvics and Management in the Lake States" by Brinkman and Roe (1975). All deal specifically with the aspen east of the Great Plains. Aspen was also given major consideration in "Growth and Utilization of Poplars in Canada" by Maini and Cayford (1968). For the western United States, Frederick Baker's (1925), "Aspen in the Central Rocky Mountain Region," remains a rich source of information, although it is clearly outdated in several respects.

The aspen-dominated forest has multiple values. It is truly a multiple-use type. In the West, it is a producer of forage for domestic livestock as well as food and cover for many wildlife species. It produces wood fiber in abundance, but has been grossly underutilized in this respect. Yields of high-quality water are greater from aspen forests than from some other forest types on similar sites in the western mountains. Esthetically, aspen is very appealing, especially when juxtaposed as groves within a mosaic of other vegetation types on the landscape. It attracts recreationists. Aspen forests also provide fire protection by acting as living firebreaks for the more flammable coniferous types.

Perhaps because aspen has not been economically appealing to wood-using industries in the West, there has been little urgency to learn the details of aspen ecology and to design effective management methods. Aspen research in the West has been somewhat piecemeal, with emphasis on specific attributes, such as forage production or water yield. However, both the utilization and research situations are changing. The sheer amount of aspen, its rapid regeneration by root sprouts after fire or logging, its rapid growth, and other characteristics that make the species distinctive are stimulating greater interest. Increasing demands are being made for the goods and services the aspen type can provide. These demands have caused forest managers and researchers, particularly in Colorado, Utah, Arizona, and New Mexico, to express a need for a synthesis of the available ecological and management information applicable to the western aspen type. This publication has been prepared in response to that increasing need.

PART I. THE TREE

PART I. THE TREE

Page

TAXONOMY

Kimball T. Harper, John D. Shane, and John R. Jones

Quaking aspen, or trembling aspen (*Populus tremuloides*), was named and described by Michaux in 1803. It exhibits marked phenotypic variability throughout its transcontinental range. Numerous authors, especially the early ones, tried to give order to the variability by subdividing it taxonomically. Quaking aspen has been subdivided by various taxonomists at one time or another into 4 species and 13 varieties or forms (Barnes 1969, Beetle 1974). However, Little (1953, 1979) recognized quaking aspen as a single heterogeneous species without subspecific taxa. Barnes (1969) found that much of the total morphological variation within the whole complex can be found in various combinations within single locales. His observation is supported indirectly by numerous observations and investigations of the variation in aspen in the West, notably by Greene (1971).

This report follows Barnes (1969), Little (1979), and current usage in accepting quaking aspen, throughout its North American range, as a single, highly variable species, *Populus tremuloides* Michx.

Paleobotany

Trees similar to quaking aspen appear to have flourished throughout western North America since middle Miocene time, almost 15 million years ago (Axelrod 1941, Chaney 1959, Smiley 1963, Wolfe 1964). In Miocene deposits, quaking aspen-like leaves have usually been designated as *Populus voyana* Chaney and Axelrod (Chaney and Axelrod 1959). Fossil specimens of *P. voyana* display large, apparently thin leaves similar to those produced by living *P. tremuloides* in the wetter portions of its range. Wolfe (1966) gave the name *P. kenaiana* to another Miocene fossil aspen from the Kenai Formation of the Cook Inlet region of Alaska. Although he did not equate his specimen to any living poplar, the leaf used to illustrate the new species seems well within the morphological limits displayed by published silhouettes of leaves from living populations of *P. tremuloides* from Utah, northern Idaho and adjacent Montana, and Vancouver Island (Barnes 1975).

Pliocene fossils referable to quaking aspen have smaller, thicker leaves than those of *P. voyana*. The Pliocene material is commonly assigned to *P. pliotremuloides* Axelrod. These leaves appear to reflect somewhat drier habitats than were common during the Miocene (Chaney and Axelrod 1959). Another fossil poplar, *P. eotremuloides* Knowlton, despite its name, apparently is not related to quaking aspen, but to *P. trichocarpa* (Chaney 1938).

Three other fossil aspen species (*P. booneana* Smith, *P. subwashoensis* Axelrod, and *P. washoensis* Brown) belong to the section *Leuce* of *Populus*. All were widespread in Miocene and Pliocene fossil floras of the western United States (Chaney 1959, Smiley 1963, Wolfe 1964, Wolfe et al. 1966). These fossil species are considered to be closely related to *P. grandidentata*, a living species now confined to eastern North America (Little 1971). Because *P. grandidentata* currently hybridizes with *P. tremuloides* where the two grow together, Barnes (1967, 1975) suggested that the modern leaf morphology of the latter species in western America may have been strongly influenced by episodes of hybridization during the late Cenozoic era, when ancestors of the two species coexisted in the West. He further emphasized that, because modern clones of quaking aspen are large and apparently very old in unglaciated parts of the central and southern Rocky Mountains, only a few sexual generations may separate living aspen from its Pliocene ancestors.

Apparently, the ancestors of both quaking aspen and bigtooth aspen (*P. grandidentata*) differed somewhat in respect to ecological requirements, because the two species rarely occur in the same fossil bed, although they overlap broadly both in time and space (Chaney and Axelrod 1959). Because the two species hybridize now and may have hybridized anciently (Barnes 1967), their continued existence as different species throughout geological times must have been related to somewhat different ecological requirements.

Upland species commonly found associated with quaking aspen-like fossils include many shrubs and trees but almost no herbaceous species. Trees that frequently occur with aspen in the fossil record include species of the following genera: *Abies*, *Acer*, *Picea*, *Pinus*, *Prunus*, *Quercus*, *Sequoia*, and *Tsuga*. Shrub genera regularly occurring with aspen include *Amelanchier*, *Arctostaphylos*, *Ceanothus*, *Mahonia*, *Rhus*, *Ribes*, and *Symphoricarpos* (Axelrod 1939, 1950, 1956; Chaney 1959; Smith 1941). Quaking aspen continues to be closely associated with most of these genera, at least somewhere within the modern range of the species.

Fossil pollen studies have made very little contribution to knowledge of aspen distribution. *Populus* pollen has a delicate exine and is, therefore, generally poorly preserved (Axelrod and Ting 1960, Sangster and Dale 1961). Also, recognition of *Populus* species by pollen alone is very difficult, as is the case with numerous other woody genera. In contrast, fossil pollen has been useful in indicating the herbaceous angiosperms that may have been associated with aspen in late Cenozoic time. It has been generally concluded that the flowering herbs did not make a significant contribution to the vegetative cover of the earth until Miocene time. During Miocene, there was a pronounced increase in percentage and taxonomic diversity of probable herbaceous pollen types, although macrofossils of herbs remained uncommon (Wolfe 1962). Wolfe (1962) concluded, on the basis of fossil pollen, that the following taxa probably were represented by herbs in a Miocene upland forest of the Oregon Cascades: *Chenopodiaceae*, *Compositae* (including *Chichoreae* and *Astereae*), Galium, *Graminae*, *Malvaceae*, *Onagraceae*, and Valeriana. The woody flora of the beds considered included a fossil quaking aspen (Chaney 1959). Aspen may have occurred in the same community as the herbaceous taxa listed previously.

Relationships

The genus *Populus* has been subdivided into several sections. Aspen belongs to the section *Leuce*, subsection *Tripidae*. In Alberta, Canada, Brayshaw (1965) found what seemed to be evidence that aspen hybridizes in nature with poplars belonging in other sections. However, Ronald et al. (1973) could find no evidence of such crosses in Manitoba, despite widespread association of quaking aspen with species of other sections. In the United States, there are no known natural hybrids of aspen and poplars belonging to other sections.

In some parts of North America, quaking aspen hybridizes naturally with *P. alba* of the subsection *Albidae*, introduced widely from Europe (Barnes 1961, Einspahr and Winton 1977, Spies 1978). However, there are no reports of natural hybrids with *P. alba* in the West.

The only species of subsection *Albidae* native to North America is *Populus monticola* (Sargent 1891), found in southern Baja California, Mexico between 2,100 and 5,100 feet (650 m and 1,550 m) elevation (Standley 1920). Aspen does not grow in that part of Mexico. Bailey (1930) suggested that *P. monticola* is not native at all, but actually *P. alba* var. *subintegerrima* introduced by early Spanish settlers and subsequently naturalized.

The subsection *Tripidae* includes, besides quaking aspen, bigtooth aspen (*P. grandidentata* Michx.) of eastern North America, the Eurasian *P. tremula* Linnaeus, and several Asian taxa. All of the species in subsection *Tripidae* are easily crossed (Einspahr and Winton 1977). Natural hybrids of quaking aspen and bigtooth aspen are fairly common in some eastern locales (Andrejak and Barnes 1969, Barnes 1961, Pauley 1956). Although the occurrence of backcrossing and introgression has been suggested (Barnes 1961, Pauley 1956), they have not been compellingly demonstrated.

Hybrids between quaking aspen and *P. tremula* may survive and grow either well or poorly (Einspahr and Benson 1964; Pauley et al. 1963c, 1963d). However, the same is true of quaking aspen seedlings planted outside their own provenance.

Middle-latitude sources of European aspen, *P. tremula*, survived and grew about as well in Massachusetts as did aspen of local and Lake States sources, while *P. tremula* from Scandinavia performed there about as poorly as western aspen (Pauley 1963, Pauley et al. 1963a, 1963b).

Before 1803, when Michaux described *P. tremuloides*, quaking aspen seems to have been regarded by some simply as an American occurrence of *P. tremula* (Marshall 1785, cited by Sudworth 1934). Pauley[1] wrote that when the full range of variability within each species is considered, there seemed to be no sharp morphological or physiological discontinuities between quaking aspen and *P. tremula*. He wrote further that, physiologically at least, *P. tremuloides* from the Lake States is probably more similar to *P. tremula* of southern Sweden than to *P. tremuloides* of Arizona or the Yukon Territory. Barnes (1975) noted that some Utah clones more closely resembled the Asian aspens *P. rotundifolia* and *P. bonati* than they do quaking aspen clones in the northern Rocky Mountains and adjacent Canada, or those typical of eastern North America.

Considering the broad variability within *P. tremuloides* and the Eurasian and Tertiary aspens, the apparent lack of traits that clearly differentiate them, and the interfertility of modern forms, a case could be made for considering most of the subsection of *Tripidae* a single circumboreal superspecies. But *P. tremuloides* itself, with the broad variability discussed more fully in the GENETICS AND VARIATION chapter, already stretches the concept of a species.

[1] *Personal communication from Scott S. Pauley, February 10, 1964.*

DISTRIBUTION

John R. Jones

Quaking aspen is the most widely distributed native North American tree species (Little 1971, Sargent 1890). It grows in a great diversity of regions, environments, and communities (Harshberger 1911). Only one deciduous tree species in the world, the closely related Eurasian aspen (*Populus tremula*), has a wider range (Weigle and Frothingham 1911).

In the humid East, aspen is distributed relatively continuously. In the West, it is confined to suitable sites on mountains and high plateaus. Aspen is one of the most common trees in the interior West, where its range (fig. 1) coincides rather closely with that of Douglas-fir (*Pseudotsuga menziesii*). In some areas, aspen forms extensive pure stands, while in others, it is a minor component of the forest landscape. For example, the geographic area over which aspen can be found is much greater in Idaho than in Colorado; but in Colorado, aspen forests cover a much greater acreage.

Despite the spotty western distribution, two Rocky Mountain states—Colorado and Utah—are among those with more than 1 million acres of aspen forest. Commercial aspen acreage in both Colorado and Utah comprises more than 25% of all commercial forests in these states. (See the WOOD RESOURCE chapter.)

Figure 1.—The range of aspen in the conterminous western United States (Little 1971).

Aspen occupies more of Utah's forested land than does any other tree species (Green and Setzer 1974). In contrast, Montana's 255,000 acres of aspen are scattered among the middle-elevation conifer forests and at the lower forest boundaries. Almost two-thirds of the aspen acreage in the West is in public ownership.

In Colorado, aspen forests are most prominent west of the Front Range and Sangre de Cristo crests. Miller and Choate (1964) describe aspen as a conspicuous forest type in Colorado, on high plateaus and mesas and on rolling mountains of intermediate elevations.

In Wyoming, Reed (1971) found aspen more prevalent on the west slope of the Wind River Range than on the east slope. In Glacier National Park, Montana, in contrast, Standley (1921) reported aspen abundant only on the east side. Lynch (1955) described the plains margin at the foot of the mountains east of Glacier National Park as the southwestern extremity of the extensive aspen parkland region of Canada.

Merriam (1891) and Patten (1963) described aspen in parts of the northern Rockies as forming scattered groves and small stands, quite different from the extensive aspen forests of northern New Mexico, western Wyoming, and especially Colorado and Utah.

Aspen is a component of several vegetation types. (See the VEGETATION ASSOCIATIONS chapter.) It is found in many young ponderosa pine (*Pinus ponderosa*) stands of the Front Range of Colorado (Gary 1975, Vestal 1917) and the Black Hills of South Dakota (Thilenius 1972). Clements (1910) described it as sharing dominance with young lodgepole pine (*Pinus contorta*) on burns in northern Colorado. Horton (1956) described mixed stands of aspen and lodgepole pine on foothills burns in Alberta, Canada. Moir (1969) found a few aspen sprouts in the understories of almost all climax lodgepole pine stands of the Front Range of Colorado. Aspen groves and individual trees are widespread and often abundant in forests of mixed conifers in the southern Rocky Mountains and Southwest (Jones 1974b). Aspen individuals and clones also are found in many spruce-fir stands in the central and southern Rockies (Alexander 1974), particularly at the lower subalpine elevations. On the Kaibab Plateau, in northern Arizona, aspen forms small, thick stands in drainageways in the ponderosa pine zone; and, in the mixed conifer and spruce-fir zones, it often forms conspicuous margins around islands of grassland (Russo 1964).

Beetle (1974) Langenheim (1962), Marr (1961), and Reed (1971) noted the tendency of aspen to grow on cerain slope aspects, at different elevations in the interior West. Generally, in the northern or the upper altitudinal imits of its range, aspen occupies southerly exposures. For example, in interior Alaska, it is common to south slopes up to 3,000 feet (900 m) altitude (Viereck and Litle 1972). Farther south, or at intermediate elevations, it grows on easterly and even northerly facing slopes as well. In the middle portions of its range, aspen can be found on virtually all exposures. Toward the southern imits of its range, aspen favors the cool northern slopes.

Aspen grows in a broad range of elevations. For example, in north-central Colorado, at about 40° north atitude, it ranges from 5,500 feet to 11,250 feet (1,700 m o 3,400 m) (Greene 1971). Cox (1933), Jones and Markstrom (1973), and Marr (1961) reported it in the Colorado "krummholz," the distorted and dwarfed stands of tree-shrubs near altitudinal timberline. Farher south, in the Pikes Peak area, Schneider (1909) gave he limits of aspen as 6,300 to 10,400 feet (1,900 m to 3,150 m).

Baker (1925) mentioned an upper limit for aspen of 12,000 feet (3,650 m) in Colorado, and equated aspen's upper limit with the spruce-fir timberline. Sudworth (1934) also stated a maximum elevation for aspen of 12,000 feet (3,650 m).

Langenheim (1962) reported that the aspen communiy type west of the continental divide, near Gunnison, Colo., was found as high as 11,200 feet (3,400 m), but only as low as 8,500 feet (2,600 m). In the same area, an extensive spruce-fir forest reached 11,500 feet (3,500 m).

In the Intermountain Region, aspen has been reported as high as 11,000 feet (3,350 m), probably in Utah, and as low as 3,000 feet (900 m), presumably in central Idaho.[1] Houston (1954) gave the upper and lower limits as 8,000 and 5,500 feet (2,450 m and 1,700 m) in southern Idaho. On the high plateaus of south-central Utah, Dixon (1935) mentioned finding dwarf aspens as high as 10,700 feet (3,250 m), in an area where Engelmann spruce (*Picea engelmannii*) was the dominant vegetation up to 11,000 feet (3,350 m).

Strain and Johnson (1963) gave the elevational range as 7,000 to 10,000 feet (2,150 m to 3,050 m) in southeastern Wyoming, where timberline is 11,000 feet (3,350 m). Similar upper elevational limits were given by Reed (1971) for the Wind River Range of west-central Wyoming. In southern Alberta, Day and Duffy (1963) reported aspen only as high as 6,000 feet (1,850 m); where the upper limit of spruce-fir forest is about 7,000 feet (2,150 m), and Douglas-fir about 5,500 feet (1,700 m).

In comparison, Sudworth (1908), described aspen in western Washington as occurring from sea level to 4,000 feet (1,200 m), and in southern California between 6,000 and 10,000 feet (1,850 m and 3,050 m). Strain (1964) described a stand of shrubby aspen at 10,700 feet (3,250 m) in southern California. Sudworth (1908) also reported that aspen in Baja California was restricted to a few locales above 8,000 feet (2,450 m) on the Sierra San Pedro Martir.

Aspen commonly reaches its lowest elevations in canyons and ravines, as noted by Vestal (1917) in Colorado, and Baker (1925) and Dixon (1935) in Utah. These observations have been confirmed by many others in various parts of the West. Seepage flow from higher elevations appears to subirrigate many of these low-elevation aspen sites.

In summary, in the interior West, aspen is confined to relatively moist sites (16 to 40-plus inches (41 cm to 102+ cm) annual precipitation) that have cold winters and a reasonably long growing season. These conditions restrict aspen to low elevations in the northern and eastern portions of its range. Aspen grows at progressively higher elevations southward along the Rocky Mountains. At the southern end of its range, it is virtually restricted to mountaintops. Most commercial sawtimber concentrations are confined to elevations between 7,000 and 10,000 feet (2,150 m and 3,050 m) in the central Rocky Mountains (Colorado, northern New Mexico, and southern Utah).

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[1] *Aspen Committee. 1965. Guidelines for coordination of uses in aspen areas. 13 p. U.S. Department of Agriculture, Forest Service, Intermountain Region, Ogden, Utah.*

MORPHOLOGY

John R. Jones and Norbert V. DeByle

The term "morphology" is used broadly here to include the exterior form of the tree above ground, the root system, and the stand.

Tree Above Ground

Sources for the following description are Barry (1971), Einspahr and Winton (1976), Fechner and Barrows (1976), Harlow and Harrar (1958), Little (1950), Preston (1961), Sargent (1890), and Viereck and Little (1972).

General Characteristics

Aspen is a small to medium-sized deciduous tree with straight trunk and short, irregularly bent limbs, making a narrow dome-like crown. Trees are commonly 20 to 60 feet (6 m to 18 m) tall and 3 to 18 inches (8 cm to 46 cm) in diameter. Occasionally, trees more than 80 feet (24 m) tall and larger than 24 inches (61 cm) in diameter are found.

The bark is smooth with a greenish-white, yellowish-white, yellowish-gray, or grayish to almost white coloration. At maturity the bark may become roughened and fissured.

Small twigs are smooth, slender, flexible, and reddish-brown. Terminal winter buds are 1/4 to 1/2 inch (0.6 cm to 1.3 cm) long, conical pointed, and covered by six to seven, sometimes resinous, reddish-brown scales. The flower buds are larger and ovate (fig. 1).

Leaf blades are thin and firm, nearly round, 1 1/2 to 3 inches (4 cm to 8 cm) in diameter, short-pointed at the apex, rounded at the base, with many small rounded to sharply pointed teeth at the margin (fig. 1). The leaves are smooth, shiny, green to yellowish-green above, and dull beneath. In autumn, the leaves turn bright yellow, gold, orange, or slightly reddish. Petioles are 1 1/2 to 3 inches (4 cm to 8 cm) long and flattened perpendicular to the plane of the blade. The flattened petiole acts as pivot for the blade, which trembles in the slightest breeze. In contrast to the leaves on mature trees, the leaves of young suckers are much larger (sometimes 7 to 8 inches (18 cm to 20 cm) long)), very succulent, often twice as long as they are broad.

Aspen is dioecious, with male and female flowers normally borne on separate trees (fig. 1). Flowering commonly occurs in April or May before the appearance of the leaves. Petalless, unisexual flowers (1/8 inch (0.3 cm) long) are arranged along drooping, flexible, modified spikes (1 to 2 1/2 inches (2.5 cm to 6 cm) long)) called catkins or aments. Individual flowers are inserted singularly on a saucer-shaped disc attached to the stalk by a short pedicle, and are subtended by a brown hairy lobed scale. Male flowers have 6 to 12 stamens. Female flowers have a single ovary composed of two carpels crowned by a short stout style with two erect stigmas.

The seed capsules mature in May and June, when the catkins are 3 1/2 to 4 inches (9 cm to 10 cm) long. They are conical, light-green, thin-walled, 2-valved, and nearly 1/4 inch (0.6 cm) long. The number of capsules per catkin varies from 70 to 100, with 6 to 8 seeds in each. Seeds are pear-shaped, light brown, about 1/32 inch (0.08 cm) long, with a tuft of white hairs attached to the basal end. (See the SEXUAL REPRODUCTION, SEEDS, AND SEEDLINGS chapter.)

The Bark

Descriptions of western aspen trees often mention several bark colors: white, yellow-brown, and green. The white bark, common in the West, results from a coating of dead cork cells that easily rub off (Strain 1961). Some yellow-brown trees have a coating of dead cork cells, too.

Chlorophyll in the bark gives the green color. In northern New Mexico, Covington (1975) found aspen bark to be darker green at higher elevations. But this darker bark actually had less chlorophyll than the lighter-colored bark of aspen at lower elevations; instead, the dead cork cells of dark green bark were more translucent.

The smooth bark characteristic of aspen results from a persistent periderm (Kaufert 1937). Rough bark on aspen in the West is restricted largely to the lower few feet of the bole and as patches higher up. Baker (1925) wrote that rough basal bark in the West results from gnawing by sheep. In the West, the rather uniform upper boundary of dark, rough, fissured bark in some stands suggests a snow line as well as a browse line. Gnawing by rodents beneath the snow surface also stimulates rough bark in aspen (fig. 2) (Hinds and Krebill 1975).

Geometry

Baker (1925) provided data on the relationship of tree height to diameter at breast height (4.5 feet (1.4 m) above ground) (table 1). Because this relationship varies strongly with site quality, there are separate values for sites 1 through 4. However, these data are from a limited geographical area, in which Baker's site 1 does not include the truly best aspen sites found elsewhere in the

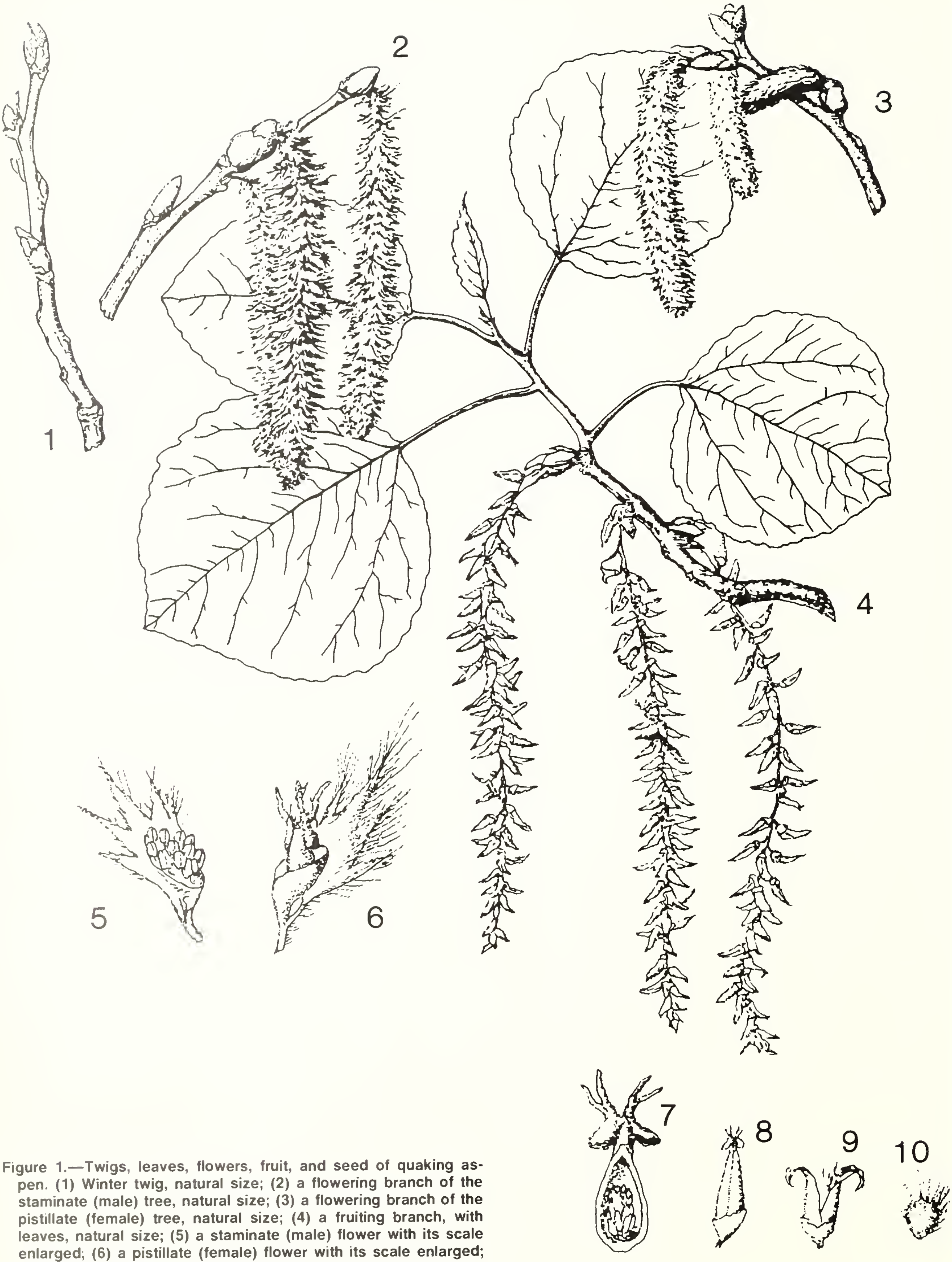

Figure 1.—Twigs, leaves, flowers, fruit, and seed of quaking aspen. (1) Winter twig, natural size; (2) a flowering branch of the staminate (male) tree, natural size; (3) a flowering branch of the pistillate (female) tree, natural size; (4) a fruiting branch, with leaves, natural size; (5) a staminate (male) flower with its scale enlarged; (6) a pistillate (female) flower with its scale enlarged; (7) vertical section of a pistil, enlarged; (8) a fruit, enlarged; (9) a fruit with open valves, enlarged; (10) a seed, greatly enlarged.

Table 1.—Average heights (feet) of aspen of different diameters (inches) on site quality classes 1-4 (Baker 1925).

	Site class			
d.b.h.	**1**	**2**	**3**	**4**
4	40	35	32	30
5	46	41	36	34
6	51	46	41	37
7	57	51	45	39
8	62	56	46	41
9	66	59	51	43
10	70	63	54	45
11	73	66	57	46
12	75	68	58	48
13	76	70	60	N/A
14	78	71	61	N/A
15	79	72	62	N/A
16	80	73	62	N/A
17	81	74	N/A	N/A
18	81	74	N/A	N/A
19	82	74	N/A	N/A
20	82	75	N/A	N/A
21	83	75	N/A	N/A
22	83	75	N/A	N/A

N/A = Not applicable.

West. On these, aspen with the given diameters would grow much taller.

In the West, old trees on mediocre or poor sites sometimes reach large diameters that give them a peculiarly stout-boled stubby appearance. Strain (1964) reported two extreme cases: a 226-year-old aspen that was 39 feet (12 m) tall and 17.3 inches (44 cm) d.b.h., and a 107-year-old tree that was only 10 feet (3 m) tall but 9.2 inches (23 cm) in diameter at the 1-foot (30-cm) height.

Beetle (1974) described the crown spread of aspen of different diameters in Wyoming stands.

d.b.h. (*inches*)	Crown spread (*feet*)
2	5
5	7
7	9
12	12
13–18	13–14

He noted that crown spread, while varying somewhat with stand density, was not great for aspen, even for mature trees.

Beetle (1974) described aspen crowns as round-topped and "one-sided," and "always developed toward the nearest edge of the stand." This crown description is not found elsewhere in the literature. There would seem to be a limit to how far from the edge that condition could occur.

Strain (1964) pointed out that aspen crowns may be either rounded or pyramidal. Clones with branches approximately at right angles to the trunk produce pyramidal tops; those with strongly ascending branches produce round tops. Those tendencies would be modi-

Figure 2.—Dark, rough bark resulting from feeding by voles. (A) Trees with rough bark extending upward to 4 feet (1.2 m). (B) Closeup. (Hinds and Krebill 1975).

fied or strengthened by the relative growth rates of terminals versus lateral shoots.

Aspen trees exhibiting pronounced drooping characteristics have been observed throughout the Rocky Mountain region along roadsides, in campgrounds, and in urban areas (Livingston et al. 1979). Trees affected with this malady "are characterized by pendant branches with shortened internodes and large nodes, large terminal leaves, and a lack of lateral foliage and branching." The pendant growth habit results from punky, rubbery wood in the branches. The cause or causal agents of drooping aspen are unknown. (See the DISEASES chapter.)

Aspen Clones

Barnes (1966) described the clonal habit of aspen. A clone is a group of individuals propagated vegetatively from a single individual of seedling origin, termed the "ortet". The members of a clone, termed "ramets," are genetically identical. (See the GENETICS AND VARIATION chapter.)

As an aspen seedling grows and matures, it develops a widespread root system. Under suitable conditions, typically after fire, this root system gives rise to many shoots, called "root suckers" that form new trees. (See the VEGETATIVE REGENERATION chapter.) These suckers (the ramets) are genetic copies of the original ortet. The genotype present in the ortet survives as a clone through many generations of ramets. In the West, clones apparently persist for thousands of years. By expansion of ramet root systems, a clone may expand over time to cover 100 acres or more, although the area occupied usually is much smaller (Kemperman and Barnes 1976).

The boundary of two adjoining clones is often abrupt and frequently conspicuous (Baker 1921, Barnes 1969, Cottam 1954, Jones and Trujillo 1975b). Because each clone consists of genetic duplicates, the mass uniformity within clones emphasizes the differences between clones.

The clonal habit is of major importance in the ecology and management of aspen. Stands are composed of clones. A stand may be a mosaic of clones or may be a single clone.

The Root System

Aspen seedlings (ortets) during their first year have fibrous, branching, lateral root systems with few taproots. In moist, sandy soil, Day (1944) found at the end of the first year that lateral roots were less than 16 inches (41 cm) long and taproots less than 6 inches (15 cm) deep. In the second year, lateral roots had grown to 4 to 6 feet (1.2 m to 1.8 m), and suckers appeared on them. He found an 18-year-old tree, 25 feet (7.6 m) tall, with a main lateral root 47 feet (14 m) long and branch sinker roots to a depth of 7 1/2 feet (2.3 m).

The root system of an aspen clone is characterized by relatively shallow, widespreading cord-like lateral roots and vertical sinker roots that descend from the laterals (Baker 1925, Buell and Buell 1959, Gifford 1966, Maini 1968). The lateral roots are cylindrical with little taper, except near the ramets (Sandberg and Schneider 1953). Undulating within the upper 2 to 3 feet (0.6 m to 1 m) of the soil profile, they show only occasional branching. Branches generally arise from the base of ramets (Gifford 1966). Lateral roots may extend for more than 100 feet (30 m) into adjacent open areas (Buell and Buell 1959). In Colorado, of eight plant species studied, Berndt and Gibbons (1958) found quaking aspen roots to have the greatest lateral extent, up to 48 feet (15 m) from the tree. The shallow laterals tend to follow minor soil surface irregularities (Sandberg 1951), so much so that Baker (1925) found them growing upward into decaying conifer stumps, where they often produced suckers Jones (1974a). Turlo (1963) found aspen roots in Wyoming growing along the soil surface beneath fallen logs as well as into the logs themselves.

Sinker roots may descend from points anywhere along a lateral root. In two Utah clones, Gifford (1966) observed that only 30% of the sinker roots originated from the base of ramets. They reached depths of more than 9 feet (2.7 m), often following old root channels (Day 1944, Gifford 1966). At their lower extremities, sinker roots branch profusely into a dense fan-shaped mat. Dense mats of fine roots often occur when tree roots encounter an impeding layer—rock, dense clay, or water saturated soil. Several studies of soil water depletion by aspen imply effective rooting depth to at least 9 feet on deep, well-drained soils (Johnston 1970, Johnston et al. 1969). This is similar to the depths reached by associated woody plant species on the same sites.

The quantity or weight of roots under aspen infrequently have been measured. Day (1944) found a root/shoot ratio of 2:1 in 6- to 8-year-old aspen. Vaartaja (1960) measured greater proportions of roots under 6-month-old seedling aspen from a northern (54° latitude) ecotype than from an ecotype from 46° latitude; the difference was attributed to adaptation to the cold soils of the north. Young and Carpenter (1967) found the ratio decreased with increasing aspen tree heights from 10 through 35 feet (3 m to 11 m). An open, mature stand of Minnesota aspen (200 trees per acre averaging 5 1/2 inches (14 cm) d.b.h.) was estimated to have 70,000 feet (21 km) of roots per acre that were larger than 0.3 inch (0.8 cm) in diameter (Sandberg 1951, Sandberg and Schneider 1953).

The stems in aspen clones usually are interconnected in small groups via their common parent root system (Barnes 1959, Day 1944, Kittredge and Gevorkiantz 1929). These connections can transmit water and solutes from tree to tree (DeByle 1961, 1964; Gifford 1966; Tew et al. 1969), but perhaps not carbohydrates (Strain 1961). The intraclonal connections, the extensive lateral root network, and the characteristic enlargement of the parent root on the distal side of suckers (Brown 1935) are illustrated in figures 3 and 4. These groups of stems may remain functionally interconnected throughout the life of the aspen stand (DeByle 1964, Maini 1968, Tew et al. 1969). The size of most groups will decrease in number as the stand matures and trees die (DeByle 1964). Also, some connections likely will decay and break (Barnes 1959, Gifford 1966). The development of interconnected stem groups in aspen clones is illustrated in figure 5.

Root grafts seldom are found in aspen. LaRue (1934) discovered numerous grafts in some species, but found none at all in aspen, even where roots had grown around one another or were otherwise in contact. Turlo (1963) found no actual grafts, even though there was a great deal of root crossover. DeByle (1964), using tracers and extensive excavation in several stands of bigtooth aspen and quaking aspen, found a few grafts in one bigtooth aspen stand but none elsewhere, although in all stands many roots were found growing tightly together.

A newly formed aspen sucker depends upon the parent root for nutrients and water. This ready-made root system gives aspen suckers a growth and survival advantage over seedlings of aspen and other species (Day 1944, Graham et al. 1963). As the sucker grows in diameter, the parent root distal to it enlarges, and branch roots arise from the base of the shoot itself and from the portion of the thickened root (Baker 1925, Brown 1935). The sucker literally adopts that portion of its parent root as its own. The degree of dependence suckers have on their parent roots diminish as they develop their own root systems. The rate of such development and independence seems to vary widely—from a couple of years (Sandberg 1951) to more than 20 years (Zahner and DeByle 1965). In the West, Schier and Campbell (1978a) examined 1- and 2-year-old suckers in 8 clones and found adventitious roots had developed under more than half of the suckers; but only 1% had well-developed root systems of their own. Those that did were on very small parent roots.

The swelling of the parent root on the distal side of suckers and the likelihood of interconnected stem groups make the root system of aspen unique among common forest tree species. The parent root and its branches often are considerably older than the sucker stems. These unique characteristics and the effect they have on both size and development of roots and stems must be taken into account when studying aspen root systems, especially those of young sucker stands.

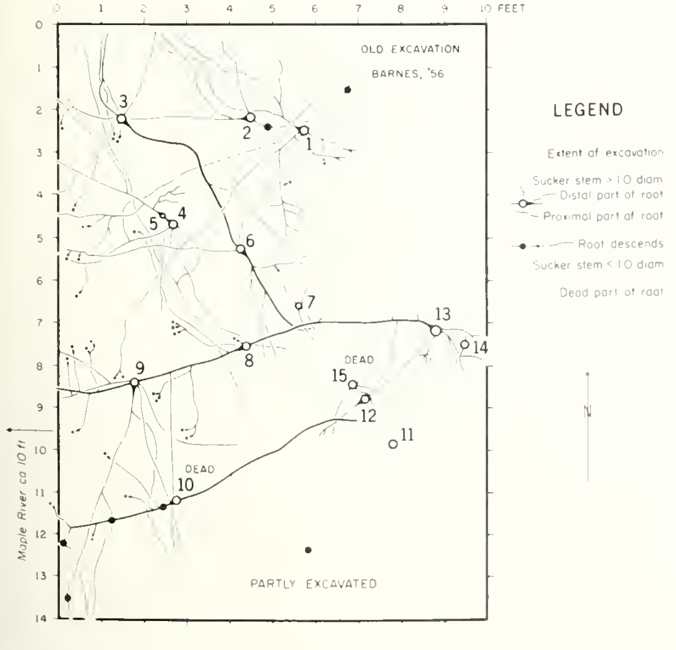

Figure 3.—Drawing of a vertical view of the root system under part of an aspen clone with 13-year-old, 3-inch (8-cm) diameter stems. (DeByle 1964).

Figure 4.—North half of the root system excavation diagrammed in figure 3.

Stand Structure

Aspen, is a shade-intolerant species that commonly grows in even-aged stands, especially on sites where competition with more shade-tolerant tree species is intense, such as throughout most of aspen's range in the East. In the West, most aspen stands are even-aged and single-storied. Nearly all of the trees in these stands originated during a period of 2 to 4 years (Baker 1918b, 1925; Jones 1975; Jones and Trujillo 1975a, 1975b; Patton and Avant 1970; Sampson 1919; Smith et al. 1972).

Sometimes these even-aged stands of aspen are the same age over some rather large areas. In the White Mountains of Arizona, for example, many aspen stands originated in 1905,[1] following widespread fires in 1904 (Kallander 1969).

The uniformity of these even-aged stands, when young, can be striking. For example, Miller (1967) found that the leaf distribution of an even-aged sapling stand in Colorado was rather homogeneous throughout the depth of the canopy, except at the very top and bottom.

In contrast, Baker (1925) described Utah stands that were only broadly even-aged, made up of trees that originated over a period of 10 or 20 years during deterioration of the previous stand. Stahelin (1943) and both Jones and Hinds[2] also found such stands in Colorado and New Mexico (fig. 6). These stands typically were mature and single-storied; their age irregularity was recognized only when the ages of individual trees were determined.

Other single-storied stands have two distinct, easily-recognized age classes. They are likely to consist of a more or less substantial scattering of old, often fire-scarred veterans standing among younger, slender trees of similar height. The old trees usually are survivors of a fire decades earlier that killed many of the aspen and gave rise to a subordinate stratum of suckers. (See the FIRE chapter.) Many of these eventually reached a height similar to the older trees, and, with them, formed a closed canopy.

Figure 6.—A single-storied stand with trees ranging from 75 to 99 years old. Dark bark near bases appears to be caused by rodent gnawing beneath the snow. White River National Forest, Colorado.

Baker (1925) described two-storied stands in Utah. Surface fire in single-storied stands had killed some trees and resulted in an understory of suckers (fig. 7). Johnston and Doty (1972) mentioned two-storied stands in which the lower stratum developed beneath an open overstory when livestock were excluded after long overuse. Similar two-storied stands probably would result if big game browsing were eliminated from severely impacted mature aspen stands (Krebill 1972).

All-aged stands are more common than expected. Davidson et al. (1959) sampled 32 aspen sawtimber plots scattered through western Colorado. Only eight were even-aged; seven were "two-aged," with ages in the lower class somewhat uneven; and the other 17 were uneven-aged, with most age spreads from 20 to 70 years. Alder (1970) selected 44 uncut aspen stands in Utah and Arizona with at least two tree strata and described their age structure. A few had an age distribution resembling the classic J-shaped curve of all-aged stands (Bruce and Schumaker 1950). Packard (1942) mentioned similar all-aged stands in Colorado. However, their health and vigor many not be the best. Betters and Woods (1981) measured reduced growth rate and increased incidence of decay in suppressed trees within uneven-aged aspen stands in northwestern Colorado.

Many stands dominated by aspen contain a mixture of other species. Authors since Weigle and Frothingham (1911) have pointed out the common occurrence of coniferous understories beneath aspen canopies. In the Southwest, where many aspen stands developed after the burning of mixed conifer forests, aspen stands often include groups and scattered individuals of overmature conifers, most commonly Douglas-fir (*Pseudotsuga men-*

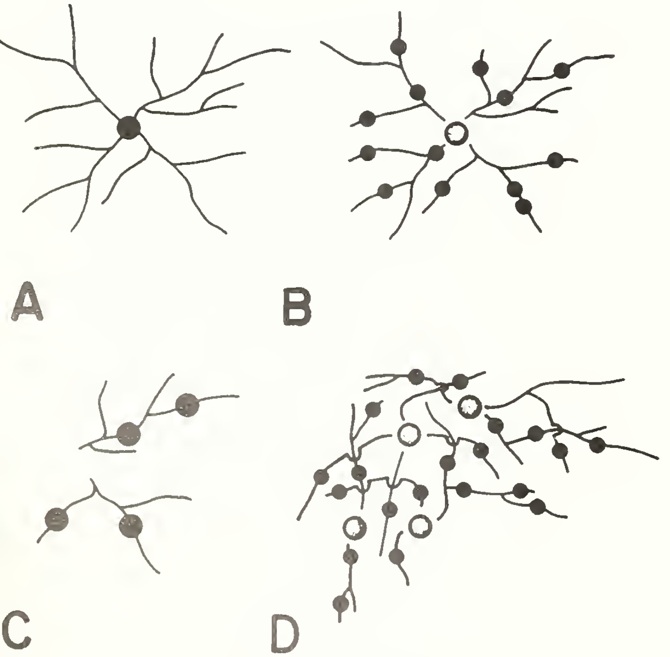

Figure 5.—The development of a hypothetical aspen clone. (A) Vertical view of a large tree of seedling origin with four superficial lateral roots. (B) The sucker pattern that developed on these roots after destruction of the ortet. The clone now consists of 13 ramets, each connected to some but not all others in the clone. (C) Four of the 13 ramets illustrated in B that survived for approximately 50 years before being removed by fire or cutting. (D) The roots of the four trees shown in (C) would give rise to numerous suckers. After 10 to 20 years, these might have thinned through natural causes to the 20 stems illustrated here. (DeByle 1964).

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[1] *Unpublished data collected by John R. Jones.*

[2] *Unpublished data.*

Figure 7.—Two-storied stand after a moderate fire in aspen (Baker 1925).

ziesii), that survived the fire. Some southwestern forests are an irregular mosaic of aspen patches and coniferous patches, reflecting in part the varying intensities of old fires.

After fire, aspen sometimes forms mixed stands with lodgepole pine. These mixes are described for northern Colorado (Clements 1910) and northern Utah (Ream 1963). Mixtures may be in small groups, with the aspen taller during early years of stand development, and the pine asserting dominance later and eventually eliminating most of the aspen (Clements 1910).

In summary, aspen in the West occurs as even-aged stands that probably originated after fire or similar perturbance, broadly even-aged stands, two-storied stands of two ages, one-storied stands of two ages, and all-aged stands. Even-aged stands predominate. For example, Shepperd (1981) sampled 140 sites in Colorado and Wyoming and found single-aged stands most frequent, two-aged stands next, and broad-aged stands made up only 4% of the sample. Choate (1966) implied that most stands in New Mexico are even-aged, too.

Stand Changes Over Time

The morphology of even-aged aspen stands changes with age. Young stands have a large proportion of their stems overtopped by others of about the same age (Pollard 1971). On six clearcut plots in Arizona heavily stocked with 3- and 4-year-old suckers, 38% were already dead—most apparently because of intense competition—and 42% of the survivors were overtopped (Jones 1975). In four fully stocked, 22-year-old-clones, 59% of the live trees were completely overtopped (Jones and Trujillo 1975a), forming a subordinate layer of very slender trees with little foliage. Conventionally, even-aged stands like these are called single-storied; the numerous overtopped trees, seriously declining, are ignored. However, in well-stocked mature and overmature even-aged stands, there are very few overtopped aspen (Stoehr 1955), except for more or less ephemeral suckers.

Barnes (1966) and Brown (1935) described stands with a somewhat domed or elliptical profile. These usually are in openings where lack of competition permits clonal expansion. The core of such stands generally consists of older trees, with progressively younger and shorter trees toward the edge. These stands often have even-aged cores surrounded by bands of younger even-aged stems. Baker (1925) ascribed these even-aged extensions to surface fires and described them as commonly only about 15 feet (5 m) wide but sometimes more than 50 feet (15 m) wide. In Wyoming, Beetle (1974) found that the older aspen in the center of such stands had died, forming what he termed a "fairy ring," or, if larger, an "aspen opening."

As an even-aged aspen stand matures, several factors may act independently or together to influence stand structure or morphology. In addition to clonal characteristics (Schier 1975a), these appear to be climate, fire history, soil or site quality, impacts of livestock and big game, incidence of disease and perhaps insects, and the presence of a conifer seed source.

Baker (1925) stated that single-storied stands regularly produced suckers. If these stands were reasonably well-stocked, the suckers normally were weak and inconspicuous and died in a few years. However, without sudden destruction by fire or a similar agent, a well-stocked, overmature, even-aged aspen stand slowly dies, the canopy opens up, and aspen suckers survive and grow in the openings. (This assumes that other species, especially conifers, do not take over the site, and that livestock or big game impacts are minimal.) These suckers typically arise over a period of several years; the resulting stand is broadly even-aged.

If such broadly even-aged stands reach old age without disturbance, their deterioration is likely to extend over a longer period than before because of the range of tree ages. That, in turn, would result in a longer regeneration period and a new stand with an even greater range of ages. Baker (1925) hypothesized that if this continued over several generations of aspen, all-aged stands would result. The all-aged stands of aspen that occur in the West probably developed through this process. The stability of aspen on some sites was recognized many years ago (Fetherolf 1917), and is considered by some as a de facto climax type (Mueggler 1976b) on these sites.

GROWTH

John R. Jones and George A. Schier

This chapter considers aspen growth as a process, and discusses some characteristics of the growth and development of trees and stands. For the most part, factors affecting growth are discussed elsewhere, particularly in the GENETICS AND VARIATION chapter and in chapters in PART II. ECOLOGY. Aspen growth as it relates to wood production is examined in the WOOD RESOURCE chapter.

LIFE-TIME PATTERNS

In the West, a stand of aspen may persist for more than 200 years. On a good site in southwestern Colorado, sample dominants in one stand averaged 215 years old and 107 feet (33 m) tall. The stand was still intact but had a very high decay frequency. That study (Jones 1966, 1967b) included 71 plots in mature and overmature aspen, mostly in Colorado but with a few plots in northern New Mexico and Arizona. The age-class distribution was as follows:

Age (*years*)	**Number of plots**
<60	1
60-79	12
80-99	22
100-119	12
120-129	8
140-159	6
160-179	6
180-199	2
≥200	2

Although that was not a random sample, it gives some idea of the ages of mature and overmature stands encountered in Colorado, New Mexico, and Arizona.

In the Lake States, aspen lives notably longer on good sites than on poor sites (Zehngraff 1947, 1949; Graham et al. 1963; Fralish 1972). This also has been reported in the West (Baker 1925).[1] But on at least some poor western sites, aspen stands survive a long time. Of the 10 plots (Jones 1966, 1967b) in stands 160 years or older, 3 had site indexes that were rather poor by Colorado standards. Strain (1964) reported an uneven-aged stand in California's White Mountains with a sample tree 226 years old and only 39 feet (12 m) tall. That indicates a very poor site; however, it has what seems to be the oldest reported quaking aspen. Greene (1971) sampled clones in Colorado over a gradient from 5,500 to 11,250 feet (1,700 m to 3,400 m) elevation. Her data suggested that although aspen may live longer near timberline, growth was very slow there because of the short growing season.

Height Growth

The result of a lifetime of aspen growth can vary from a shrub in the Colorado krummholz to a tree in central Utah 120 feet (37 m) tall and 54 inches (137 cm) d.b.h. (Harlow and Harrar 1958). Beetle (1974) reported that in Jackson Hole, Wyo., aspen seldom grows taller than 60 to 70 feet (18 m to 21 m), or in marginal climates 20 to 40 feet (6 m to 12 m). Baker (1925) described a stand in central Utah as representative of better stands in the region. Its dominants averaged 64 feet (20 m) tall at age 80 and 75.5 feet (23 m) at 150. In a few southwestern areas, trees taller than 100 feet (30 m) are common, notably in the White Mountains of eastern Arizona and part of the San Juan Mountains near Pagosa Springs, Colo. Aspen taller than 90 feet (27 m) are frequent in various parts of the San Juans, in the Jemez Mountains of northern New Mexico, and on the San Francisco Peaks in northern Arizona. Aspen occasionally reaches these sizes elsewhere in the West (Hofer 1920).

Early Growth Rates

Stem analyses of mature and overmature dominants on Jones' (1967b) 71 plots show that most took 2 to 5 years to reach breast height (4.5 feet (1.5 m)); but some had taken only 1 year. A few had taken more than 5 years, perhaps because of dieback, browsing, or competition from shrubs, herbs, or residual overstory.

Dominant saplings on a 4-year-old Arizona clearcut averaged 10.5 feet (3 m) tall, and most were only three summers old (Jones 1975). The tallest, four summers old, was 17.4 feet (5 m). That was better than juvenile growth determined on other southwestern areas by stem analysis of mature dominants, and indicates the growth rate that can be attained under good circumstances (Jones 1975). Some of the dominants came up the same summer after the spring cut. Their first-year growth averaged somewhat less than that of dominants which came up the following year (fig. 1); but 3 years later, they still had a greater average height because of their earlier start. The greatest growth made by any sucker during its first summer was 4.9 feet (1.5 m).

However, early (1-5 years) height growth of aspen is not necessarily an indication of later growth potential of a stand. Jones and Trujillo (1975a), examining dissected

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[1] *USDA Forest Service. 1962. Timber management guide for aspen. 14 p. USDA Forest Service, Rocky Mountain Region, Denver, Colo.*

stems of trees from a well-stocked 22-year-old Arizona stand, found that trees on poorer sites reached 10 feet (3 m) tall almost as soon as those on good sites. On several sites in Colorado and the Southwest, Jones (1967b) found only a weak correlation (R = 0.41) between the height of dominant aspen at age 80 (site index) and the number of years it had taken them to reach breast height.

Site Index as a Measurement of Growth

For stands beyond the small sapling stage, site index is commonly used to represent the course of height growth for the dominant aspen trees in the stands of a given region. Site index curves are generalized regional representations and are unlikely to portray the growth curves of a specific site or stand very closely (Spurr 1952, 1956).

Baker (1925) presented a table of height-age coordinates for four aspen site classes in the Interior West. They were developed about 1912, mostly from measurements made on a single watershed. The methods widely used in later years to develop site index curves had not yet been described. Baker's height-age coordinates did not, nor were they intended to, represent the curves of height growth for any actual or hypothetical stand.

Jones (1967b) dissected many dominant aspens in the southern Rocky Mountains and reconstructed the course of their height growth. Each of his site index curves (fig. 2) is based on height-age data from plots whose dominant heights at age 80 were near the age-80 height for that site class. Curves were smoothed with the help of data from adjacent classes. Age was defined as the number of rings at breast height. This avoided the poor relationship of initial growth to apparent site quality, as well as the problems of counting rings at the base of trees with butt rot. The curves are available as an equation for computer application (Brickell 1970) and as a table for easy field and office use (Jones 1966).

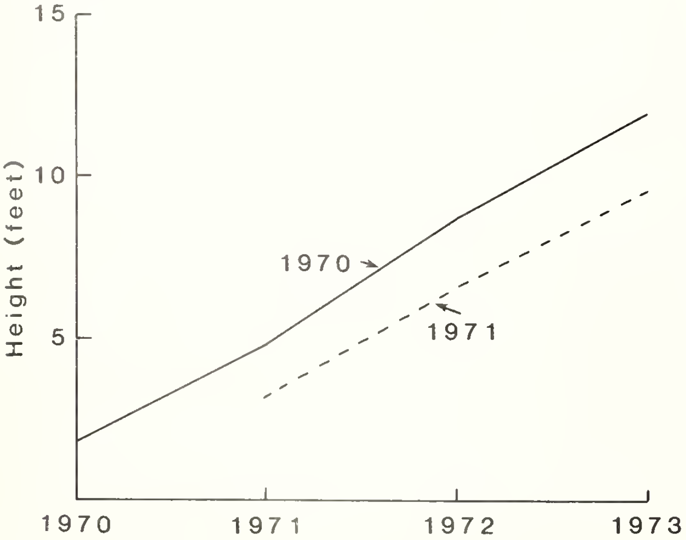

Figure 1.—Height growth of dominant 1970- and 1971-origin suckers on an Arizona clearcut (Jones 1975). Apache National Forest.

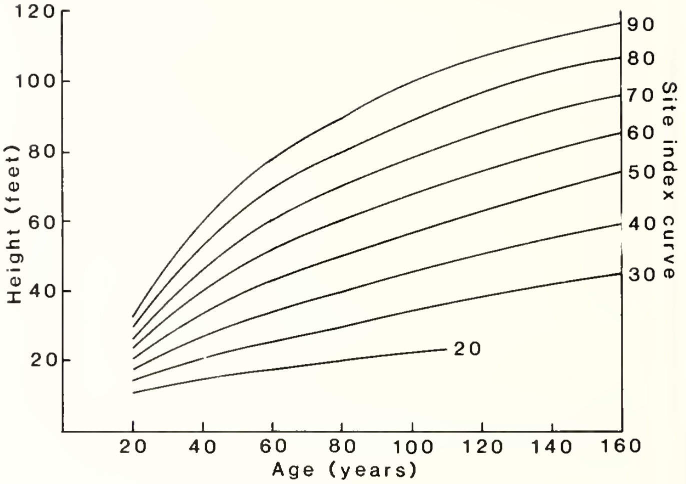

Figure 2.—Aspen site index curves for Colorado and New Mexico, using breast height age (Jones 1967b). The index age is 80 years.

The shape of actual plot curves varied from these. In figure 3, comparison of Plots 14 and 71, and of Plots 12 and 69, show how different heights at maturity may be on plots where heights had been similar at age 30 or 40. Each plot probably was within a single clone.

Even stands that grow rapidly in height the first few decades often grow somewhat more slowly in height at maturity. The factors which cause height growth to slow as stands get older may be related more to the size than the age of trees.

The difference in mature height between some tall stands and some that are much shorter sometimes results entirely from large differences in immature height growth. Later growth rates may be quite similar. This is reflected in Jones' (1967b) site index curves (fig. 2), which are roughly parallel beyond the index age (80 years).

Diameter Growth

There is little information on patterns of diameter growth in aspen. Presumably, progressive crown or root deterioration results in markedly reduced diameter growth near the end of a tree's life. But there is no strong evidence that diameter growth of healthy, dominant aspen declines substantially with age.

At least during the first few decades, changes in the diameter growth of dominant trees seem to be short-term responses to external factors instead of forming a strong, age-conditioned pattern. Various workers, for example Churchill et al. (1964), have documented the severe diameter growth reduction in aspen caused by outbreaks of defoliating insects. Such reductions typically are followed by complete recovery. In Michigan, Graham et al. (1963) described periods of intensifying competition between immature canopy trees. These periods, ending with marked mortality, cause short-term diameter growth fluctuations which tend to obscure any possible long-term patterns.

In subordinate crown classes, however, diameter growth rates decline over time. This reflects not age, but decreasing availability of growth requisites as competitive position deteriorates. In an Arizona study (Jones and Trujillo 1975a), 22-year-old intermediates had been codominants earlier, and some were dominants before that. With each reduction in competitive position, their supply of sunlight and perhaps also of water and nutrients became less, and relative ring widths decreased. Trees that became overtopped formed still narrower rings; and, during their final years, these light-deprived trees formed rings that were barely visible under a microscope.

In a particular year, weather may cause exceptionally good or poor diameter growth. In widespread samples from throughout the southern Rocky Mountains, Jones (1967b) found that on a given plot, the rings for certain years were notably wider or narrower than the several rings on both sides. Often there were several such distinctive rings common to every sample dominant on a plot.

Aspen diameter growth is not related to site the same way that height growth is. A stand may have much larger diameters, yet, may be considerably shorter than another of similar age (fig. 4). The site characteristics that limited heights on Plot 15, in comparison to heights on Plot 14, did not limit relative diameter growth. Stand density has only a modest effect on the final diameters of dominants (see the INTERMEDIATE TREATMENTS chapter).

SEASONAL PATTERNS

Shoot Growth

Aspen buds begin to swell during the first warm period in spring, when minimum temperatures are still below freezing (Ahlgren 1957). Photoperiod is not a critical factor in determining the timing of bud opening. The beginning of bud activity may vary several weeks

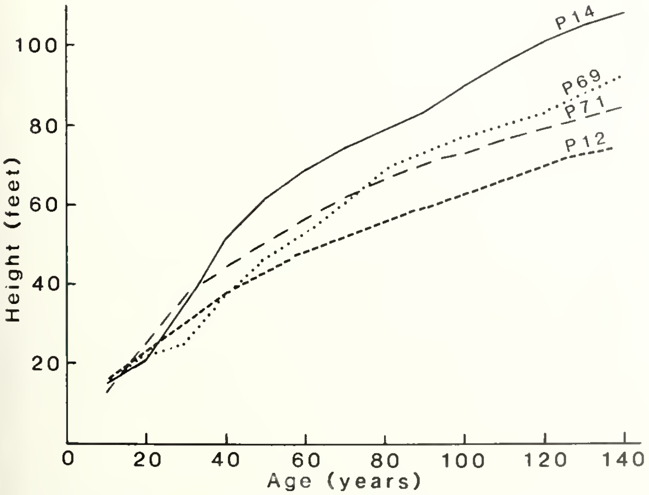

Figure 3.—Later height divergence on plots with similar heights at age 30 (Plots 14 and 71) and age 40 (Plots 69 and 12).

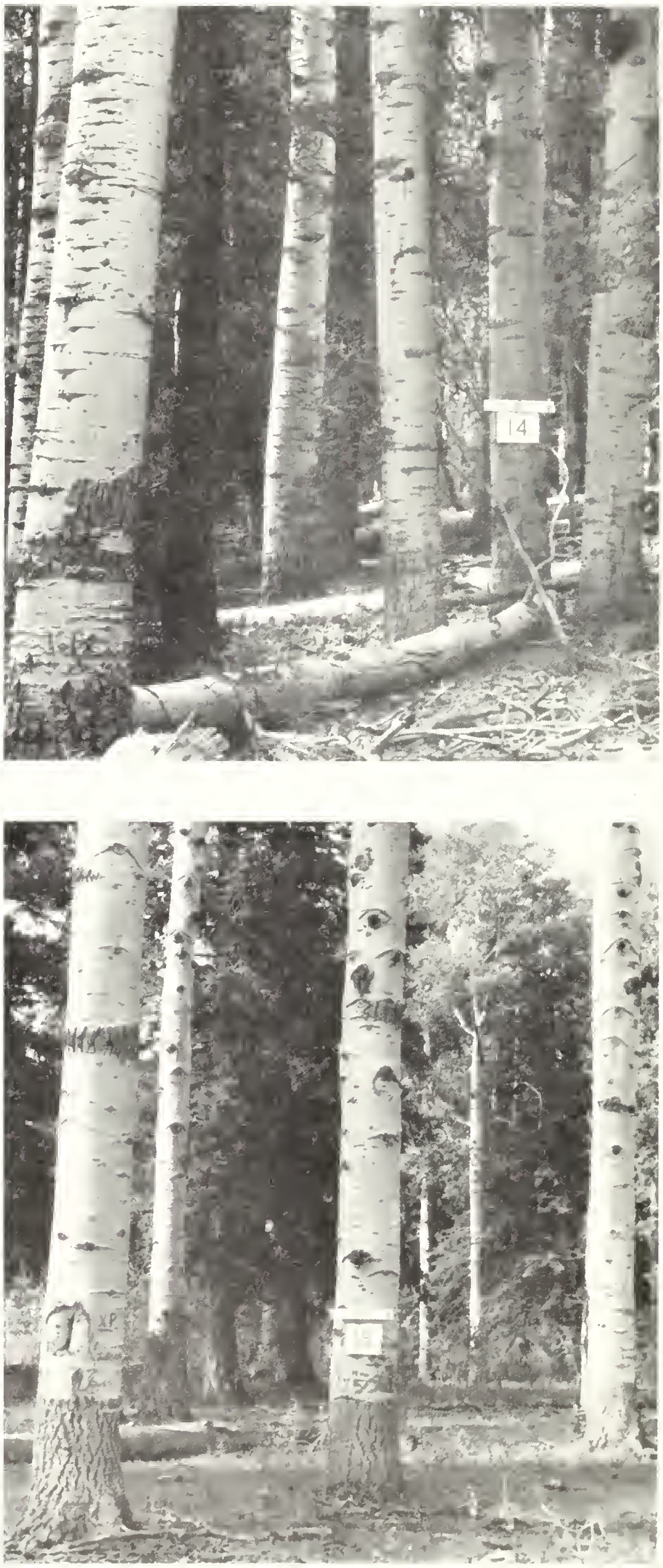

Figure 4.—Diameter comparison of two stands. The scale board above the plot numbers is 2 feet (61 cm) long. Each sample dominant on Plot 15 (bottom) exceeded 24 inches (61 cm) d.b.h. at 137 years, with an average height of 84 feet (26 m). No tree on Plot 14 (top) was larger than 20 inches (51 cm) d.b.h. at 148 years, although the sample dominants averaged 110 feet (34 m) tall. Apache National Forest, Arizona.

from one year to the next, depending on the weather. Warm weather early in the spring will advance the time of flushing; cold weather will retard it. Adjacent clones may show marked differences in timing and progression of leaf flushing (Barnes 1969).

Observation suggests that at typical aspen elevations in Colorado and the Southwest, aspen commonly leafs out in late May or early June, depending on locale and clone. In a southern Wyoming study at 8,700 feet (2,650 m) , aspen leaves were unrolled but not fully expanded on June 1 (Strain 1961, Strain and Johnson 1963). In south-central Utah, Dixon (1935) reported that the highest elevation aspen observed, a dwarfed gnarled stand at 10,000 feet (3,050 m), was just leafing out on June 21. In northwestern Wyoming, Beetle (1974) noted that new terminal growth in aspen began in early to late June, depending on year and site. On the east slope of the Front Range in Colorado, Greene (1971) found that low-altitude (below 7,000 feet (2,150 m)) clones generally leaf out in early May, middle-altitude (8,000 to 10,000 feet (2,450 m to 3,050 m)) clones in late May or early June, and high altitude (above 10,500 feet (3,200 m)) clones at the end of June.

Observing shoot development of 60 aspen clones from 9,800 to 10,200 feet (3,000 m to 3,100 m) in elevation, on a southeast facing slope in northern Colorado, Egeberg (1963) found that more than 3½ weeks elapsed between the times the first and last clones flushed out. This wide clonal variation in timing of bud break resulted in clonal differences in susceptibility to frost damage.

Genetics strongly influence duration of shoot growth in aspen, which generally correlates with the frost-free season prevailing in the native habitat of each clone. Day length appears to determine duration of height growth. Clones from high latitudes or high elevations are among the first to cease growing and form terminal buds. Maini (1968) reported that basal branches ceased growth first; some 3 to 4 weeks later the branches in mid-crown stopped growing; and finally, some 3 or 4 weeks still later, the terminal stopped growing.

There is limited information on when shoot extension in western aspen ceases. Observation of trees in yards in Logan, Utah, indicates that bud set occurs in late July or early August. Strain (1961) found that aspen on a poor site in southern Wyoming ceased growing in height by June 26. In the Upper Peninsula of Michigan, the average period of height growth was about 80 days (Strothman and Zasada 1957). In Utah, Schier (1978c) found that 2-year-old aspen ramets were fully dormant by late August, as indicated by the failure of axillary buds to break following defoliation. (The shoots of dormant aspen require a cold period before they resume growth.)

Cambial Growth

Five to eight layers of undifferentiated cells overwinter in the cambial zone of aspen (Davis and Evert 1968). In the Lake States, cells on the phloem side of the cambial zone begin to divide in late March or early April. Early cell division proceeds relatively slowly and primarily produces phloem. When xylem begins forming in mid-May, cambial activity increases and reaches a maximum in late May and June. Cambial activity drops sharply in early July; and by the end of July or early August dividing cells can no longer be found.

Cambial activity in bigtooth aspen (*Populus grandidentata* Michx.) begins about 3 weeks before the buds leaf out (Wilcox 1962). Brown (1935) reported that cambial activity in quaking aspen (*Populus tremuloides* Michx.) begins immediately below the leaf buds as they begin to swell, then progresses gradually down the stem and outward toward the root tips. It reaches the base of the trunk about the time the leaves emerge (Ahlgren 1957, Brown 1935), varying with the distance from the leafy crown to the tree base (Brown 1935). Cell division in the cambium probably is triggered by auxins from the elongation of new shoots (Wilcox 1962), which begins after the small early leaves have expanded (Strain 1961).

Cambial activity in aspen ends in different parts of the tree in the same order that it starts, stopping first in the twigs and persisting longest in the roots (Brown 1935). In general, the fastest growing trees have the longest growing season (Kozlowski and Winget 1962b).

SHOOT TYPES

Aspen trees have two types of shoots: short shoots and long shoots (Critchfield 1960, Kozlowski and Clausen 1966, Pollard 1970b). Short shoots are preformed or predetermined in the winter bud. Their growth is fixed, because it is completed when the preformed stem units have elongated. Growth of long shoots involves the elongation of preformed stem units, followed by a period of free growth during which new stem units begin and elongate simultaneously. Short shoots complete their growth during a brief period in the spring, whereas long shoots may continue elongating until late summer. Lateral long shoots vary from those growing slightly longer than short shoots to those growing as much as the terminal shoot.

The occurrence of both fixed and free growth in aspen results in leaf dimorphism (Critchfield 1960). The two basic types of leaves are called "early" or "late" depending on their time of initiation and differentiation. Both leaf types grow on long shoots (for this reason they are called heterophyllous shoots), whereas short shoots have only early leaves. Early leaves are embryonic leaves in the winter bud, and are the first set of leaves that appear in the spring (Critchfield 1960). The first late leaves are also present in the winter bud, but are arrested primordia. Succeeding late leaves begin and develop during free growth. Late leaves vary in shape more than early leaves and have gland-tipped teeth along their margins, which are lacking in early leaves (Barnes 1969).

The tendency for free growth and production of heterophyllous long shoots diminishes as the tree ages. The terminal and main lateral shoots of young aspen are comprised almost entirely of long shoots. As the crowns increase in size, short shoots soon outnumber long shoots, and most of the foliage consists of early leaves. Pollard (1970b) found that long shoots made up 13% of the canopy in a 6-year-old stand, whereas they made up only 6% of the canopy in a 15-year-old stand. There were no long shoots at all in a 52-year-old stand. Kozlowski and Clausen (1966) also found that all shoots of adult aspen were preformed, and, therefore, all leaves were of the early type.

Aspen shoots normally do not begin branching until the second year. Elongation of lateral buds on the current year's growth is inhibited. Strain (1964), however, reported that suckers from an exceptionally shrubby clone branched during their first summer.

Free growth of leaders and many lateral shoots enables young aspen to grow rapidly and develop a canopy in a few years. Continuing height growth and branch extension far into the summer on good sites is not shared by any of the associated conifers, making aspen's rapid juvenile growth and stand development unique among the upland forest species in the Interior West.

PHOTOSYNTHESIS AND GROWTH

Aspen is classified as very shade intolerant when compared to other North American tree species (Baker 1949). Aspen's inability to survive under shade results from a low ratio of photosynthesis to respiration under low light intensity (Bazzaz 1979). Tolerant species have a more favorable carbon balance under low light than aspen, because they have higher photosynthetic rates and/or lower respiration rates.

Loach (1967) found that hardwood species ranging from very tolerant (beech) to very intolerant (aspen) all had lower photosynthetic rates in the shade. Respiratory adaptations to shade, however, were not similar. Leaves of tolerant species showed reduced respiration rates in the shade, but those of aspen did not.

Farmer (1963a) found that temperature regime has an important effect on response of aspen to low light intensity. Reduction of light intensity from 1,700 to 500 foot-candles reduced both height growth and dry weight increment at a 76°F (24°C) day/71°F (22°C) night regime. At a cooler regime (70°/66°F) (21°/19°C), however, dry weight increment was reduced, but height growth was not.

Attached aspen leaves attain their light saturation point at about 3,000 to 3,500 foot-candles (Loach 1967, Okafo and Hanover 1978). At this light intensity Okafo and Hanover (1978) found that the average net photosynthesis rate of Michigan aspen was 33.9 mg CO_2 dm^{-2} hr^{-1}. There was considerable variation between genotypes. It ranged from 10.4 to 50.4 mg CO_2 dm^{-2} hr^{-1}. Net photosynthesis rates for individual leaves exceeded the rates observed for the whole seedling by about four times. This was a result of mutual leaf shading and the occurrence on whole seedlings of young and old leaves, both of which have lower rates of photosynthesis.

Because aspen produces new leaves over the entire growing season, the tree uses both reserves and currently synthesized carbohydrates for apical growth. The amount of current photosynthate utilized in shoot expansion depends upon the relative timing of leaf development and internode elongation. For about 2 weeks after spring bud break, elongating shoots largely depend upon reserve carbohydrates that move upward from storage tissue in stem and branches (Donnelly 1974). First-developing leaves begin to photosynthesize soon after bud break; but they assimilate and respire more metabolites than they produce. They begin to export substantial amounts of photosynthate when they are about 50% of their full size. More than half of the photosynthate is at first transported to the developing shoot, where it is utilized in intermode elongation and in the expansion of terminal leaves. Then, as other leaves closer to the stem tip begin exporting photosynthate, meristems below the developing shoot become the major sinks for carbohydrates from the first formed or basal leaves.

There is a seasonal change in the relative proportion of photosynthate transported from the leaves to the stem tip and to the lower stem and roots (Donnelly 1974). Early in the growing season, most of the photosynthate is transported to vigorous sinks in developing shoots and leaves. As the season progresses, the downward translocation of photosynthate increases because of the increase in number of leaves exporting photosynthate and the decline in rate of shoot elongation. Channeling of photosynthate to the roots during the second half of the growing season is indicated by the buildup of carbohydrate concentrations in the roots (Schier and Zasada 1973).

The occurrence of chloroplasts in phelloderm and cortical parenchyma cells of the bark enable aspen stems and branches to carry on photosynthesis (Barr and Potter 1974). Foote and Schaedle (1976) reported that in 5-to 7-year-old aspen stems gross photosynthesis ranged from 0.0 mg CO_2 dm^{-2} hr^{-1} on winter days when the temperature was below 27°F (−3°C) to 5.5 mg CO_2 dm^{-2} hr^{-1} in July. The stem was not capable of net photosynthesis; but the respiratory loss of CO_2 from the stem was reduced all the way to zero, depending on the time of year and the level of illumination. Photosynthate produced in the bark is transported laterally in rays to xylem, phloem, and cambium (Shepard 1975).

The annual contribution of bark photosynthesis to the carbohydrate supply of a tree has been estimated to be only 1-2% (Foote and Schaedle 1978). This small contribution, however, may not reflect the actual importance of bark photosynthesis in satisfying the respiratory needs of the stem for maintenance and biosynthesis. During periods of high insolation, bark photosynthesis nearly equals stem respiration and could increase the chances of recovery of stressed trees after insect defoliation or after a severe late spring freeze.

DISTRIBUTION OF GROWTH WITHIN THE TREE

Diameter growth of woody stems typically is greatest near the source of photosynthates. In forest trees this is within or at the base of the live crown. Aspen is no exception. The annual diameter growth of the bole of mature Wisconsin aspen was considerably greater at 19 feet (6 m) than at 4.5 feet (1.5 m), with most of the difference developed late in the growing season (Kozlowski and Winget 1962b). In New Brunswick, "relatively young" aspen growing in the open had maximum ring widths for the year within the first five internodes from the apex (McDougall 1963). Jones and Trujillo (1975a) found that, in 22-year-old Arizona aspen, maximum diameter growth occurred in the upper bole within the crown.

Most of the aboveground biomass of mature aspen trees is made up of woody bole, bark, and branches. A sampling of trees in northern Utah and western Wyoming (Johnston and Bartos 1977) showed that the woody bole made up 50% or more of the aboveground biomass, the bark from 20% to 25%, and live branches from 10% to 17% of the biomass. The dry weight ratio of branches to bole decreases modestly with age (Schlaegel 1975a, Zavitkovsky 1971). The branch-to-bole ratio is greatest in dominants.

Much less is known about root growth than about top growth. Almost 20% of the total biomass of 40-year-old aspen consisted of roots greater than 0.2 inch (5 mm) diameter (Alban et al. 1978). Apparently the proportion of the tree that is below ground declines with age (Young and Carpenter 1967). Young trees 10 feet (3 m) tall had a ratio of 0.46, those 20 feet (6 m) tall 0.31, and older trees 35 feet (11 m) tall only 0.25. From an exploratory study in a small aspen population, Young et al. (1964) found that, for a given diameter, the taller trees have the greater root-to-top ratios; and, for a given height, trees with larger diameters have smaller ratios.

STAND DEVELOPMENT

Uneven-aged aspen stands are common in many western areas, but their growth has not been studied (see the MORPHOLOGY chapter).

The development of even-aged stands has not received much attention aside from the yield studies that are reviewed in the WOOD RESOURCE chapter. The following generalized characteristics of even-aged stand growth are based on findings from the Great Lakes region (Graham et al. 1963, Pollard 1971), and a few western case histories (Jones 1975, Jones and Trujillo 1975a):

1. Rapid sucker growth. Early sucker growth ranges from less than 1 foot (30 cm) to more than 3 feet (1 m) per year for shoots having good competitive position. Rapid extension of lateral shoots on suckers more than 1 year old accompanies leader growth and results in early crown closure.
2. Quick definition of crown classes. After the canopy closes, trees stratify into crown classes quickly, despite genetic uniformity within clones (fig. 5). There is a fairly continual adjustment of trees to growing space, and a loss in competitive position of many trees making up the codominant, intermediate, and overtopped classes.

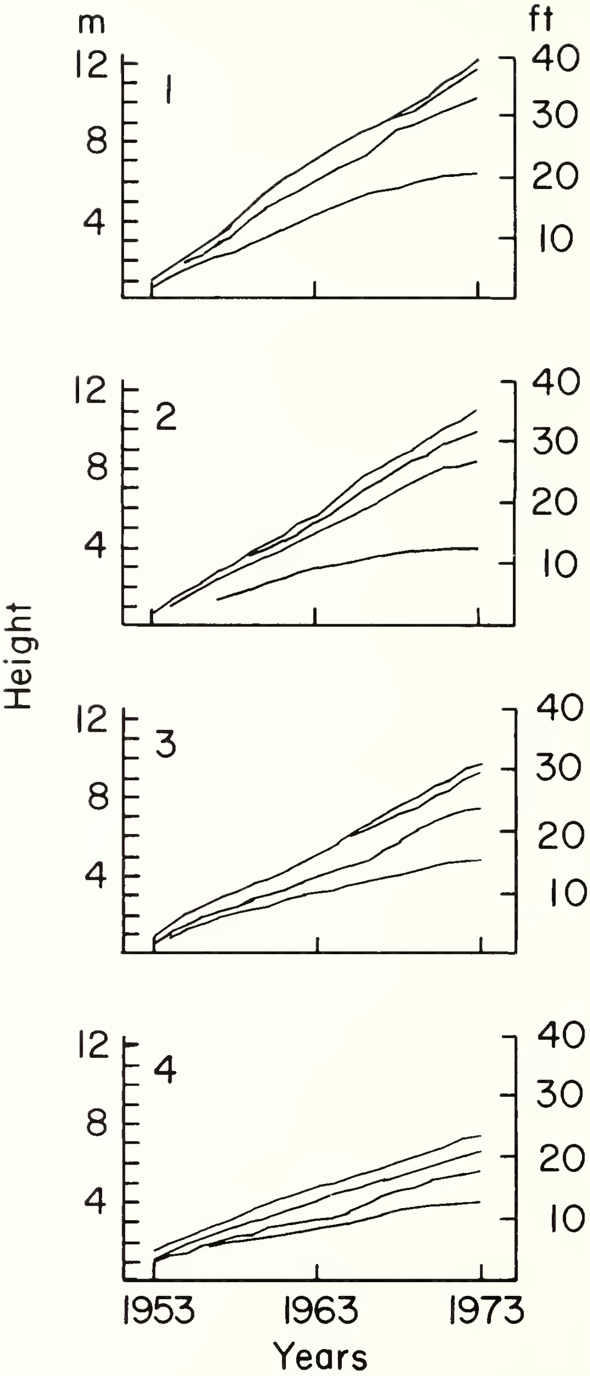

Figure 5.—Height growth curves for each live crown class on four Arizona plots (Jones and Trujillo 1975a).

3. Rapid natural thinning. When competition becomes intense enough to appreciably affect the diameter growth of dominants, mortality quickly reduces the number of trees in the lower crown classes. There are periodic surges in mortality, with a disproportionate number of trees, mostly those overtopped, dying within a short time. The adjustment in stocking may be severe enough to reduce dry weight increment for a time. Diameter growth, however, shows strong recovery with reduced competition.

SEXUAL REPRODUCTION, SEEDS, AND SEEDLINGS

Walter T. McDonough

Natural genetic interchange and extensive colonization of aspen by seed strongly depends upon favorable climatic and microclimatic conditions and upon human intervention. At times, in regions with the right combination of environmental conditions, there is significant reproduction by seed; elsewhere such establishment is rare. Seed production generally is profuse; but this potential for regeneration is considerably reduced by the exacting survival requirements of aspen seedlings. Under the marginal conditions that prevail in some regions, aspen can consistently reproduce only vegetatively (Cottam 1954, Graham et al. 1963). (See the VEGETATIVE REGENERATION chapter.) Despite this, studies of the mechanism of sexual reproduction in aspen are valuable for increasing knowledge of the species' reactions to stable and changing environments. Where reproduction of aspen by seed is desirable in areas that are naturally inhospitable, the existing environmental conditions may be modified, or by selective plant breeding, the seedling reaction to existing conditions may be changed so as to increase the probability of successful reproduction.

Sexual Reproduction

Aspen flowers have either pistils or stamens, but generally not both as is common among other flowering plants. As a result of extensive vegetative reproduction and constancy of genetic composition, all trees within a clone generally are either staminate or pistillate. However, perfect flowers possessing both parts occasionally have been observed (Lester 1963, Pauley and Mennel 1957, Strain 1964). Estimates of the number of trees in clones that have some perfect flowers range from 5% to 20% (Santamour 1956, Schreiner 1974).

Although the staminate-pistillate ratio among clones in a given locality is generally 1:1, the ratio may vary considerably and may be as high as 3:1 or more (Pauley and Mennel 1957). Also, instances have been reported of clones within localities that produce only staminate flowers (Strain 1964), and clones which alternate between staminate and pistillate in different years (Graham et al. 1963), or show various combinations of perfect, staminate, or pistillate flowers within or between inflorescences on the same tree (Einspahr and Winton 1976). Apparently, determination of reproductive structures is unstable in clones with certain genetic combinations. Otherwise, it occasionally is influenced by local environmental conditions, or results from competition among reproductive branches on individual trees for water and nutrients.

Aspen reach reproductive maturity and begin flowering by 10 to 20 years of age, with a peak in seed production at 50 years and with 3- to 5-year cyclic variations in light to heavy seed crops (Fechner and Barrows 1976, Maini 1968, Moss 1938, Schreiner 1965). Individual reproductive shoots produce 2-10 inflorescences (catkins) each with 50-100 flowers, and 2-10 seeds per flower (Einspahr and Winton 1976, Henry and Barnes 1977). The seeds (1-2 million/kg) are provided with a tuft of dispersal hairs at the basal end, and have an air-dry water content of 6%. The plumose seeds are thereby adapted for wind dispersal to distances of 1,600 feet (500 m), or several miles under high wind conditions (Stoeckler 1960). The seeds are not damaged by water transport and will germinate while floating or submerged (Faust 1936). Water dispersal is important for deposition on suitable wet sites.

In common with all other seed plants, sexual reproduction in aspen involves two distinct entities—sporophytes and gametophytes (Lester 1963). The asexual sporophyte (the aspen tree) which reproduces directly by root sprouting is interposed between successive generations of the sexually reproducing gametophyte. Within certain parts of the flower, the sporophyte produces two kinds of spores by meiosis, a process that involves a halving of the number of chromosomes per cell during nuclear and cell division. The spores can be distinguished, using a microscope, as large and small—megaspores within the ovaries of pistillate flowers and microspores within the anthers of staminate flowers, respectively. Still in place, the spore nuclei undergo several nonreductional chromosomal divisions to form megagametophytes (female) and microgametophytes (male).

Gametophytes are multinucleate microscopic plants, rendered nearly vestigial by evolutionary reduction in size and complexity. Among the nuclei are the egg and sperm that are later randomly joined by nuclear fusion (fertilization) to initiate a sporophyte embryo. This restores the original number of chromosomes found in the sporophyte. As a result of these twin processes of halving and doubling of the number of chromosomes, the constituent genes are recombined in ways that differ from those of the previous sporophyte generation. Because genes largely control morphology and physiology of the individual clones, such recombinations insure sufficient variety among progeny to adapt to long-term climatic changes and to a wider range of potential habitats (see the GENETICS AND VARIATION chapter).

During one growing season, the various parts of the flower and spore-producing tissues are progressively differentiated. Buds located on short shoots below a vegetative (leaf) bud begin differentiation into floral and spore-producing tissues that will become visible as staminate and pistillate flowers during the following spring (Beetle 1974, Fechner and Barrows 1976). Within staminate flower buds, the four-lobed stamens are first differentiated in early summer, followed by spore-producing tissue within each lobe. Formation of microspores is delayed until the buds are subject to several weeks of freezing temperatures in winter. A similar differentiation occurs within the pistillate flower buds during late summer, except that the megaspore nucleus divides once to initiate megagametophyte development before undergoing the winter dormant period.

Gametophytes complete development, floral parts enlarge, and flowers open during April-May of the following spring. First, pollen is wind-dispersed from the anthers of the staminate flowers. At least one of the vast numbers of pollen generally comes into contact with a receptive portion of the style of a pistillate flower. A tube-like growth of the pollen then proceeds to the vicinity of the ovary with its enclosed female gametophyte. Shortly after contact, a mobile sperm nucleus fuses with an egg nucleus. By repeated cell divisions, the fusion nucleus develops into the embryo of the seed—the sporophyte of the next generation.

These events are completed during a 4- to 6-week interval. The strings of capsules (catkins) developed from the ovaries of pistillate flowers open along two slits. The tufted seeds are exposed to wind for dispersal over a wide area (fig. 1). Meanwhile, other reproductive buds begin, repeating the annual process of spore and gametophyte formation and sexual reproduction.

Figure 1.—Maturing pistillate catkins. Aspen woodland in mid-June at 7,200 feet (2,200 m) elevation on the Wasatch National Forest of northern Utah.

Seed Germination

Seeds can tolerate a broad range of temperatures during germination. In various collections, high germination percentages have been reported between 0° and 39° C (Faust 1936), 5° and 37° C (Strain 1964), 5° and 25° C (Zasada and Viereck 1975), and 2° and 30° C, with limited germination to 40° C (McDonough 1979). However, temperature extremes are detrimental. At 2° to 5° C, germination rates are sharply lowered; and at temperatures above 25° C, total germination is reduced progressively to near zero. High temperatures inhibit germination, decrease emergence through a covering soil layer, and retard seedling growth. The percentage of abnormal germination—failure of any root growth or expansion of the cotyledons (seed leaves)—is increased also. Dark soil seedbeds, when exposed to sunlight, may reach temperatures that significantly inhibit germination and growth.

Standardized seed testing rules (International Seed Testing Association 1966) specify germination temperatures between 20° and 30° C, light, and first counts after 3 days. Somewhat in contrast, the aspen seed examined from northern Utah had optimum temperatures for both rate and total germination between 15° and 25° C, with no light requirement, and with earliest germination between 12 and 20 hours (McDonough 1979).

Early Growth

Several studies (Faust 1936, McDonough 1979, Moss 1938, Strain 1964) provide detailed information on germination and early seedling growth in aspen. Swelling of the root tip and the junction between root and hypocotyl (basal stem segment) without rupture of the seedcoat (incipient germination) are the earliest observed events (fig. 2). Further progress is either delayed or prevented by incubation at temperatures below 10° C, by placement in osmotic media, by cyclic wetting and drying the seeds, or by the presence of inhibitor compounds.

Normal germination over a 30- to 48-hour period progresses by rupture of the seed coat, root protrusion, formation of root crown hairs, growth and geotropic curvature of the root, and, lagging slightly, growth of the hypocotyl (fig. 2). Growth of the crown is terminated by adhesion to the surface with the completion of root curvature. Root growth slows perceptibly after the initial thrust. Hypocotyl growth tends to proceed uniformly at a rate and extent that strongly depends on light levels. Chlorophyll synthesis in the cotyledons is completed as root and hypocotyl growth proceed (fig. 2). The seed coat then is cast off, and the cotyledons unfold (fig. 2). The plumule, the cluster of developing leaves and stem segments above the cotyledons, is apparent at this time. However, there is a 6- to 10-day delay before growth is perceptible.

Figure 2.—Germination of an aspen seed: (1) incipient germination, (2) initial root protrusion, (3) initiation of root hairs, (4) elongation and curvature of the root-hypocotyl axis, (5) an "S"-shaped axis and development of chlorophyll in the cotyledons, and (6) unfolding of the cotyledons and extensive growth of the hypocotyl.

Abnormalities in germination are common and are conditioned by high temperature, presence of inhibitors, and wet-dry cycling of the seeds. These conditions damage or kill the active growth area of the root and result in extension of the hypocotyl only. Abnormal germination always kills the seedling.

Limitations on Seedling Growth

Established seedlings are found in the field (Barnes 1966, Faust 1936, Larson 1944), but this is believed to be uncommon (Einspahr and Winton 1976, Maini 1968). Only in regions where climatic and site conditions are particularly favorable does reproduction from seed contribute significantly to maintenance and spread of the species (Andrejak and Barnes 1969, Maini 1974). Therefore, Baker's (1918b) suggestion that sexual reproduction is defective because of failure of seed set or low germinability of seeds was widely accepted for many years. However, studies with seed collections from various regions of North America (Einspahr and Winton 1976, Maini 1968, Moss 1938) demonstrated that the paucity of established seedlings in nature results from rapid loss of seed germinability and from exacting requirements for seedling growth and survival, rather than from low or defective seed production.

Optimum conditions for germination and survival include an alluvial seedbed with adequate drainage, moderate temperature, and freedom from plant competition. Maini (1968) listed several factors involved in the failure of aspen seedlings to become established: (1) rapid loss of germinability with age; (2) presence of inhibitors in the seed hairs, soil, or litter; (3) rapid drying of the soil at and near the surface; and (4) unfavorably high surface temperatures.

Seeds deteriorate rapidly, except under optimum storage conditions of low temperature and humidity (Faust 1936, Zasada and Densmore 1977). In western Canada, seeds remained viable for 2-4 weeks after maturation (Moss 1938), a duration that is probably representative of longevity in the field. Seeds stored in air-dried soil, from mid-spring through early summer, on a mountain site in northern Utah, protected from precipitation but not from fluctuating temperature and humidity, declined 40% to 60% in germination after 4 weeks, and 75% to 100% after 8 weeks (McDonough 1979). The extent of loss also depends upon incubation temperature during germination, deterioration increasing with increasing temperature.

Inhibitors do not occur in the seed hairs, as suggested by Maini (1968). If the hairs were wetted and the seeds were fully imbibed, seeds germinated equally well whether they were embedded in masses of hairs or were isolated (McDonough 1979).

Lack of optimum seedbed conditions (i.e. a flat, well-watered, mineral soil surface) decreases germination and emergence. A heterogenous seedbed strands some seeds on rapidly drying surfaces, such as particles of litter or soil prominences. There, either seeds do not germinate, or else root hair growth is insufficient to make firm contact with the water-supplying substrate.

Germination and emergence also are reduced when the remains of particular understory species predominate in the litter. Naturally occurring inhibitors in litter (e.g. coumarin) severely inhibit root growth at concentrations of 10 ppm (McDonough 1979).

In addition to physical and chemical seedbed effects, emergence is decreased by relatively shallow burial. Emergence is reduced 20% to 80% from a 4-mm depth at optimum temperatures; there are greater reductions at higher temperatures (McDonough 1979). Such sensitivity is a disadvantage, because even minor disturbance loosens surface-germinated seeds. Also, the likelihood of desiccation by extreme temperatures and fluctuating soil water content is greater at the surface.

Germination and early seedling growth are highly sensitive to small soil water deficits. Pot culture and field plantings require regular and carefully controlled irrigation to prevent wilting and desiccation (Einspahr and Winton 1976, Moss 1938). On osmotic media, normal germination is reduced 20% at -2 to -3 bars and 50% at -4 to -5 bars. This range of water potentials had much less effect on germination of many other range and pasture plants (McDonough 1971, 1975). Osmotic inhibition is even more pronounced on aspen seeds previously stored under suboptimal conditions (McDonough 1979). This high water requirement is necessary to pass from incipient to normal germination, and for the hypocotyl and root to penetrate the substrate. Maximum growth is reduced by soil solutes, by high incubation temperature, and by aging of the seeds.

The exacting seedbed requirements for successful germination and early seedling growth illustrate several problems of seedling development. One involves failure of the root hairs to penetrate the soil surface. These hairs perform the critical water-absorbing function until significant root growth occurs (Day 1944, Moss 1938); but they are subject to rapid drying. Other disadvantages include weak anchorage to the surface, slow growth of the root and plumule, and etiolation (spindly growth) of the hypocotyl under reduced light. Despite these limitations, however, aspen seedlings effectively colonize regions other than western United States where environmental and land use conditions meet the species' requirements.

VEGETATIVE REGENERATION

George A. Schier, John R. Jones, and Robert P. Winokur

Aspen is noted for its ability to regenerate vegetatively by adventitious shoots or suckers that arise on its long lateral roots. It also produces sprouts from stumps and root collars; but they are not common. In a survey of regeneration after clearcutting mature aspen in Utah, Baker (1918b) found that 92% of the shoots originated from roots, 7% from root collars, and 1% from stumps. Stump and root collar sprouts are more common when sapling-sized or younger aspen are cut; but even then, they probably do not exceed 20% of the regeneration (Maini 1968).

Origin of Suckers

Biological Development

Aspen root suckers develop from meristems that begin in the cork cambium anytime during secondary growth (Brown 1935, Sandberg 1951, Schier 1973c). This contrasts with balsam and black poplars, where most buds originate in the pericyle zone during early life of the root (Schier and Campbell 1976). These meristems may develop into buds and then elongate into shoots; but frequently, growth is arrested at the primordial stage or after a bud forms. When the stems in a clone are cut, suckers arise from new or preexisting meristems (buds and primordia) on the roots. At the same time that shoots are developing, the vascular strand is extending, by dedifferentiation of bark tissue, to the root cambium. Eventually, vascular connections are established between the shoot and the parent root.

Many thousands of suppressed shoot primordia can be found on the roots of most aspen clones. They occur as small mounds protruding from the cork cambium (Schier 1973b), and can be seen without magnification by peeling off the cork (fig. 1). Primordia occur in various stages of ontogeny—from those that are essentially small masses of meristematic cells with no tissue differentiation, to those in which procambium and protoxylem elements have been differentiated. The length of time an adventitious meristem remains in the primordial stage is unknown.

Figure 1.—The cork has been peeled away to uncover preexisting primordia on the surface of an aspen root.

Buds that have been suppressed for more than 1 year have vascular traces that extend into the secondary xylem. They grow enough each year to keep pace with the radially increasing cambium. Buds occasionally emerge as short shoots and then remain dormant for several years before developing into long shoots above the ground (Sandberg 1951). The year a bud has formed can be determined by locating the annual ring in the secondary xylem where the vascular trace originated.

Buds are not as important a source of suckers as are newly initiated meristems or preexisting primordia (Sandberg 1951, Schier 1973b). Sandberg (1951) observed that suppressed buds on roots often remained inhibited while numerous newly initiated meristems and preexisting primordia on the same root developed into suckers. In addition, suckers that originated from suppressed buds elongated much less vigorously than suckers recently initiated from meristems or primordia.

Parent Roots

Aspen root suckering is affected by the depth and diameter of the parent roots. On study areas in Utah and Wyoming, Schier and Campbell (1978a) found that 25% of all suckers arose from roots within 1.6 inches (4 cm) of the surface, 70% within 3.2 inches (8 cm), and 92% within 4.7 inches (12 cm) (fig. 2). The maximum depth of parent roots was 11 inches (28 cm). Compared with parent roots of aspen in the Lake States, those of aspen in the West were deeper. On burned areas, high burn severities increased the depth of the parent roots from which suckers were initiated.

In their study of parent roots of aspen suckers, Schier and Campbell (1978a) found that the range in diameter of roots producing suckers was 0.04 to 3.7 inches (0.1 cm to 9 cm) (fig. 3). On a Utah site, 60% of the suckers grew from roots smaller than 0.4 inch (1 cm) in diameter, 88% from roots smaller than 0.8 inch (2 cm) in diameter, and 93% from roots smaller than 1.2 inches (3 cm) in diameter. On a Wyoming site, the percentages were 38%, 68%, and 86%, respectively.

Factors Affecting Suckering

Apical Dominance

Sucker development on aspen roots appears to be suppressed by auxin transported from aerial parts of the tree (Eliasson 1971b, 1971c; Farmer 1962a, 1962b; Schier 1973d, 1975b; Steneker 1974). This phenomenon is termed "apical dominance." When movement of auxin into roots is halted or reduced by cutting, burning, girdling, or defoliation of the trees, auxin levels in the roots decline rapidly (Eliasson 1971c, 1972). This permits new suckers to begin; it also allows preexisting primordia, buds, and shoots, whose growth had been suppressed by auxin, to resume growth.

Deteriorating, overmature aspen clones often fail to regenerate because apical dominance is maintained over a shrinking root system (Schier 1975a).

Apical dominance also is important in limiting regeneration after an aspen stand is cut or burned. Elongating suckers produce auxins whose translocation into the root inhibits the initiation and development of additional suckers (Eliasson 1971a, Schier 1972).

The relatively large number of suckers that arise regularly in many undisturbed aspen clones indicates that apical dominance is not absolute (Schier 1975b, Schier and Smith 1979). This is not surprising, because auxin is a relatively unstable compound that must be transported a considerable distance from its source in developing buds and young leaves to the roots for it to have its effects. Apical dominance weakens as auxin travels down the stem because of immobilization, destruction, and age (Thimann 1977).

During normal seasonal tree growth, there are periods when apical dominance is weak enough to permit suckering. For example, in spring, before bud burst and translocation of auxin to the roots, temperatures often are high enough for suckers to begin and grow (Schier 1978c). Sucker formation is inhibited later, after the leaf buds open and apical dominance is reasserted.

Hormonal Growth Promoters

Factors stimulating root sucker initiation and growth have not been as thoroughly studied as apical dominance. Research with other plants (Peterson 1975, Skene 1975), exploratory studies in aspen (Barry 1971, Schier 1981, Williams 1972), and culture of plantlets on aspen callus (Winton 1968, Wolter 1968) all indicate that cytokinins synthesized in root meristems are involved in suckering. High ratios of cytokinins to auxins favor shoot initiation; low ratios inhibit it (Winton 1968, Wolter 1968). Changes in these ratios occur when an aspen tree is cut, because auxins no longer move into the roots, and cytokinins no longer move out of them.

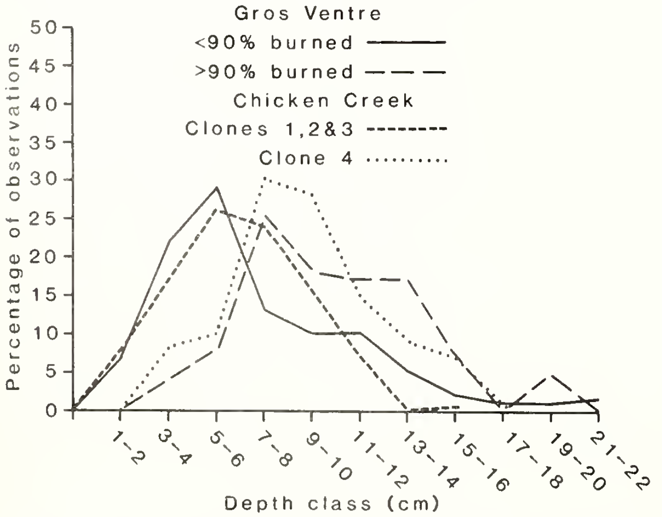

Figure 2.—Frequency distribution of root suckers in relation to parent root depth after burning in the Gros Ventre area in Wyoming and clearcutting in the Chicken Creek Watersheds in Utah (Schier and Campbell 1978a).

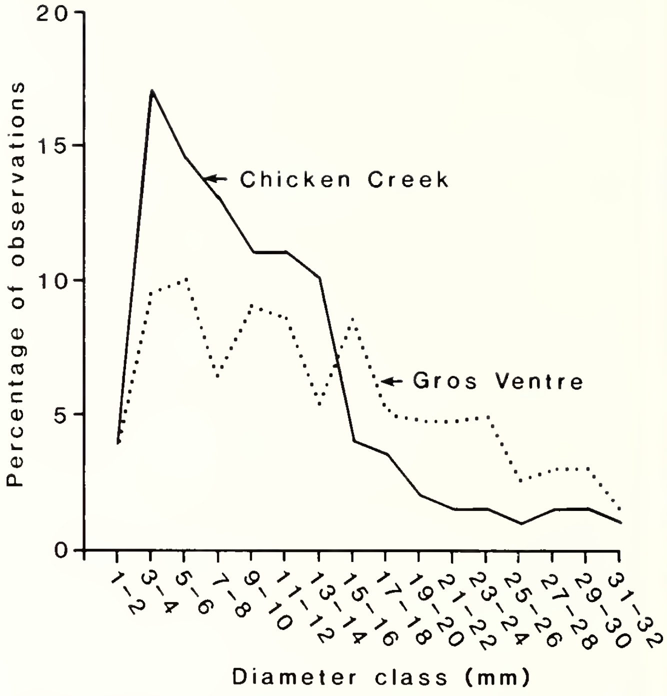

Figure 3.—Frequency distribution of root suckers in relation to parent root diameter after burning in the Gros Ventre area in Wyoming and clearcutting in the Chicken Creek Watersheds in Utah (Schier and Campbell 1978a).

Another growth regulator, a compound resembling gibberellic acid, appears to promote sucker production by stimulating shoot elongation after suckers have begun (Schier 1973a, Schier et al. 1974). Therefore, interference with its biosynthesis can reduce regeneration, even if cytokinin concentrations are high.

Abscisic Acid

Abscisic acid (ABA) may have a role in inhibiting sucker growth in dormant aspen. When young aspen were decapitated after going dormant in late summer, buds formed on the roots; but they did not elongate until the next spring (Schier 1978c). Regulation of dormancy generally seems to be controlled by a balance between endogenous inhibitors, such as ABA, and growth promoting substances, especially gibberellins. Dormancy is broken by low winter temperatures, which lower the inhibitor:growth-promoter ratio.

Carbohydrate Reserves

After a change in hormone balances triggers new shoots, carbohydrate reserves supply the energy necessary for bud development and shoot outgrowth. Primordia actually may be stimulated only in those areas of the root where there has been a heavy accumulation of starch (Thorpe and Murashige 1970).

An elongating sucker remains dependent upon parent root reserves until it emerges from the soil surface and can photosynthesize (Schier and Zasada 1973). The number of suckers developing on aspen roots generally is not limited by the concentration of stored carbohydrates. However, because sucker growth through the soil is sensitive to slight changes in carbohydrate concentration, the density of actual regeneration can be limited by low levels of carbohydrate reserves. Low supplies of carbohydrates might be expected to have more effect on regeneration from clones whose horizontal roots are deeper, because their suckers require more energy to push through to the soil surface.

After the parent stand has been removed, repeated destruction of the new suckers (such as by repeated browsing, cutting, burning, or herbicide spraying) can exhaust carbohydrate reserves and drastically reduce production of more suckers (Baker 1918b, Sampson 1919). This accounts for the dwindling sucker production on heavily browsed cutovers.

Environmental Factors

Soil temperature is important to suckering (Maini and Horton 1966b, Zasada and Schier 1973) and may account for sucker invasions of grassland adjacent to aspen stands (Bailey and Wroe 1974, Maini 1960, Williams 1972). High temperatures increase cytokinin production by root meristems (Williams 1972) and may also lower auxin concentrations in roots by speeding its degradation. The effect is a higher ratio of cytokinins to auxins, which stimulates suckering, as noted previously.

Root cuttings in a medium that is either very dry or saturated with water produce few suckers. Sucker production in the forest, however, is not inhibited by dry surface soils, because water is translocated upward through parent roots from moist soil deeper in the profile (Gifford 1964). (See the EFFECTS OF WATER AND TEMPERATURE chapter.)

Although light is not essential for sucker initiation, it is necessary for good sucker growth (Farmer 1963a). Baker (1925) compared the number of suckers under various light intensities. He found that under full sunlight in clearcuts, there were 40,000 suckers per acre (98,840 per ha). Where shading from residual aspen reduced light intensity to 50% of full sunlight or less, the number of suckers decreased to fewer than 3,000 stems per acre (7,400 per ha). (See the OTHER PHYSICAL FACTORS chapter for a more detailed discussion of the effects of light on aspen regeneration.)

Potential Sucker Production

The potential for suckering is enormous. Almost any segment of an aspen root, except newly formed root parts, can sucker under favorable conditions (Sandberg 1951). Schier and Campbell (1980) found that under artificial conditions, the number of suckers produced from 1/4- to 1/2-inch (0.6-cm to 1.3-cm) diameter root cuttings of 20 Utah aspen clones was 0.25 to 15.7 per lineal inch (0.1 per cm to 6.2 per cm); the mean number was 2.0 per inch (0.8 per cm). Barry and Sachs (1968) found a maximum of 600 sucker buds on an 18-inch-long (45-cm) root segment of 1/2-inch (1.3 cm) diameter.

Clearcutting the aspen overstory usually results in profuse, relatively rapid aspen suckering. In southwestern Colorado, commercial clearcutting of mature quaking aspen on blocks ranging from 3 to 17 acres (1 ha to 7 ha) resulted in 31,000 sprouts per acre (76,600 per ha) 1 year after clearcutting, compared to the 1,000 per acre (2,500 per ha) on the uncut blocks (Crouch 1983). In a northwestern Colorado study, clearcutting mature aspen on 5-acre (2-ha) blocks resulted in 18,000 sprouts per acre (44,500 per ha) compared to 531 stems per acre (1,300 per ha) before clearcutting (Crouch 1981). In a northern Utah study (Bartos and Mueggler 1982), the number of suckers per acre increased nearly twentyfold 2 years after clearcutting (fig. 4). Similar large increases in numbers of suckers after clearcutting were reported in other studies (Baker 1925, Hittenrauch 1976, Jones 1975, Mueggler and Bartos 1977, Sampson 1919, Smith et al. 1972). One reason for such large numbers of suckers is that they often emerge in clumps from a single point of origin on the parent root (Benson and Einspahr 1972, Sandberg 1951, Smith et al. 1972, Turlo 1963).

Jones (1976) indicated that 20,000-30,000 suckers per acre (49,400-74,100 per ha) is not excessive, because early natural thinning is heavy and effective. The number of suckers rapidly declines when suckers are

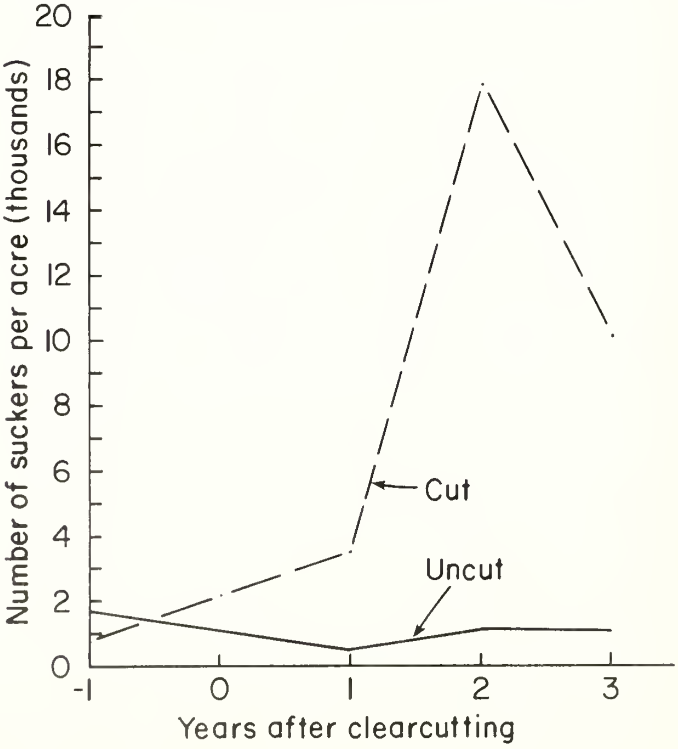

Figure 4.—Changes in the number of aspen suckers per acre on clearcut and uncut control areas from 1 year before cutting to 3 years after cutting (data from Bartos and Mueggler 1982).

extremely numerous after clearcutting (fig. 4) (Baker 1925; Bartos and Mueggler 1982; Crouch 1981, 1983; Sampson 1919; Smith et al. 1972). The least vigorous suckers die during the first 1-2 years, leaving one or two dominant suckers in each clump. Competition reduces most clumps to a single stem by the fifth year after cutting, and almost all to a single stem by the tenth year (Sandberg 1951, Turlo 1963). Competition also is a major factor in thinning out young stands of suckers. As stands develop, some of the trees become overtopped and die off (Jones 1976, Moir 1969). Diseases, insects and other invertebrates, mammals, and snow damage (Crouch 1983) also are factors (see the related chapters in PART II. ECOLOGY).

Sucker production also is affected by the stocking of the parent stand before cutting. Poorly stocked aspen produce few suckers after logging, because they do not have the necessary root densities. In Michigan, Graham et al. (1963) found the following relationship between the basal area per acre of parent stands and mean sucker production 1 year after clearcutting: less than 50 square feet, 5,200 suckers per acre (12,850 per ha); 51 to 100 square feet, 7,000 suckers per acre (17,300 per ha); and more than 100 square feet, 9,900 suckers per acre (24,450 per ha).

Where aspen stocking is low, sucker production sometimes may not peak until several years after cutting or burning. On a mixed conifer burn in New Mexico, number of suckers from the intermixed aspens increased from 11,800 stems per acre (29,150 per ha) 1 year after the fire to 14,500 stems per acre (35,800 per ha) 3 years afterwards (Patton and Avant 1970).

Occasionally, heavily cut aspen stands in Colorado produced few suckers (Hessel 1976).[1] This also has been observed in the Lake States (Fralish and Loucks 1967, Stoeckeler and Macon 1956). In some of these cases, heavy and repeated deer browsing of young suckers may have been responsible.

The failure of aspen to regenerate also has been observed in deteriorating aspen clones where production of suckers is often insufficient to replace overstory mortality (Schier 1975a). On many sites, these clones are rapidly replaced by conifers. Dry sites, however, revert to rangeland dominated by shrubs, forbs, and grasses.

Although there may be only a few scattered residual aspen in coniferous stands, aspen root suckers generally will dominate the regeneration after logging or fire if aspen root density is adequate (fig. 5). Often, the residual aspen are large veterans surviving from a time of aspen dominance (fig. 6). However, in other coniferous stands, aspens are so few they might escape casual observation (Marr 1961). On Colorado spruce-fir burns occupied by aspen stands, aspen often had been represented only sparingly before the fires (Stahelin 1943). After the fires, aspen suckers formed patches around where aspen had stood previously. The patches tended to coalesce over time by the extension and suckering of roots. The resulting stands, therefore, were only broadly even-aged. Perhaps scarcity of parent trees also accounted for the 5- to 10-year age range reported by Loope and Gruell (1973) for mature aspen stands near Jackson Hole, Wyo.

Figure 5.—A 23-year-old mixed conifer burn with dense aspen. The burned-out snag in the center was a large Douglas-fir. Most of the fallen snags were Engelmann spruce and Douglas-fir. Escudilla Mountain, Apache National Forest, Arizona.

In the lower foothills of the Canadian Rockies, Horton (1956) found aspen suckers in almost every stand regardless of age, density, or species composition. Even under very dense canopies, he found weak, inconspicuous suckers, most of which probably would live only a few years. These observations suggest that, in some areas, aspen roots occasionally may persist in the absence of canopy aspen, nurtured only by transient suckers beneath the coniferous canopy.

Figure 6.—A southwestern mixed conifer stand with aspen scattered throughout. Canopy trees on this site were primarily Douglas-fir, Engelmann spruce, corkbark fir, and aspen. Harvest of nearly all the merchantable conifers (23,000 board feet per acre) resulted in widespread suckering and aspen dominance of the regeneration stand (Gottfried and Jones 1975). Apache National Forest, Arizona.

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[1] *Betters, David R. 1976. The aspen: Guidelines for decision making. Report, Routt National Forest, Rocky Mountain Region, USDA Forest Service, 100 p. Steamboat Springs, Colo.*

Variation Among and Within Clones

The number of suckers produced can vary markedly among clones (Barnes 1969, Tew 1970a). Barry and Sachs (1968) reported large differences in sucker production among California aspen clones. Similarly, the relative capacities of different clones to produce suckers varied greatly when suckers were propagated from root cuttings in controlled environments (Farmer 1962a, Maini 1967, Schier 1974, Schier and Campbell 1980, Tew 1970a, Zufa 1971). The magnitude of these differences varied with date of root collection because of variation in the seasonal trend in sucker production among clones (Schier 1973d, Schier and Campbell 1980).

The number of suckers produced by a clone probably is related to the levels of carbohydrate reserves (Schier and Johnston 1971, Tew 1970a) and hormonal growth promoters in the roots. In the West, where single clones frequently cover several acres, such clonal differences may account for large differences in the density of suckering (Jones 1975).

Genotype probably also strongly influences suckering capacity. However, nongenetic factors, such as clone history, stem age, and environmental factors could have the major influence. Some clones, despite a high suckering capacity, produce few viable suckers when propagated from root cuttings, because their excised roots are highly susceptible to decay (Schier 1981).

The fact that some clones have an all-aged stand structure indicates that, even in undisturbed stands, suckers that die can be replaced quickly by new ones (Alder 1970). Also, apical control may be so weak, or the concentration of growth promoting substances may be so high in some clones, that they sucker vigorously after the slightest disturbance.

There also is considerable variation in suckering capacity among lateral roots within an aspen clone (Schier 1978a). Intraclonal differences among roots probably are caused by differences in the physiological condition (e.g., water content, hormone levels and ratios, concentration of nutrients), which, in turn, are caused by microclimate variability and root position in the clonal root system. Temperature, an important microclimatic element noted previously, varies with soil depth and exposure to radiation. Physiological condition as controlled by root position depends upon proximity and attachment to trees of various ages and vigor. This position determines the quantity of photosynthates and auxins and other growth regulators translocated to a particular root.

There is no evidence of a gradient in suckering capacity in a segmented root; that is, cuttings from a lateral root that were taken further from the stem did not significantly differ in suckering capacity from those taken from the same root closer to the stem (Schier 1978a). This indicates that neither distance from the parent tree, nor root age regulate suckering within lateral roots.

GENETICS AND VARIATION

John R. Jones and Norbert V. DeByle

The broad genotypic variability in quaking aspen (*Populus tremuloides* Michx.), that results in equally broad phenotypic variability among clones is important to the ecology and management of this species. This chapter considers principles of aspen genetics and variation, variation in aspen over its range, and local variation among clones. For a more detailed review of the genetics of quaking aspen, especially with wider geographic application and with emphasis on tree breeding, see Einspahr and Winton (1976).

General Principles

Cytogenetics

Aspen is typically dioecious—forming either male or female flowers on a tree, but seldom both. The haploid number of chromosomes in the gametophytes formed in these flowers is 19. Through sexual union, the nucleus in the cells of the resulting sporophyte (tree seedling) has a diploid number of chromosomes—38 in aspen (Einspahr and Winton 1976).

Sometimes the normal process of chromosome splitting and recombining during cell division goes awry. This can result in triploid, or even tetraploid or monoploid sporophytes. Polyploidy occurs in aspen, and can be induced for breeding purposes (Einspahr and Winton 1976). Triploid trees (clones) at times occur in nature.

Hybridization

Quaking aspen crosses readily with other species of *Populus* within the section *Leuce*, producing hybrids. Where quaking aspen grows near bigtooth aspen (*Populus grandidentata* Michx.) (Barnes 1961) or near introduced species, hybrids sometimes occur (Einspahr and Winton 1976). Quaking aspen also has been hybridized with other species, particularly *P. tremula*, *P. alba*, and *P. canescens* in tree breeding programs (Einspahr and Winton 1976).

Population Genetics

A population persisting in an environment has become genetically adapted to survive there. A species growing in a wide variety of environments exhibits genetic variation associated with the pattern of environmental variation (Spurr and Barnes 1973). Typically, tree species have a clinal or continuous pattern of genetic variation.

The term "aspen ecotypes" often is used. Ecotype implies a degree of genetic discontinuity between one population and other populations of the species, as distinguished from the more continuous variability across a cline (Ford-Robertson 1971, Society of American Foresters 1958, Spurr and Barnes 1973). The pattern of genetic variation in aspen, however, appears to be clinal. Therefore, the term "ecotype," although commonly used in reference to aspen, is not entirely correct.

Genetic differences among populations usually reflect existing environmental differences, especially day length and other similar environmental gradients across the cline. They also can reflect past differences, past or current introgression of genes from other species, and genetic changes that accompanied past or existing barriers to gene flow.

Some selection of genotypes can be expected by different environments within a region, and even within a localized area, such as different elevations. However, even where local environmental differences are large, populations usually do not differ as much as those on different parts of the continent because of past gene flow between local sites.

Aspen has certain peculiarities that may have affected its evolution and certainly affect its ecology and management. In the West, a whole aspen stand may be a single genetic entity—a clone (see the MORPHOLOGY chapter). If clones are large, some areas with considerable acreage of aspen, therefore, may have only a few individuals (clones) available for sexual reproduction (Strain 1964).

In much of the West, even where there are many genotypes, the rarity of successful sexual reproduction results in restricted gene recombination, and, therefore, very limited selection of new genotypes in current environments. Local populations of aspen genotypes are virtually fixed on most western aspen sites.

Given occasional fire or comparable disturbance, aspen clones (genotypes) perpetuate themselves readily and abundantly by root suckering (see the VEGETATIVE REGENERATION chapter). Cottam (1954) suggested that most current clones in the Great Basin are at least 8,000 years old. Barnes (1975) speculated that an occasional Utah and Colorado clone may have originated as a seedling during the Pliocene, surviving the intervening 1 million years or more by suckering. Suitable conditions for widespread aspen seedling establishment apparently can be thousands of years apart without serious genetic impoverishment.

Except during periods of widespread seedling establishment, there may be essentially no competition between aspen genotypes except along clonal boundaries. There is no genetic competition within a stand of pure aspen consisting of a single clone. Such a clone may not be as well adapted to its site as are other clones in the vicinity. But it became established under a set of previous conditions; and, once established, it was well enough adapted to persist.

Geographic Variation

Pauley et al. (1963a, Pauley 1963) grew quaking aspen seedlings in Massachusetts from seed sources throughout most of its range. Seedlings of Lake States origin survived and grew as well as seedlings from local New England sources. But western seedlings from a large range of latitudes (Arizona to the Yukon Territory) were weak, and almost all died by age 12. Daylength at different latitudes is important, as shown by Vaartaja (1960), who compared seedlings from Wisconsin and northern Saskatchewan sources. He found very different growth responses to short-day conditions.

Barnes (1975) studied phenotypic variation of leaves of western aspen from southern Utah and Colorado northward to the Canadian border. While there was a great deal of variation within areas, the differences between areas were even more striking. Proceeding northward, he found that leaves tended to be smaller, and narrower, with one exception—aspen leaves were largest on Vancouver Island and the coast of Washington. Leaves in northern Idaho and northern Montana resembled those of central Canada and the Great Lakes region. Leaves from the Columbia and Colorado Plateaus, however, closely resembled those of preglacial aspens. He suggested that this resemblance to Tertiary aspens reflects the relatively small number of sexual generations over the hundreds of thousands of intervening years. In contrast, in northern Idaho and northern Montana, aspen regeneration from seed is comparatively common, as it is in central Canada and in the glaciated East. Presumably, many more sexual generations in these areas have been exposed to the evolutionary pressures of environmental stresses and competition than those in the Columbia and Colorado Plateaus.

Airborne aspen pollen has been found 200 miles (320 km) from its nearest possible source (Bassett and Crompton 1969). Most female trees, however, probably are pollinated by nearby male trees. Gene flow between widely separated populations of aspen must be slow and uncertain, even under the most favorable conditions.

Local Variation Among Clones

Patterns

Almost every conceivable combination of morphological and phenological characteristics has been reported[1] in aspen clones (Cottam 1954, Egeberg 1963, Morgan 1969, Strain 1961).

There is strong evidence of selection of genotypes by extreme sites. Aspen is morphologically, and presumably genetically, most uniform at its lowest and highest elevations, where environmental stresses are most severe. The greatest variation in form occurs at intermediate elevations (Greene 1971), suggesting a broader spectrum of genotypes there. However, the occurrence of large differences in ecologically adaptive characters between neighboring clones on the same site indicates that selection through much of the aspen elevational zone has not been rigorous.

Phenology

Adjacent clones of the same sex show considerable interclonal variation in bursting of floral buds (Greene 1971). Generally, clones that break dormancy relatively early in one year do the same in other years.

Marked differences in timing of leaf flushing between clones have been observed (Baker 1921, Barnes 1969, Cottam 1954, Egeberg 1963, Strain 1966). The clonal variation does not result entirely from genetic differences between clones; site has a considerable effect on leaf flushing, also.

Egeberg (1963) sampled 60 clones on one Colorado hillside, all at similar elevations and facing the same direction. They leafed out over a 3-week period. Morgan (1969) reported clones that leafed out 2 weeks earlier than neighboring clones, but also turned yellow 2 weeks earlier. Greene (1971), however, found that clones which flushed earliest were not necessarily the first to change color in autumn. Cottam (1954) found that saplings transplanted to the University of Utah campus retained their leafing differences.

A tendency to later leafing and earlier yellowing could be expected at higher elevations. Near Santa Fe, N. Mex., Covington (1975) found that clones at the lowest elevations (8,000 feet (2,450 m)) leafed out as much as 5 weeks earlier than those at the highest (10,700 feet (3,250 m)), and turned yellow 3 to 5 weeks later. He attributed this largely to climatic difference across the 2,700 feet (800 m) of elevation.

Growth Rates

Growth rates are of major interest to foresters. (See the GROWTH chapter for a discussion of the specific characteristics of the growth and development of aspen trees and stands.) Zahner and Crawford (1965) documented large differences in growth rates of adjacent bigtooth aspen clones on the same site. Barnes (1969) found that growth rates varied among different quaking aspen clones on the same sites in Michigan. When differences were adjusted for crown class, he found heritabilities of 0.58 and 0.43 for total height and diameter at breast height, respectively.

In Utah, Warner and Harper (1972) commonly observed large height differences between contiguous clones on apparently uniform sites. Clonal differences in

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[1] *Montgomery, D. H. 1957. A phenological study of aspen in the Medicine Bow Mountains. 25 p. Unpublished paper at the University of Wyoming, cited by Strain (1961, 1964).*

diameter growth also have been found. In many clones in the Colorado Front Range, Mitton and Grant (1980) found a significant positive relationship between clone heterozygosity and mean annual diameter growth.

Jones and Trujillo (1975a, 1975b) dissected dominant aspen along the common boundaries of paired clones in Arizona. Their data suggested that, while substantial differences are often seen, most clones which share a site do not differ much in height. Where there are height differences between clones on a shared site, they often develop during the early to mid-sapling stage. Subsequent height growth in both clones may be similar, and the height difference may remain about the same for many years (fig. 1). Height contrasts often are most conspicuous, therefore, when the stand is young (Jones and Trujillo 1975a, 1975b).

Zahner and Crawford (1965) pointed out that clonal height variation can introduce a major error when site index is used to characterize the production potential of a site. That is a problem primarily where the site is occupied by several to many clones, and site index is unwittingly based on only one or two.

In the West, however, a site will often be occupied entirely by one clone. The site index of that clone is normally the only relevant one, unless the area is to be regenerated by planting. Perhaps the best aspen site indexes in the West are the result of superior genotypes growing on good to excellent sites. Conversely, the poorest result from inferior genotypes growing on poor sites. (See the section on site index in the GROWTH chapter.)

Regeneration

In Arizona and Utah, regeneration and subsequent stocking sometimes differ among clones (Jones and Trujillo 1975a, Schier 1975a, Schier and Campbell 1980). In Arizona, at age 22, some clones with more trees per acre also had larger trees, in both height and diameter, than neighboring clones on the same site, despite considerably greater crowding (Jones and Trujillo 1975a).

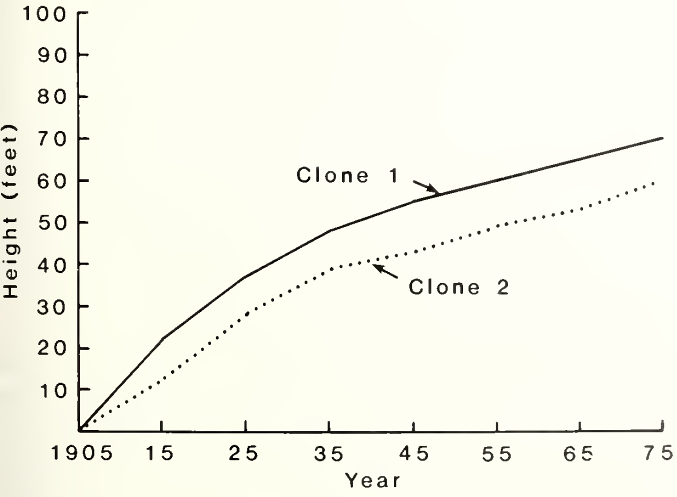

Figure 1.—Height growth curves of two clones on the same plot and site (Jones and Trujillo 1975b). Apache National Forest, Arizona.

There are numerous reports of clonal differences in the suckering capacity of excised roots (Farmer 1962a, Maini 1967, Schier 1974, Schier and Campbell 1980, Tew 1970a, Zufa 1971). Sucker cuttings also show clonal differences in rooting ability (Schier 1974, Schier and Campbell 1980). (See the VEGETATIVE REGENERATION chapter for a fuller discussion of variation in suckering potential within and among clones.)

Susceptibility to Diseases and Insects

In Manitoba, Wall (1971) found that the incidence of decay, percent of volume decayed, position of rot columns in the trunks, and shape of rot columns, differed among clones. Where clonal boundaries crossed the boundaries of different sites, clonal responses to site change were not always the same. Decay might increase in some clones but decrease in others. In Michigan, susceptibility to Hypoxylon canker varied markedly among clones on four different sites (Copony and Barnes 1974).

A late-flushing clone in Alberta was damaged by leaf beetles year after year. The older and less succulent leaves of nearby clones were less attractive to the beetles and were not damaged.[2] In contrast, populations of tortricid caterpillars infested primarily the leaves of early-flushing clones (Witter and Waisanen 1978).

Polyploidy

Differences in growth rates and wood characteristics have been demonstrated between naturally occurring triploid clones and associated diploid clones (Einspahr et al. 1967; Van Buijtenen et al. 1958a, 1958b). But it was not established that the differences were greater than those between some diploid clones. Van Buijtenen et al. (1958b) reported that clues for recognizing triploids were their larger trees and larger leaves. But the triploids they described presumably were found and recognized because they looked different. There may have been other triploid clones in the vicinity that were not recognized, whose trees and leaves were not larger than many of the nearby diploid clones. This is suggested by Every and Wiens (1971). In studying 18 Utah clones, they found that three were triploids and one was a tetraploid. Yet, there were no morphological differences that distinguished them from the associated highly varied diploid clones. This suggests that polyploids may be more common and some of them less conspicuous than generally realized.

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[2] *Personal communication from A. K. Hellum, University of Alberta.*

Other Characteristics

In Manitoba, Wall et al. (1971) noted that some clones became chlorotic on nutrient-deficient sites where others did not. Research with cottonwood clones (Curlin 1967) suggests that differences among aspen clones in response to soil fertilization might be expected.

Carbohydrate reserves in roots vary from clone to clone (Schier and Johnston 1971, Tew 1970a) (see the VEGETATIVE REGENERATION chapter). Tew (1970b) found differences between clones in chemical composition of leaves that would influence their browse quality for animals.

Some clones have very slender twigs, while the twigs are relatively stout on others. On some they are quite crooked; on others they are comparatively straight. Barnes (1969) and Strain (1964) mentioned clonal differences in branching habit. Barnes (1969) also noted variation in time of flowering.

As discussed in the MORPHOLOGY and GROWTH chapters, young aspen stands generally thin themselves effectively. Occasionally, however, a mature clone may be found which has not thinned itself (fig. 2). At age 70, the clone in figure 2 still had about 8,000 live but stunted stems per acre (19,800 per ha), despite several years of western tent caterpillar attacks. Nearby clones on the same ridge had typical stocking and much larger trees.

Sex-Related Differences

Reviewing genetics research on the genus *Populus*, Pauley (1949) felt there was considerable evidence that male *Populus* clones tend to grow faster and have better form and disease resistance than female clones. Rohmeder and Schonbach (1959) reported a tendency in male clones of European *P. tremula* to have better vigor and form than female clones. In a Saskatchewan study, female trees flowered and leafed out 4 to 5 days earlier than males, and the leaves also yellowed earlier (Maini 1968). Morgan (1969) reported that the female trees he saw flowering in an apparently small sample of Colorado clones all leafed out early, while no early-leafing male trees were seen. In the Snowy Range, in Wyoming, Montgomery found that the time of flowering did not differ with sex.[1]

Figure 2.—An unusual, 70-year-old clone that had not become self-thinned. About 8,000 live stems per acre (19,800 per ha). Carson National Forest, New Mexico.

Einspahr (1962) compared 49 male and 42 female clones in Upper Michigan and northern Wisconsin. He found no statistically significant difference between the sexes in any of the characteristics compared—age, height, diameter at breast height, volumes, form class, branch angle, branch weight, natural pruning, or crown volume. Barnes (1969) found sex and growth unrelated in Lower Michigan. In Colorado, however, Grant and Mitton (1979) found that at all elevations, female clones showed a consistently higher radial growth increment than male clones.

Whether clonal differences in form, growth, etc. tend to be sex-related seems generally unimportant from a management viewpoint. Clones usually are selected for the desired characteristics—form, vigor, phenology, etc. The sex of the clone usually is not a consideration except for seed collection or production.

Distinguishing Clones

The great genotypic variation in aspen is reflected in an equally great phenotypic variation among clones. Yet, the genotype uniformity within clones is equally striking—all the trees within a clone appear almost alike. This, plus the large size of most western clones, produces a mosaic on the western landscape (fig. 3). These clones can be distinguished by many characteristics, some very noticeable, and some quite subtle.

Forest managers seldom may be interested in the less noticeable clonal differences, such as leaf morphology. If a clone is markedly superior or inferior in terms of growth rate, stocking, stem form, pruning, beauty, or disease incidence, it usually will be easily recognized. Researchers, however, may want to distinguish clones that are not conspicuously different.

In Minnesota, Blake (1964) outlined what appeared to be different clones on low level color aerial photographs taken in spring. Ground checking confirmed the identification.

Barnes (1969) presented a summary of identifying characteristics for clones in northern Lower Michigan. They are equally applicable in the West. Modified slightly, they are presented in table 1, listed in order of decreasing usefulness within each season. Some characteristics, such as bark color, are useful only when viewing both clones from the same direction. The same tree often looks markedly different on opposite sides.

Leaves differ greatly within a clone, depending on the size, age, and crown class of the tree. They also differ on determinate and indeterminate shoots, on shoots of different lengths, and at different positions on the shoot. But within those subdivisions, they are relatively uniform within a clone. For example, a tree may be assigned to a clone on the basis of two leaves from the lower crown, taken from the central portion of a determinate shoot 1 to 5 inches (3 cm to 13 cm) long.

Figure 3.—A mosaic of aspen clones on Utah's northern mountains.

Greene (1971) listed six prominent features useful in differentiating clones in Colorado: (1) sex, (2) time of leafing and of leaf fall, (3) spring and autumn leaf color, (4) shape and size of leaves, (5) leaf serration, and (6) pubescence of dormant buds.

When possible, the ideal times to identify clones are the period of leafing out in late spring and the period of color change and leaf-fall in early autumn. Many clones that look much alike in midsummer contrast sharply at those times.

Table 1.—Criteria for distinguishing clones, by season and in order of usefulness. Adapted from Barnes (1969).

---------------------- All Seasons ----------------------

Bark
  1. Texture
  2. Color

Stem Characteristics
  3. Form
  4. Branching habit (angle, length, and internode length)

Susceptibility to injury
  5. Sunscald
  6. Frost crack
  7. Insect and disease injury

Miscellaneous
  8. Self-pruning
  9. Galls

------------------------ Spring ------------------------

  1. Sex
  2. Time of flowering, and flower characteristics
  3. Time, color, and rate of leaf flushing

------------------------ Summer ------------------------

  1. Leaf shape (width/length ratio), color, and size
  2. Shape of leaf blade base
  3. Leaf margin; number, size, and shape of teeth
  4. Shape of leaf tip
  5. Leaf rust infection

------------------------ Autumn ------------------------

  1. Leaf color
  2. Time and rate of leaf fall

PART II. ECOLOGY

PART II. ECOLOGY

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VEGETATION ASSOCIATIONS

W. F. Mueggler

Aspen trees grow along moist stream bottoms as well as on dry ridges and southerly exposures, on talus slopes, and on shallow to deep soils of varied origins. Quaking aspen is one of the few plant species that can grow in all mountain vegetational zones from the alpine to the basal plain (Daubenmire 1943). As a consequence, aspen dominated communities are found intermixed with such divergent vegetation as semiarid shrublands and wet spruce-fir forests.

The broad latitudinal and environmental range of aspen (discussed in the DISTRIBUTION chapter) brings it into association with a diversity of other plant species. Consequently, understory composition varies from place to place and reflects both regional floristics and adjacent vegetation types.

A characteristic element among aspen communities in the West is the luxuriant undergrowth that it supports compared to that in adjacent coniferous forests. This undergrowth frequently consists of three layers: tall shrubs, medium shrubs/tall herbs, and low herbs. Forbs generally dominate the herb component; but occasionally, grasses and sedges are equally abundant.

The complexity and diversity of aspen-dominated communities are compounded by the occurrence of aspen as a dominant seral as well as climax tree. The proportion and even presence of many understory species changes drastically as the climax trees (usually conifers in the West) regain dominance and alter the microenvironment and competitive relationships.

There have been only a few, geographically narrow attempts to classify aspen communities into recognizable associations based upon floristics and/or environment. Although interest in classifying aspen communities is increasing (Hoffman and Alexander 1980, Mueggler and Campbell 1982, Severson and Thilenius 1976, Youngblood and Mueggler 1981), descriptions of community composition are too incomplete to permit reliable categorization of aspen associations throughout the West or even on a regional basis.

Figure 1.—A seral aspen community in northern Utah rapidly being replaced by Engelmann spruce and subalpine fir climax forest.

Seral Versus Stable Aspen Communities

Aspen generally has been regarded as a fire-induced successional species able to dominate a site until it is replaced by less fire-enduring but more shade tolerant and environmentally adapted conifers. (The role of fire in aspen succession is discussed in the FIRE chapter.)

The successional status of much western aspen land is evidenced by aspen's relatively rapid replacement by conifers within a single aspen generation (fig. 1). This is a major concern to many resource managers who anticipate the loss of multiple resource values (grazing, wildlife habitat, water production) accompanying such type conversion. In many areas, however, conifer invasion can be so slow that more than 1,000 years without fire may be required for aspen stands to progress to a conifer climax.

Recent studies suggest that although the majority of aspen forests may be seral to other types of vegetation, climax aspen communities occur throughout the West. Lynch (1955) described stable aspen groves in northern Montana; aspen appears to be a climax dominant in parts of western Wyoming (Beetle 1974, Reed 1971, Youngblood and Mueggler 1981), southern Wyoming (Wirsing and Alexander, 1975), eastern Idaho (Mueggler and Campbell 1982), and in parts of northern Utah (Henderson et al. 1977); both Hoffman and Alexander (1980) and Langenheim (1962) concluded that many of the aspen forests in central and northern Colorado are stable; and Severson and Thilenius (1976) found stable aspen communities in the Black Hills of North Dakota.

The uneven age distribution of aspen trees in some stands (fig. 2) indicates that aspen can be self-perpetuating without necessarily requiring a major rejeuvenating disturbance such as fire. Whether such stands qualify as "climax" is unclear. An uneven-aged structure of the aspen overstory, lack of evidence of successional change in the understory, and absence of invasion by trees more shade tolerant than aspen are indicators of community stability. Such relatively stable stands that are able to persist for several centuries without appreciable change should be considered at least *de facto* climax, and should be managed as stable vegetation types.

The environmental conditions which differentiate stable and seral aspen communities have not been determined. Harper[1] found that seral aspen stands were not consistently associated with soil parent material. Instead, they appeared to be associated with sandstone soils on the Wasatch Plateau of central Utah, with basaltic soils on the Aquarius Plateau, and with granitic soils in the LaSal Mountains of south-central and southeastern Utah. Aspen tends to form relatively stable communities at mid-elevations and on southerly exposures; at high elevations and on northerly exposures, it usually is seral to conifers. However, these relationships have not been verified.

The most valid indicator of a seral aspen situation appears to be incipient or actual prominence of conifers, which suggests active replacement of the aspen overstory by more shade tolerant trees. Conifers, however, must be prominent, not merely present. Occasional conifers can be found in a basically stable aspen community because of highly unusual and temporary conditions which favored their establishment. In such cases, a stable aspen community might contain a few scattered conifers but lack subsequent conifer reproduction, even though a seed source is present. An uneven-aged conifer understory generally is reliable evidence of a seral aspen site.

Seral aspen communities in the West usually change eventually to forests dominated by coniferous trees if plant succession is permitted to progress without disturbance. Conifers such as *Picea engelmannii*, *P. pungens*, *Abies lasiocarpa*, *A. concolor*, *Pinus contorta*, *P. ponderosa*, and *Pseudotsuga menziesii* form an increasing part of the tree canopy as succession progresses.

Figure 2.—A stable, uneven-aged aspen community in northern Utah.

Figure 3.—A degenerating aspen community in southern Montana being replaced by mountain grassland vegetation.

Sometimes, however, aspen communities are replaced by grasslands and shrublands (fig. 3). This usually occurs where aspen fails to regenerate on sites not suited for the establishment and growth of conifers. Regeneration can fail when apical dominance prevents suckering during gradual deterioration of the clones (Schier 1975a) (see the VEGETATIVE REGENERATION chapter). Regeneration also can fail because of animal use. Where suckering does occur in a decadent clone, continued heavy browsing by wildlife or livestock can prevent suckers from developing into trees and cause a gradual conversion to grasslands or shrublands. (See the ANIMAL IMPACTS chapter.)

Community Structure

All aspen communities are multilayered. Sufficient light is able to penetrate the canopy to support abundant undergrowth, in contrast to the general paucity of herbs and shrubs in adjacent coniferous forests.

Most aspen stands are even-aged because of the rapid reproduction by suckering after major disturbance. Uneven-aged stands are likely to form under stable aspen conditions where the overstory gradually disintegrates with disease or age and is replaced by suckers. Uneven-aged stands also occur where individual clones gradually expand into adjacent grasslands or shrublands. At maturity (80 to 100 years) tree heights range from roughly 30 to 100 feet (10 m to 30 m), depending upon site and clonal genotype. A tall shrub stratum sometimes grows beneath this tree canopy layer. Where present, tall shrubs form a very open and intermittent layer from 6 to 12 feet (2 m to 4 m) in height. Medium height shrubs and tall herbs frequently form a rather continuous layer at about 3 feet (1 m). An even lower layer of herbs is always part of the understory. Although scattered mosses and lichens may be on the forest floor, they seldom form a conspicuous layer. Some aspen communities in the West consist of only a tree layer and a low herbaceous layer of forbs and/or graminoids; more commonly, however, a medium shrub and/or tall herb layer also is present.

In seral aspen stands, the tree canopy usually consists almost exclusively of aspen for 50 to 150 years, un-

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[1] *Personal communication from K. T. Harper, Department of Botany and Range Science, Brigham Young University, Provo, Utah*

til the slower growing conifers are able to penetrate the aspen canopy. As the conifer layer thickens, less light penetrates to lower levels of vegetation, competitive relationships are altered, and the understory shrubs and herbs progressively decrease in abundance until few remain.

A tall shrub undergrowth component can be found associated with aspen along the Rocky Mountains and high plateaus from Canada to Mexico. Species of *Prunus* and *Amelanchier* frequently are major constituents of this layer throughout the range of aspen in the West. Other genera, such as *Acer, Quercus,* and *Corylus,* however, are more restricted geographically. Usually the shrubs are scattered and do not form a well-defined layer. Occasionally, however, these tall shrubs are so abundant that they impede movement of livestock and humans through the stands. The environmental controls on the tall shrub component are uncertain; but, for whatever reasons, this layer appears to frequent aspen communities more on southerly than on northerly exposures, and more at lower than at upper elevations.

Most aspen stands contain an undergrowth layer consisting of a mixture of medium-high shrubs and tall herbs. A variety of shrub genera may be found in this layer (e.g. *Pachistima, Ribes, Shepherdia, Juniperus, Ceanothus,* and *Spiraea*). Various species of *Symphoricarpos* and *Rosa,* however, usually are most frequent and abundant. These latter two genera appear to typify the shrub component of aspen communities throughout the West. The tall herb component in this layer consists of a wide variety of genera. Those most common are: *Agastache, Aster, Delphinium, Senecio, Ligusticum, Hackelia, Heracleum,* and *Rudbeckia.* Species composition of the medium shrub/tall herb layer varies greatly between locations. In some stands, it may be composed almost exclusively of *Symphoricarpos oreophilus.* In others, shrubs may be lacking, and the layer will be composed of tall forbs, such as *Senecio serra, Rudbeckia occidentalis, Agastache urticifolia,* and *Delphinium occidentale.*

The low herb layer, always present in aspen communities, varies in composition. It generally is composed of an abundance of forbs and lesser amounts of graminoids. Occasionally, low-growing shrubs, such as *Berberis* and *Arctostaphylos,* also are present. The graminoids associated throughout the geographical distribution of aspen consist of members of the genera *Agropyron, Bromus, Poa, Elymus,* and *Carex.* The most generally encountered forb genera in this layer are *Thalictrum, Achillea, Aster, Fragaria, Osmorhiza, Lupinus, Galium,* and *Valeriana*; however, the diversity of forbs is great. *Thalictrum* is the only low forb that really typifies aspen communities throughout the West. Annual forbs, such as *Nemophila breviflora* and *Galium bifolium,* are rather common in this layer. In some locations, species of *Lathyrus* and *Vicia* form a rather unique, sprawling net of lush growth partly elevated by their tendency to cling to and climb over low shrubs and upright forbs.

Aspen Associations

An understanding of the similarities and differences in aspen communities throughout the West can be facilitated by a regional summarization of available information. The regional breakdown used here (fig. 4) is based primarily on broad physiographic provinces (Fenneman 1931). The amount of information available on aspen communities for any one region differs considerably and tends to reflect the prevalence of aspen in the region.

The undergrowth of aspen communities is highly diverse even within subregional areas. Extensive surveys of aspen communities indicate that only about 10% of the species encountered are found in more than 50% of the stands (table 1). For example, of 114 important shrubs and herbs found in eastern Idaho aspen communities, only 11 were present in more than one-half of the 319 stands sampled (Mueggler and Campbell 1982). Frequently, species that dominate the undergrowth of some stands are absent in others. This reflects the ability of aspen to serve as an overstory dominant under a broad range of environmental conditions.

Despite the highly varied composition of undergrowth in aspen communities throughout the West, certain genera appear repeatedly regardless of geographical location. Shrub genera typically growing in aspen communities are *Symphoricarpos, Rosa, Amelanchier, Prunus,* and *Berberis.* Forbs that repeatedly are found in aspen communities regardless of region are *Thalictrum, Osmorhiza, Geranium, Aster, Lathyrus, Achillea, Ligusticum, Galium,* and *Senecio.* The few graminoids commonly found in aspen understory are members of the genera *Bromus, Elymus, Poa,* and *Carex.*

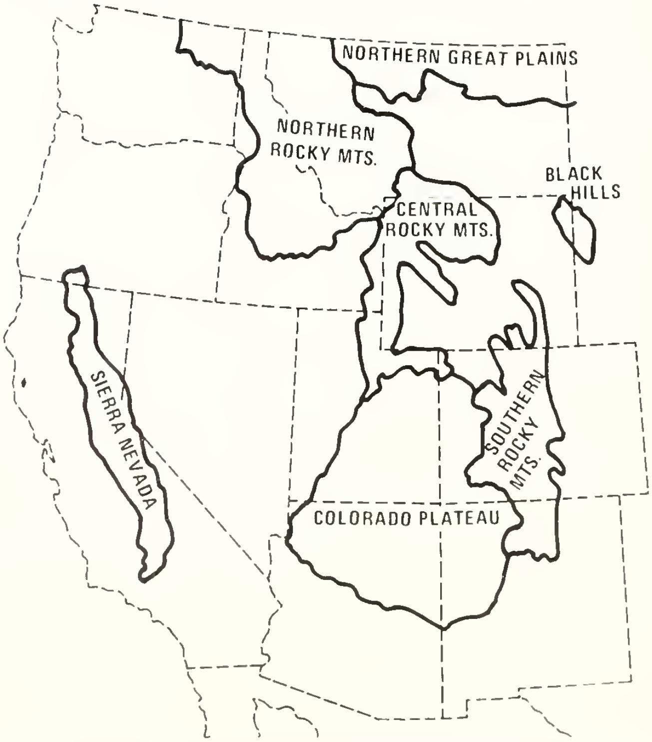

Figure 4.—Regions of western United States in which aspen exists in unique, described vegetation associations (Fenneman 1931).

Table 1.—Percentage cover[1] by undergrowth species growing in 50% or more of the aspen stands sampled in separate studies in the central Rocky Mountains (southeastern Idaho and western Wyoming) and southern Rocky Mountains (northern Colorado).

Species	Central Rocky Mountains		Southern Rocky Mountains
	(E. Idaho)[2]	(W. Wyoming)[3]	(N. Colorado)[4]
Achillea millefolium	1	1	4
Amelanchier alnifolia	12		
Aster engelmannii			4
Bromus ciliatus			8
Carex geyeri			15
Calamagrostis rubescens	33		
Elymus glaucus	9	5	13
Fragaria spp.		4	3
Galium boreale			2
Geranium richardsonii			9
G. viscosissimum	12	8	
Lathyrus leucanthus			6
Ligusticum porteri			16
Lupinus argenteus	7	5	
Osmorhiza spp.	6		6
Rosa woodsii	4	7	
Symphoricarpos oreophilus	14	9	
Taraxacum spp.	2		7
Thalictrum fendleri	10	13	20
Vicia americana			6
Total stands sampled	319	177	47
Total species reported	114	99	103

[1] *Average canopy cover of the species in those stands where present.*
[2] *Data compiled from Mueggler and Campbell (1982).*
[3] *Data compiled from Youngblood and Mueggler (1981).*
[4] *Data compiled from Hoffman and Alexander (1980).*

Northern Great Plains

The aspen parklands that sweep across Canada as a broad ecotone between the northern boreal forests and the prairies of the Northern Great Plains penetrate southward into northern Montana. Aspen groves on the eastern edge of Glacier National Park, where the east slope of the Northern Rocky Mountains meet the plains, are a southwesterly extension of these parklands (Lynch 1955).

Aspen in the northern parklands is considered a climax species that was held in check naturally by repeated wildfires (Moss 1932). It now appears to be aggressively expanding into adjacent prairies. Between 1907 and 1966, aspen groves in the parkland regions of south-central Alberta expanded 60% (Bailey and Wroe 1974). This invasion by aspen appears partly related to periods of higher than normal growing season temperatures. Expansion of the aspen groves is a major concern of livestock producers in Canada, because only 10% to 25% as much forage is produced in the aspen understory as was produced in the prior grasslands (Bailey and Wroe 1974).

The dynamics of these northern parkland aspen communities contrasts with those for the aspen forests in the Rocky Mountains and Colorado Plateau regions. Fire apparently suppressed expansion of aspen in the northern parklands; but fire perpetuated the seral aspen forests farther south. The herbaceous understory in mature aspen parkland communities is characteristically meager; but it is usually lush in the aspen forests farther south.

Moss (1932) described what he termed an aspen consociation in the parklands of Alberta. This consociation contained a mixed understory of shrubs, forbs, and grasses (table 2). Such a simplistic categorization inevitably has substantial within-category differences in composition.

Table 2.—Common plants occurring in the undergrowth of aspen communities in the parklands of Alberta (Moss 1932).

SHRUBS

Symphoricarpos pauciflorus
Amelanchier alnifolia
Prunus sp.
Rosa sp.
Corylus rostrata
Viburnum pauciflorum

GRASSES

Agropyron richardsonii
A. tenerum
Bromus ciliatus
Calamagrostis canadensis

FORBS

Aralia nudicaulis
Aster lindleyanus
Cornus canadensis
Epilobium angustifolium
Fragaria americana
Galium triflorum
Lathyrus ochroleucus
Vicia americana
Mertensia pilosa
Rubus triflorus
Thalictrum venulosum

The southerly extension of parklands into Montana consists of a rather narrow mosaic of aspen groves and grasslands where the mountains meet the plains. Lynch 1955) recognized three stable aspen associations in this area (table 3). His *Populetum Symphoricarpetosum* association occupies sloping lands and has a pronounced shrub stratum. His *Populetum Asteretosum* association occurs in intermorainal troughs and depressions and has an understory consisting principally of forbs; shrubs are of minor importance. Lynch's *Populetum Osmorhizatosum* association is restricted to moist slopes and narrow valley bottoms; it is conspicuous, because the ree layer consists of a mixture of *Populus tremuloides* and *P. trichocarpa*.

Northern Rocky Mountains

Aspen communities in the Northern Rocky Mountains and adjacent Columbia Plateau are relatively infrequent and small. Generally, they are small clones along mounain streams and meadow fringes, or are a very patchy ransitional type between coniferous forest and grassands on mountain slopes. The size of individual stands seldom exceeds 5 acres (2 ha). Habeck (1967) considered much of the aspen in the mountains of northwestern Montana to be seral to *Pseudotsuga menziesii* and *Picea engelmannii*, but acknowledged the existence of stable groves. Pfister et al. (1977) indicated that small patches of climax aspen probably occur farther south in Montana near the Continental Divide. Permanent or climax aspen communities also have been identified in central Idaho (Schlatterer 1972) and in the Blue Mountains of eastern Oregon (Hall 1973).

Descriptions of aspen communities of the Northern Rocky Mountains and Columbia Plateau are sketchy. Those in Montana mentioned by Habeck (1967) contain a distinct shrub layer consisting of such species as *Symphoricarpos occidentalis, Amelanchier alnifolia, Rosa woodsii, Prunus virginiana, Shepherdia argentea,* and *Ribes setosum*; the herb layer consists of an unspecified mixture of grasses and forbs. Peek (1963) indicated that dominant understory species in some southwestern Montana aspen stands were *Thalictrum occidentale, Geranium viscosissimum, Heracleum lanatum, Bromus marginatus,* and *Calamagrostis rubescens*.

Schlatterer (1972) described a single *Populus tremuloides/Symphoricarpos oreophilus-Carex geyeri* habitat type for central Idaho. This habitat type represents the climax aspen communities (table 4), in contrast to those in central Idaho which are seral to *Pseudotsuga menziesii* and *Abies lasiocarpa*. Occurrence of climax aspen in this area appears to be strong-

Table 3.—Prominent undergrowth species in three aspen associations east of Glacier National Park, Montana (Lynch 1955).

	Associations		
	Populetum Symphoricarpetosum	***Populetum Asteretosum***	***Populetum Osmorhizetosum***
SHRUBS			
Amelanchier alnifolia	[1]X*	X	
Berberis repens	X		X
Prunus virginiana	X		
Rosa acicularis	X*	X	
Symphoricarpos albus	X*	X	
S. occidentalis		X	X
GRAMINOIDS			
Agropyron subsecundum			X
Bromus carinatus			X
Calamagrostis rubescens	X*		
Carex spp.	X		X
Elymus glaucus		X*	X
FORBS			
Achillea millefolium	X	X	
Aster foliaceus	X	X*	X
A. conspicuus	X	X	X
Fragaria virginiana	X	X*	X
Galium boreale	X	X	X
Geranium richardsonii		X*	X
G. viscosissimum	X		
Heracleum lanatum		X	X*
Lathyrus ochroleucus	X*	X	X
Osmorhiza occidentalis			X
Smilacina stellata	X	X	X*
Thalictrum occidentale		X*	X
Vicia americana	X	X	X
Viola canadensis		X	X*

[1] *An asterisk denotes where the species is most abundant.*

Table 4.—Undergrowth plants common in the *Populus tremuloides/Symphoricarpos oreophilus-Carex geyeri* habitat type in central Idaho (Schlatterer 1972).

SHRUBS	FORBS
Symphoricarpos oreophilus	*Achillea millefolium*
Artemisia tridentata ssp. *vaseyana*	*Fragaria virginiana*
	Geranium viscosissimum
GRAMINOIDS	*Hydrophyllum capitatum*
	Lupinus spp.
Agropyron subsecundum	*Osmorhiza occidentalis*
Carex geyeri	*Potentilla glandulosa*
Festuca idahoensis	*Senecio serra*
Poa nervosa	*Smilacina stellata*
Stipa columbiana	*Thalictrum occidentale*
	Valeriana sitchensis

ly governed by temperature and the amount of available soil moisture. Schlatterer (1972) noted that species composition of the habitat type varied greatly, depending upon amount of disturbance by livestock grazing.

Hall (1973) described a *Populus tremuloides*-meadow community type in northeastern Oregon that occurs most often as groves on moist meadow sites. The understory of these meadow groves consists primarily of the following graminoids: *Deschampsia caespitosa*, *Carex festivella*, *Danthonia californica*, *Poa pratensis*, and *Agrostis* spp. Forbs such as *Veratrum californicum* become abundant with overgrazing.

Central Rocky Mountains

Aspen communities of western Wyoming and adjacent portions of Idaho and northern Utah can be either small patches or large stands. This central Rocky Mountain region appears to be a zone of transition from the sporadic, small groves in the northern Rocky Mountains to the extensive aspen forest of the Colorado Plateau and southern Rocky Mountains. The typical small, scattered aspen stands of southern Montana and northwestern Wyoming are replaced by larger and more frequent stands farther south. Extensive aspen forests are frequently found in southeastern Idaho, southern Wyoming, and northern Utah.

Most descriptions of aspen communities in this region are generalizations from community composition in local areas. Reported composition of understory vegetation differs greatly. For example, only *Symphoricarpos oreophilus*, *Senecio serra*, and *Thalictrum fendleri* are common to at least half of the descriptions from 18 different sources. Although species composition is highly varied, the communities can be categorized according to structure. Some contain a tall shrub layer, others are without tall shrubs but possess a conspicuous layer of medium to low shrubs, and others have a predominantly herbaceous understory.

The most prevalent species in the tall shrub layer in this region are *Prunus virginiana* and *Amelanchier alnifolia*. Aspen communities containing a dispersed stratum of these tall shrubs were observed by Beetle (1974), Gruell and Loope,[2] and Youngblood and Mueggler (1981) in the Jackson Hole area, and by Reed (1971) in the Wind River Mountains of western Wyoming. Mueggler and Campbell (1982) found tall-shrub undergrowth in eastern Idaho, as did Crowther and Harper (1965) and Henderson et al. (1976) in northern Utah. A community with tall shrubs almost always has a medium to low shrub layer as well. The herb layer in the tall shrub aspen communities (table 5) is composed of a mixture of forbs and grasses that generally decrease in productivity as the density of the shrub layer increases.

Communities that lack a tall shrub stratum but have a distinct medium to low shrub stratum have been noted in the Bighorn Mountains of northern Wyoming (Hoffman and Alexander 1976), throughout western Wyoming (Youngblood and Mueggler 1981), eastern Idaho (Mueggler and Campbell 1982), in the Uinta Mountains of Northern Utah (Hayward 1945, Henderson et al. 1977, Winn 1976), and generally throughout the central Rocky Mountains (Houston 1954). Such communities contain most of the species listed in table 5, except the tall shrubs. In addition, *Juniperus communis*, *Poa nervosa*, *Galium boreale*, and *Geranium viscosissimum* frequently grow in these communities. The medium and low shrubs, particularly species of *Symphoricarpos*, may form a rather dense cover. Productivity of the herb stratum usually varies inversely with the density of shrubs.

Aspen communities lacking a well-defined shrub layer, although infrequent, are found in the central Rocky Mountains. Both Reed (1952) and Youngblood and Mueggler (1981) found such communities on moist sites in western Wyoming, as did Mueggler and Campbell (1982) in eastern Idaho. Beetle (1974) mentioned "aspen savannah" communities in Teton County, Wyoming, with an understory dominated by the grass *Calamagrostis rubescens* and the forb *Lupinus argenteus*.

[2] *Gruell, G. E., and L. L. Loope. 1974. Relationships among aspen, fire, and ungulate browsing in Jackson Hole, Wyoming. USDA Forest Service, Intermountain Region, and U.S. Department of the Interior, National Park Service, Rocky Mountain Region. 33 p.*

Table 5.—Typical undergrowth species present in tall shrub aspen communities in the central Rocky Mountains.

SHRUBS	FORBS
Amelanchier alnifolia	*Achillea millefolium*
Berberis repens	*Agastache urticifolia*
Pachistima myrsinites	*Aquilegia coerulea*
Prunus virginiana	*Aster engelmannii*
Rosa nutkana	*Geranium* spp.
Rosa woodsii	*Lathyrus* spp.
Shepherdia canadensis	*Lupinus* spp.
Symphoricarpos albus	*Osmorhiza* spp.
S. oreophilus	*Rudbeckia occidentalis*
S. vaccinioides	*Senecio serra*
	Thalictrum fendleri
GRASSES	*Valeriana occidentalis*
Agropyron subsecundum	
A. trachycaulum	
Bromus anomalus	
B. marginatus	
Calamagrostis rubescens	
Elymus glaucus	

Table 6.—Aspen community types according to seral status on the Caribou and Targhee National Forests in eastern Idaho (Mueggler and Campbell 1982).

STABLE
Populus tremuloides/Amelanchier alnifolia-Pachistima myrsinites
Populus tremuloides/Amelanchier alnifolia-Spiraea betulifolia
Populus tremuloides/Amelanchier alnifolia-Symphoricarpos oreophilus
Populus tremuloides/Amelanchier alnifolia-Calamagrostis rubescens
Populus tremuloides/Pachistima myrsinites-Calamagrostis rubescens
Populus tremuloides/Pachistima myrsinites-Geranium viscosissimum
Populus tremuloides/Spiraea betulifolia-Calamagrostis rubescens
Populus tremuloides/Symphoricarpos oreophilus-Calamagrostis rubescens
Populus tremuloides/Artemisia tridentata-Festuca idahoensis
Populus tremuloides/Calamagrostis rubescens
Populus tremuloides/Geranium viscosissimum
Populus tremuloides/Wyethia amplexicaulis
SERAL (to conifers)
Populus tremuloides-Abies lasiocarpa/Symphoricarpos oreophilus
Populus tremuloides-Abies lasiocarpa/Thalictrum fendleri
Populus tremuloides-Pseudotsuga menziesii/Amelanchier alnifolia
Populus tremuloides-Pseudotsuga menziesii/Symphoricarpos oreophilus
Populus tremuloides-Pseudotsuga menziesii/Calamagrostis rubescens
Populus tremuloides-Pinus contorta/Calamagrostis rubescens
SERAL (abusive grazing)
Populus tremuloides/Symphoricarpos oreophilus-Poa pratensis
Populus tremuloides/Symphoricarpos oreophilus-Rudbeckia occidentalis
Populus tremuloides/Calamagrostis rubescens-Poa pratensis
Populus tremuloides/Poa pratensis
Populus tremuloides/Rudbeckia occidentalis

Although Beetle suggested that such stands represented a grazing disclimax situation, similar composition has been found where ungulate use has been minimal historically.[3] In northern Utah, the understory may be dominated by a luxuriant mixture of such tall forbs as Senecio serra, *Agastache urticifolia*, *Hackelia floribunda*, and *Delphinium occidentale*. These aspen/tall forb communities frequently also possess an abundance of low forbs such as *Valeriana occidentalis*, *Thalictrum fendleri*, *Osmorhiza occidentalis*, *Osmorhiza depauperata*, *Osmorhiza chilensis*, *Nemophila breviflora*, *Galium triflorum*, and *Galium boreale*.

Several researchers have attempted to develop phytosociological classifications for stable aspen communities in various parts of the central Rocky Mountain region. Hoffman and Alexander (1976) named stable aspen communities in the Bighorn Mountains of Wyoming the *Populus tremuloides/Lupinus argenteus* habitat type. These communities contain a rich mixture of grasses and forbs with the shrubs *Juniperus communis*, *Ribes lacustre*, and *Potentilla fruticosa* conspicuous in some stands. Reed (1971) classified the aspen forest in the Wind River Mountains of Wyoming into a single *Populus tremuloides/Symphoricarpos oreophilus* habitat type. However, only 10 of the 19 stands so classified contained *S. oreophilus*; and shrubs as a class were prominent in only 13, suggesting considerable compositional variability within the habitat type. Henderson et al. (1977) discerned two climax aspen habitat types in the Uinta Mountains of northern Utah: *Populus tremuloides/Carex geyeri* h.t. and *Populus tremuloides/Juniperus communis* h.t. Both are found in the lower forest zone—the former on easterly and southerly exposures and the latter primarily on north slopes.

Comprehensive classifications of aspen communities have been developed for eastern Idaho (Mueggler and Campbell 1982) and western Wyoming (Youngblood and Mueggler 1981). The Idaho classification was based upon a detailed examination of 319 aspen stands on the Caribou and Targhee National Forests. Of 23 community types described, 11 were considered stable and 12 seral, either to coniferous forests or because of major alteration caused by abusive livestock grazing (table 6). The Wyoming classification, based on 177 aspen stands sampled on the Bridger-Teton National Forest, identifies 26 community types of which 9 were considered stable and 17 seral (table 7).

Colorado Plateau

Aspen forests in the Colorado Plateau region of central and southern Utah, western Colorado, northwestern New Mexico, and northern Arizona frequently cover broad areas. According to Cottam (1954), aspen dominates more mountainous terrain between 7,000 and 10,000 feet (2,100 m and 3,000 m) elevation in Utah than any other forest tree. Although the aspen in much of this area is gradually being replaced by conifers, many of the extensive aspen stands show little evidence of such

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[3] *Personal observation by Walter F. Mueggler, Principal Plant Ecologist, Intermountain Forest and Range Experiment Station, Forestry Sciences Laboratory, Logan, Utah*

Table 7.—Aspen community types according to seral status on the Bridger-Teton National Forest, Wyoming (Youngblood and Mueggler 1981).

STABLE

Populus tremuloides/Artemisia tridentata
Populus tremuloides/Symphoricarpos oreophilus
Populus tremuloides/Wyethia amplexicaulis
Populus tremuloides/Juniperus communis
Populus tremuloides/Thalictrum fendleri
Populus tremuloides/Astragalus miser
Populus tremuloides/Calamagrostis rubescens
Populus tremuloides/Heracleum lanatum
Populus tremuloides/Ranunculus alismaefolius

SERAL

Populus tremuloides/Spiraea betulifolia c.t.
Populus tremuloides-Pseudotsuga menziesii/Spiraea betulifolia c.t.
Populus tremuloides-Pseudotsuga menziesii/Calamagrostis rubescens c.t.
Populus tremuloides/Berberis repens c.t.
Populus tremuloides-Abies lasiocarpa/Berberis repens c.t.
Populus tremuloides/Shepherdia canadensis c.t.
Populus tremuloides-Abies lasiocarpa/Shepherdia canadensis c.t.
Populus tremuloides/Arnica cordifolia c.t.
Populus tremuloides-Abies lasiocarpa/Arnica cordifolia c.t.
Populus tremuloides/Rudbeckia occidentalis c.t.
Populus tremuloides-Abies lasiocarpa/Rudbeckia occidentalis c.t.
Populus tremuloides/Prunus virginiana c.t.
Populus tremuloides-Abies lasiocarpa/Prunus virginiana c.t.
Populus tremuloides/Ligusticum filicinum c.t.
Populus tremuloides-Abies lasiocarpa/Ligusticum filicinum c.t.
Populus tremuloides-Abies lasiocarpa/Pedicularis racemosa c.t.
Populus tremuloides/Equisetum arvense c.t.

a successionary trend. Understory vegetation may provide clues to successional status of these stands. In central Utah, for example, the presence of *Bromus polyanthus, Collomia linearis, Galium bifolium, Stellaria jamesiana, Vicia americana,* and *Viola nuttallii,* suggests stable aspen communities, whereas *Berberis repens, Pachistima myrsinites,* and *Viola adunca* indicate seral communities.[1]

Barnes (1975) found that aspen on the Colorado Plateau not only is more abundant but exhibits larger individual clones than it does farther north. Kemperman (1970) measured a single clone in southern Utah that occupied 107 acres (43 ha) and consisted of 47,000 stems. Stands composed of numerous contiguous clones are common in this region; whereas in the Northern Rocky Mountain region, the clones are relatively small and frequently isolated. Regional floristics contribute to the uniqueness of aspen communities in the Colorado Plateau region. Species such as *Quercus gambelii, Symphoricarpos palmeri, Festuca thurberi,* and *F. arizonica* may be present in the understory there, but not farther north.

Despite the prevalence of aspen forests in this region, few descriptions of community composition have been published. Mueggler and Bartos (1977) described an aspen community at 8,500 feet (2,600 m) and another at 10,500 feet (3,200 m), near its lower and upper elevational limits, in the Tushar mountains of southern Utah (table 8). The lower elevation community possessed a pronounced medium to low shrub stratum consisting of *Symphoricarpos vaccinioides, Rosa woodsii,* and *Berberis repens.* The upper elevation community lacked a shrub stratum; the understory consisted of approximately 10% graminoids and 90% forbs.

Elevationally related differences in understory composition also are apparent on the Wasatch Plateau in central Utah. Data from 14 stands near 8,000 feet (2,450 m) elevation, near the lower limits of the aspen zone in this area, show a pronounced shrub stratum in contrast to data from 10 stands at about 10,000 feet (3,050 m) near the upper limits of the zone.[4] Differences in composition of the herbaceous layer at the different elevations is equally pronounced (table 9).

Warner and Harper (1972) found understory composition differences between sites of high and low quality for aspen growth (table 10), as determined from Jones' (1967b) site index curves. Warner and Harper's determinations were based on 43 stands in northern and central Utah within both the Central Rocky Mountain and Colorado Plateau regions. They found that low quality sites were characteristically more shrubby than high quality sites; the understory of high quality sites was dominated by forbs.

Paulsen (1969) described an aspen community at 9,500 feet (2,900 m) on Black Mesa, in western Colorado that had an almost exclusive herbaceous understory. The primary component was the sedge *Carex geyeri,* which accounted for about 25% of the total herbage production. Prominent grasses were *Bromus carinatus, Bromus anomalus, Festuca thurberi,* and *Agropyron trachycaulum.* Forbs comprised about 60% of the her-

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[4] *Data furnished by K. T. Harper, Department of Botany and Range Science, Brigham Young University, Provo, Utah*

Table 8.—Differences in prominent undergrowth species in aspen stands at two elevations in the Tushar mountains of southern Utah (Mueggler and Bartos 1977).

8,500 feet elevation	Common to both	10,500 feet elevation
Agropyron caninum	*Achillea millefolium*	*Carex* spp.
Berberis repens	*Astragalus bourgovii*	*Festuca idahoensis*
Cirsium undulatum	*Bromus anomalus*	*Helenium hoopesii*
Erigeron speciosus	*Castilleja linariaefolia*	*Potentilla pulcherrima*
Helianthella uniflora	*Fragaria americana*	*Solidago decumbens*
Rosa woodsii	*Frasera speciosa*	
Smilacina stellata	*Lupinus leucophyllus*	
Stipa lettermani	*Poa fendleriana*	
Symphoricarpos vaccinioides		

Table 9.—Differences in undergrowth species[1] in aspen communities at two elevations on the Wasatch Plateau in central Utah.

8,000 feet elevation	Common to both	10,000 feet elevation
Aster engelmannii	*Achillea millefolium**	*Androsace septentrionalis*
Aster foliaceus	*Agropyron riparium* (upper*)	*Artemisia ludoviciana*
*Berberis repens**	*Bromus polyanthus* (upper*)	*Chenopodium fremontii*
Bromus ciliatus	*Lathyrus lanzwertii*	*Collomia linearis*
Carex rossii	*Osmorhiza obtusa**	*Descurainia californica**
Cynoglossum officinale	*Stellaria jamesiana* (upper*)	*Galium bifolium**
Dactylis glomerata	*Taraxacum officinale**	*Melica bulbosa*
Elymus glaucus	*Vicia americana**	*Osmorhiza occidentalis*
Fragaria bracteata	*Viola nuttallii* (upper*)	*Poa reflexa*
*Galium boreale**		*Polemonium foliosissimum*
Gentiana heterosepala		*Polygonum douglasii*
*Geranium fremontii**		*Ribes montigenum*
*Lathyrus pauciflorus**		*Stipa lettermani*
*Pachistima myrsinites**		*Thalictrum fendleri*
*Poa pratensis**		*Trisetum spicatum*
Rosa sp.		
Rudbeckia occidentalis		
Stipa columbiana		
Swertia radiata		
*Symphoricarpos oreophilus**		
*Viola adunca**		

[1] *All listed species had at least 5% average frequencies; those with asterisks had frequencies of at least 20%.*

Table 10.—Effect of site quality differences on prominent undergrowth species in Utah aspen communities (Warner and Harper 1972).

Low quality site	Common to both	High quality site
Aster engelmannii	*Achillea millefolium*	*Elymus glaucus*
Gayophytum ramosissimum	*Agropyron trachycaulum*	*Lathyrus lanzwertii*
Pachistima myrsinites	*Bromus polyanthus*	*Mertensia arizonica*
Polygonum douglasii	*Chenopodium fremontii*	*Osmorhiza chilensis*
Symphoricarpos oreophilus	*Collomia linearis*	*Thalictrum fendleri*
	Collinsia parviflora	*Viola nuttallii*
	Descurainia californica	
	Galium bifolium	
	Nemophila breviflora	
	Stellaria jamesiana	
	Vicia americana	

Table 11.—Major undergrowth components of two major types of aspen communities in the Jarbridge mountains of Nevada.

Populus/forb type	Common to both	*Populus/Symphoricarpos* type
Agropyron trachycaulum	*Agastache urticifolia*	*Amelanchier alnifolia*
Osmorhiza occidentalis	*Aster perelegans*	*Carex hoodii*
Potentilla glandulosa	*Bromus marginatus*	*Ceanothus velutinus*
Senecio serra	*Geranium viscosissimum*	*Erigeron speciosus*
Thalictrum fendleri	*Hackelia mierantha*	*Prunus virginiana*
	Symphoricarpos oreophilus	*Ribes cereum*
	Valeriana occidentalis	

bage; the most abundant were *Ligusticum porteri*, *Lathyrus leucanthus*, *Thalictrum dasycarpum*, *Fragaria glauca*, *Osmorhiza obtusa*, *Geranium fremontii*, and *Galium boreale*.

Northwest of the Colorado Plateau region, in the Jarbridge Mountains of Nevada, Lewis (1975) found two major types of aspen communities. He designated those with an understory dominated by tall forbs the *Populus tremuloides*/forb type. He called those dominated by shrubs the *Populus tremuloides/Symphoricarpos* type (table 11). Lewis (1971) indicated that stable aspen communities in the nearby Ruby and East Humboldt Ranges had the following species common in the understory: *Agastache urticifolia*, *Agropyron trachycaulum*, *Bromus polyanthus*, *Castilleja miniata*, *Lupinus argenteus*, *Symphoricarpos oreophilus*, and *Thalictrum fendleri*.

Southern Rocky Mountains

The southern Rocky Mountain region extends along the mountain chain from southwestern Wyoming, through Colorado, and into north-central New Mexico. The majority of aspen forests in this region are along the west slope of the Rocky Mountains. As in adjacent regions, both seral and stable communities exist in small groves and as extensive forests. Many of the aspen forests in the region are successional to *Picea engelmannii* and *Abies lasiocarpa*.

Severson (1963) concluded that the aspen stands on the Hayden Division of the Medicine Bow National Forest in southeastern Wyoming are successional to coniferous forests. The most prominent species in the understory of these seral aspen communities are *Vicia americana*, *Carex geyeri*, *Taraxacum officinale*, *Stipa lettermani*, and *Calamagrostis rubescens*. Severson (1963) observed that variation in understory composition is influenced more by biotic factors, such as grazing, than by climatic or edaphic factors, with the exception of elevational extremes. Although Wirsing and Alexander (1975) indicated that aspen on the Medicine Bow National Forest may be a seral species in the *Abies lasiocarpa/Vaccinium* and *Abies lasiocarpa/Carex* habitat types, it also is found in stable communities, which they classified as the *Populus tremuloides/Carex geyeri* habitat type. This stable type generally occurs in small patches at the lower fringe of the coniferous forest zone. The understory of the type consists of a mixture of shrubs and herbs. Prominent members of the shrub layer are *Juniperus communis*, *Rosa woodsii*, *Amelanchier alnifolia*, and *Berberis repens*. In contrast to most aspen communities elsewhere, *Symphoricarpos* is conspicuously absent as an important member of the shrub layer. Herbs characterizing the understory of this habitat type are *Carex geyeri*, *Elymus glaucus*, *Osmorhiza depauperata*, *Galium boreale*, and *Achillea millefolium*.

A complete description of aspen communities occurring in any portion of the southern Rocky Mountains is given by Hoffman and Alexander (1980). They identified five aspen-dominated habitat types on the Routt National Forest, in northwestern Colorado: *Populus tremuloides/Symphoricarpos oreophilus* h.t., *P. tremuloides/Thalictrum fendleri* h.t., *P. tremuloides/Heracleum sphondyllium* h.t., *P. tremuloides/Veratrum tenuipetalum* h.t., and *P. tremuloides/Pteridium aquilinum* h.t. The majority of the 47 stands used to develop this classification were in the *P. tremuloides/T. fendleri* type. Species prominent in the undergrowth of most stands were *Bromus ciliatus*, *Elymus glaucus*, *Carex geyeri*, *Geranium richardsonii*, *Osmorhiza* spp., *Thalictrum fendleri*, and *Vicia americana*.

Both Langenheim (1962) and Morgan (1969) described relatively stable aspen forests in the Gunnison area of central Colorado, that have predominantly herbaceous understories. Characteristic species in these mature aspen communities are: *Bromus ciliatus*, *Erigeron elatior*, *Geranium richardsonii*, *Lathyrus leucanthus*, *Ligusticum porteri*, *Senecio serra*, *Thalictrum fendleri*, and *Vicia americana*. Morgan (1969) recognized that some communities differed because of the abundance of *Symphoricarpos utahensis*, *Aster engelmannii*, and *Pteridium aquilinum*. Langenheim (1962), however, identified situations where aspen is a transitional type with adjacent communities dominated by *Festuca thurberi* and *Artemisia tridentata*, and situations where aspen dominates talus slopes. Understory in the ecotonal and talus slope types contains shrubs such as *Symphoricarpos* spp., *Artemisia tridentata*, *Pachistima myrsinites*, *Acer glabrum*, and *Rosa* spp.

Moir and Ludwig (1979) considered aspen to be a major seral tree in 6 of the 8 spruce-fir habitat types and in 7 of the 11 mixed conifer habitat types that they identified for New Mexico and Arizona. They did not recognize aspen as either a major or minor climax dominant. Layser and Schubert (1979) also recognized the seral status of aspen in the *Picea pungens*, *Abies lasiocarpa*, *A. concolor*, *P. engelmannii*, *Pseudotsuga menziesii*, and

Pinus ponderosa climax forest series in New Mexico and Arizona. Although they did not identify situations where aspen achieves climax status, they suggested that a climax aspen series might exist in certain edaphic situations.

Black Hills

Aspen is a conspicuous element in the vegetation of the Black Hills of South Dakota. The relatively low elevation of this isolated mountain mass, less than 7,480 feet (2,280 m), confines aspen almost entirely to the northerly exposures (Severson and Thilenius 1976). Both Kranz and Linder (1973) and Thilenius (1972) recognized aspen as seral to *Pinus ponderosa* in this area; however relatively stable communities also exist.

Severson and Thilenius (1976) classified 28 aspen stands in the Black Hills and adjacent Bear Lodge Mountains of north-eastern Wyoming into the following nine "aspen groups":

1. *Populus tremuloides/Spiraea lucida/Lathyrus ochroleucus*
2. *Populus tremuloides/Symphoricarpos albus/ Pteridium aquilinum*
3. *Populus tremuloides/Berberis repens/Oryzopsis asperifolia/Aster laevis*
4. *Populus tremuloides/Ribes missouriense/ Oryzopsis asperifolia/Aster laevis*
5. *Populus tremuloides/Rosa woodsii/Poa pratensis/Trifolium repens*
6. *Populus tremuloides/Physocarpus monogynus/ Poa pratensis/Smilacina stellata*
7. *Populus tremuloides/Rubus parviflorus/ Agropyron subsecundum/Aralia nudicaulis*
8. *Populus tremuloides/Corylus cornuta/Aralia nudicaulis*
9. *Populus tremuloides/Ostrya virginiana/ Oryzopsis asperifolia/Aralia nudicaulis.*

Groups 8 and 9 are considered relatively stable aspen types. Groups 3 and 4 are seral stages that will revert to *Pinus ponderosa* or *Picea glauca*. The successional status of stands in the remaining groups was not defined. The indicator species for each group are contained in the name. As suggested by names, shrubs are generally important in the understory of most groups. Plants most commonly occurring as understory to aspen communities in this isolated mountain mass are shown in table 12.

Sierra Nevada

Aspen is only a minor element in the vegetation of the Sierra Nevada Mountains of California and northward into the Cascades of Oregon and Washington (Barry 1971, Franklin and Dyrness 1973). Scattered groves grow along riparian zones and on transitional areas between coniferous forests and mountain meadows. Occasionally, aspen can be found intermixed as scattered individuals or small clones within the coniferous forest types. Barry (1971) considered most such groves in the Sierra Nevada to be relatively stable communities particularly adapted to ecotonal areas between forest and meadows. He indicated that aspen is a truly seral species only in the *Abies magnifica* forests where it may gain temporary dominance after logging.

Table 12.—Common undergrowth species found in aspen communities in the Black Hills of South Dakota (Severson and Thilenius 1976).

SHRUBS	FORBS
Amelanchier alnifolia	*Aster laevis*
Berberis repens	*Fragaria ovalis*
Rosa woodsii	*Galium boreale*
Spiraea lucida	*Lathyrus ochroleucus*
Symphoricarpos albus	*Monarda fistulosa*
	Thalictrum venulosum
GRASSES	*Smilacina stellata*
	Vicia americana
Oryzopsis asperifolia	
Poa pratensis	

Barry (1971) found substantial understory differences in four aspen parkland stands, in the Lake Tahoe area, on the California-Nevada border. The understory varied from very sparse to very dense. Of the total 54 species encountered in these communities, only *Thalictrum fendleri* was in the understory in all four stands. Other plants reported in the understory in at least two of the four stands were *Achillea millefolium, Alnus tenuifolia, Bromus marginatus, Lupinus* spp., *Poa pratensis, Monardella odoratissima, Osmorhiza chilensis,* and *Osmorhiza occidentalis.*

Grazing Disclimax

Aspen communities have long been recognized for their value as livestock range. However, a long history of sometimes abusive grazing on some areas has led to certain changes in undergrowth composition that persists despite conservative grazing in recent years. These changes often resulted in a more simple flora of fewer plant species than originally present in the undergrowth (Beetle 1974, Costello 1944, Houston 1954). The plants that remained, usually low in palatability to livestock, increased in abundance as competition from the more palatable plants decreased (see the FORAGE chapter).

With extreme abuse, the undergrowth may consist primarily of perennials such as *Rudbeckia* spp., *Lathyrus* spp., *Wyethia* spp., *Poa pratensis*, and *Taraxacum officinale*, and annuals such as *Madia glomerata, Nemophila breviflora, Galium bifolium*, and *Polygonum douglasii* (Beetle 1974, Houston 1954). The particular combination of species will differ with the environment.

Some of the current combinations of species in aspen communities might be considered relatively stable grazing disclimaxes. Such communities apparently are no longer able to return to their original compositions in the foreseeable future, either because of environmental changes caused by abusive grazing, or because of the competitive dominance of the invader species.

CLIMATES

John R. Jones and Norbert V. DeByle

The broad range of aspen in North America is evidence of its equally broad tolerance of wide variations in climate (Fowells 1965). Given open space for establishment and not too severe competition from other plants, aspen can survive from timberline on the tundra's edge to very warm temperate climates, and from the wet maritime climates of the coasts to very severe and often quite dry continental climates of the interior. Therefore, to describe the climates typical of this species' range is extremely difficult, especially in the mountainous West, where climates vary greatly. However, aspen grows much better and competes more successfully under some climatic regimes than under others. Ecotypes of aspen have developed that perhaps are best adapted to the climatic regime in which they are growing (see the GENETICS AND VARIATION chapter).

It is difficult to relate climate measured at a standard weather station to optimum or limiting conditions for aspen growth and development. Topography markedly influences climate. There often is a large difference in climate from the point of measurement at an instrument shelter or raingage to the effective climate at the nearest aspen sites.

In the West, it is unusual for weather measurements to be taken at the actual site where aspen stands are common. Therefore, an assumption usually is made that measurements taken at the nearest station are representative of conditions in the aspen forest. This seldom is true in mountainous terrain. Under average conditions in Utah, for example, a 1,000-foot (300-m) change in elevation is roughly equivalent to a 20-day change in the length of the growing season. These changes may be much more rapid or even reversed within the air inversion zone of mountain valleys.

Differences in precipitation isohyets also are found in mountainous terrain. Depending on the synoptic pattern producing the precipitation, the same isohyet may be as much as 1,000 feet (300 m) higher on the leeward side of mountains than on their windward side.

Even more important than these major variations of climate with elevation are the local microclimate differences in available soil moisture that are associated with topography and soil characteristics. Available soil moisture may be much greater than measured precipitation in a swail or canyon site and much less on a rocky ridge or hillside. Aspect also is critical. Temperature and available soil moisture on a southwest facing slope will be quite different from those at the same elevation on a north facing slope. (See the EFFECTS OF WATER AND TEMPERATURE chapter for a discussion of the effects of these climatic factors on aspen.)

Despite data interpretation difficulties, climatic descriptions are presented here for selected sites within the range of quaking aspen in the western conterminous United States. Similar descriptions for Alaska and Canada were not attempted.

A Representative Climate

Price and Evans (1937) described climates along an elevational gradient on the west front of the Wasatch Plateau, in central Utah. The lowest station cited, at 7,660 feet (2,350 m), represents the elevational zone dominated by Gambel oak (*Quercus gambelii*). The Gambel oak zone in Utah and western Colorado occupies a position equivalent to that of ponderosa pine (*Pinus ponderosa*) in other areas—intermediate between pinyon-juniper below and aspen or mesophytic conifers such as Douglas-fir (*Pseudotsuga menziesii*) and white fir (*Abies concolor*) above. The second station, at 8,850 feet (2,700 m), represents the zone of extensive aspen dominance. This station, in the midst of the aspen forest, probably provides the best available characterization of the climates of major aspen areas in Utah and western Colorado. Those climates have been compatible with, and perhaps conducive to, the most widespread aspen dominance in the West. The third station, at 10,100 feet (3,100 m), was near the mountain top, in the spruce-fir zone, above any extensive stands of aspen. All three stations were in forest openings.

Based upon 20 years of record, there was little difference between the aspen station and the spruce-fir station in amount or monthly distribution of precipitation. Both received between 28 and 30 inches (71 cm and 76 cm) average annual precipitation, with two-thirds falling largely as snow between November and April. Growing season precipitation at the aspen station was greatest in May (2.4 inches (6 cm)), least in June (0.8 inch (2 cm)), and averaged 1.8 inches (5 cm) in each of the following four months. Both locations received much more precipitation than the oak station, especially in winter. Snowfall comprised 60% of the total precipitation at the oak station, 70% at the aspen station, and 80% at the spruce-fir station.

Snow cover usually began before November 1 at all three stations, and remained on the average until April 18 at the oak station, May 6 at the aspen station, and May 26 at the spruce-fir station. Even though the winter pack had melted, almost one-half the precipitation in May fell as snow at the aspen station. Average snow depths there were 14 inches (36 cm) on December 1, 28 inches (71 cm) on January 1, and a peak of 48 inches (122 cm) on April 1.

Summer temperatures at the aspen station were moderate. The average hours per day above 70°F (21°C) were 1 in May, 3 in June, 4 in July, 3 in August, and 1 in September. About twice as many hours per day above 70°F (21°C) were recorded at the oak station; whereas, at the spruce-fir station, no month had more than 1 hour per day above 70°F (21°C). The hours above 32°F (0°C) were more alike among the stations. At both the oak and aspen stations, more than 18 hours per day were above 32°F (0°C) from May through September. July and August continuously remained above 32°F (0°C).

The overall picture of aspen climate in this area is of cool summers with modest rainfall, and of long, snowy winters that are only moderately cold. However, the details vary from place to place in Utah and western Colorado, and differ substantially in other parts of the West.

Precipitation

Strain (1964) reported data from a weather station at 10,150 feet (3,100 m) elevation in southern California that illustrates a very dry aspen site, perhaps an extreme. For 10 years there, the annual precipitation averaged only 12.5 inches (32 cm), with 10 inches (25 cm) falling as snow. Aspen was abundant in the vicinity, although it grew poorly.

Most aspen areas, however, receive at least 15 inches (38 cm) of precipitation a year. Table 1 shows the average monthly and annual precipitation at several stations with aspen growing nearby at similar elevations. The locations of these stations are shown in figure 1, on which monthly precipitation of selected stations also has been noted to illustrate the geographic variation in seasonal distribution of moisture.

There are marked seasonal differences in precipitation across the West. In a south-to-north transect through Arizona, Utah, and Idaho, winter precipitation generally increases and summer precipitation decreases from south to north. This pattern may reflect the distance from major sources of summer rainfall, (i.e., the Gulf of California and the Gulf of Mexico) (Green and Sellers 1964, Hales 1974), and position relative to major winter storm tracks. In Colorado and New Mexico, the most notable south-north trend is in spring precipitation. Spring is exceedingly dry in southern New Mexico but is the wettest season in northern Colorado. Further north, in Montana for example, the spring wet season occurs later, in May and June.

Mountain barriers concentrate precipitation on the windward sides of mountains, and local topographic features funnel moist air. This causes marked variability in precipitation within relatively small geographic areas. This phenomenon is illustrated in northern Utah, where the west side of the Wasatch Range gets heavy orographically enhanced snowfall, while winter precipitation is greatly reduced on the east side. The November-April precipitation at Silver Lake Brighton (8,740 feet (2,650 m) elevation) on the western slopes is 30.27 inches (77 cm), compared to only 21.80 inches (55 cm) at Park City Summit (9,270 feet (2,800 m)), and only 8.03 inches (20 cm) at Moon Lake (8,150 feet (2,500 m)) on the east side.

Such contrasts are not unique to the Wasatch. Even more extreme is the contrast between two southern Colorado stations only 25 miles apart, on opposite sides of the San Juan crest. Wolf Creek Pass 4W (9,425 feet (2,850 m)) averages 45.55 inches (116 cm) per year, and Santa Maria Reservoir (9,706 feet (2,950 m)) averages only 15.37 inches (39 cm) per year. Winter averages (November-April) are 29.45 inches (75 cm), and only 5.71 inches (15 cm), respectively.

Ives (1941a) pointed out that precipitation varies fairly consistently among locales in the Rocky Mountains because of interactions of topography and local as well as large-scale air movements. The same presumably is true elsewhere in the mountainous West.

There is a sparsity of weather stations in the West at the higher elevations occupied by aspen. Because of large precipitation variability in these uplands, precipitation records from stations in the valleys, even a few miles away, do not accurately describe the climate of most aspen stands. Therefore, for most higher elevations in the West, an estimate of annual or seasonal precipitation at any point is best made using large-scale precipitation maps.[1]

Monthly precipitation sometimes may be of interest. Equations for estimating monthly precipitation are available in Jones (1971a) for the southern Rocky Mountains. They are based on relationships of precipitation with several physiographic variables.

In addition to usual forms of precipitation, heavy rime sometimes accumulates in the crowns of trees when supercooled winter clouds move through the forest (fig. 2). From a 3-year study in the Sangre de Cristo Mountains of New Mexico, Gary (1972) estimated that rime collection in the canopy of a dense stand contributed at least 1 inch (3 cm) of water per year to the moisture regime. Grover[2] reported a similar phenomenon on the west slopes of the central Wasatch Mountains in Utah.

Temperature

In the interior West, high elevation weather stations with fairly long periods of temperature records are even more sparse than are locations with precipitation records. Table 2 lists several stations with long-term temperature records within or near elevations where aspen grows. Station locations are shown in figure 3.

[1] *Summer (May-September), winter (October-April), and annual precipitation maps are variously available from: (Arizona) University of Arizona, Room 102, West Stadium Building, Tucson, Ariz. 84721; (Colorado) Colorado Water Conservation Board, 215 State Services Building, 1525 Sherman Street, Denver, Colo. 80203; (New Mexico) State Engineer Office, State Capitol Building, Santa Fe, N. Mex. 87501; (Utah) State Engineer Office, State Capitol Building, Salt Lake City, Utah 84101. The isohyets are drawn on topographic maps with scales of 1:500,000. The maps were prepared by the Water Supply Forecast Unit of the USDA Soil Conservation Service in cooperation with the State Climatologists' Offices of the U.S. Department of Commerce Weather Bureau.*

[2] *Personal communication from Dr. Ben Grover to E. Arlo Richardson, both with Utah State University, Logan.*

Table 1.—Precipitation (in inches) at some stations with aspen nearby at a similar elevation. Stations are listed in north-south order within states and are number-coded to map locations (figure 1).[1]

Station	Elev. (feet)	Months												Total annual	Class[2]
		J	F	M	A	M	J	J	A	S	O	N	D		
MONTANA															
1 Babb 6NE	4,300	0.79	0.84	0.97	1.47	2.79	4.44	1.60	1.65	1.93	1.01	0.81	0.82	19.12	1
2 Whitefish 5NW	3,080	2.33	1.81	1.38	1.53	2.36	3.38	1.18	1.55	1.61	1.69	2.15	2.18	23.15	3
3 Lewistown AP	4,145	0.68	0.59	0.71	1.00	3.08	4.08	1.62	1.70	1.64	1.00	0.71	0.66	17.47	2
4 Ovando	4,109	1.71	1.04	0.85	0.83	1.98	2.47	1.00	0.99	1.22	1.18	1.47	1.69	16.43	3
5 Red Lodge	5,575	1.20	1.00	2.09	3.50	3.42	3.49	1.25	1.18	2.22	1.35	1.57	0.94	23.21	2
6 Lakeview	6,710	1.70	1.19	1.60	1.48	2.58	3.28	1.22	1.43	1.48	1.45	1.55	1.56	20.52	2
IDAHO															
7 McCall	5,025	4.04	2.81	2.53	2.04	2.47	2.39	0.44	0.82	1.43	2.34	3.18	3.69	28.18	3
8 Ashton	5,260	1.85	1.80	1.30	1.22	1.87	2.21	0.64	1.04	1.15	1.29	1.86	2.04	18.27	3
9 Willow Flat	6,100	4.34	4.13	3.53	4.01	2.68	2.52	0.92	1.07	1.89	2.21	3.52	4.08	34.90	2
WYOMING															
10 Moran 5WNW	6,798	2.81	2.10	1.82	1.72	2.03	1.85	0.88	1.30	1.46	1.40	2.32	2.69	22.38	1
11 Kendall	7,645	1.65	0.98	1.24	1.09	1.93	2.05	1.03	1.33	1.39	1.00	1.26	1.57	16.52	1
12 Foxpark	9,065	1.37	1.37	1.71	1.68	1.55	1.57	1.68	1.49	1.16	0.97	1.11	1.03	16.69	3
UTAH															
13 Red Butte No. 6	7,200	4.06	3.82	3.92	4.89	3.02	2.14	0.78	1.34	1.87	2.95	3.02	3.93	35.74	2
14 Silver Lake Brighton	8,740	5.35	4.80	5.53	4.50	2.87	2.65	1.28	1.95	1.74	3.05	4.75	5.34	43.81	2
15 Moon Lake	8,150	1.20	1.00	1.29	1.53	1.63	1.85	1.24	2.23	1.64	1.54	1.25	1.76	18.16	3
16 Timpanogos Div. No. 4	8,140	4.90	4.41	3.50	3.97	2.33	2.06	0.70	1.82	2.14	2.94	4.26	5.47	38.50	1
17 Ephraim GBRC HQ	8,800	2.83	3.51	3.55	4.13	2.33	1.41	1.07	1.84	1.77	2.42	2.66	3.16	30.68	1
18 Ephraim Alp. Mead.	9,850	3.80	4.36	4.56	4.78	2.77	1.73	1.17	2.01	1.88	2.91	3.24	3.94	37.15	3
19 Beaver Canyon PH	7,275	1.75	1.97	2.38	2.13	1.49	1.05	1.58	1.88	0.99	1.30	1.28	1.63	19.43	1
20 Bryce Canyon NPHQ	7,915	1.28	1.21	1.42	1.19	0.85	0.73	1.30	2.41	1.50	1.50	1.05	1.39	15.83	1
COLORADO															
21 Longs Peak	8,956	1.34	1.26	2.33	2.89	2.76	2.03	2.36	2.35	1.50	1.39	1.06	0.69	21.96	3
22 Silver Lake	10,200	1.81	2.46	3.03	3.37	3.42	2.36	2.91	2.42	1.54	1.73	1.72	1.54	28.31	2
23 Winter Park	9,058	2.24	2.42	2.84	3.35	2.88	1.70	2.29	2.07	1.33	1.88	2.00	1.86	26.86	3
24 Dillon	9,065	1.43	1.55	2.08	2.17	1.71	1.20	1.89	1.63	1.17	1.11	1.18	1.30	18.42	3
25 Leadville	10,200	1.32	1.51	1.71	1.83	1.44	1.13	2.73	2.11	1.35	1.11	1.07	1.17	18.48	2
26 Crested Butte	8,800	2.68	2.56	2.36	1.73	1.31	1.43	1.95	2.27	1.66	1.43	1.52	2.10	23.00	1
27 Fremont Exp. Stn.	8,900	0.51	0.82	1.64	2.41	2.96	2.33	3.27	3.08	1.47	0.99	0.78	0.46	20.72	2
28 Pitkin	9,200	1.45	1.36	1.41	1.41	1.15	0.91	1.86	1.82	1.23	1.00	0.89	1.19	15.68	1
29 Knott Ranch[3]	9,300	2.48	2.23	2.68	1.85	1.21	1.01	1.57	2.18	1.35	1.52	1.69	2.43	22.20	1
30 Trout Lake	9,700	2.48	2.51	2.86	3.00	1.89	1.24	2.62	3.07	2.26	2.35	1.59	1.87	27.74	3
31 Rio Grande Reservoir	9,495	1.54	1.06	1.44	1.68	1.63	1.17	1.96	2.55	2.17	2.43	1.26	1.25	20.14	1
32 Rico	8,840	2.46	2.46	2.49	2.23	1.61	1.19	2.39	2.80	2.49	2.40	1.66	2.31	26.49	2
33 LaVeta Pass	9,200	1.75	1.73	2.42	3.02	2.56	1.14	1.63	1.72	1.22	1.60	1.62	1.08	21.49	2
34 Terminal Dam	8,300	2.17	1.58	1.81	1.51	1.35	1.02	2.21	2.65	2.43	2.05	1.15	1.92	21.85	2
35 Wolf Creek Pass 4W	9,425	6.08	4.64	5.77	4.06	2.13	1.25	2.79	3.60	3.02	3.31	3.64	5.26	45.55	3
36 North Lake	8,800	0.92	1.14	1.76	2.30	2.53	1.38	2.95	2.98	1.43	1.26	0.92	0.77	20.34	3
37 Cumbres Pass	10,000	3.76	4.17	3.94	3.45	1.74	1.23	2.45	3.45	2.19	2.11	2.93	2.89	34.31	1
NEW MEXICO															
38 Red River	8,676	1.07	1.10	1.35	1.60	1.80	1.24	2.56	3.07	1.49	1.47	0.98	0.93	18.66	2
39 Bateman Ranch	8,900	1.94	1.98	2.18	1.56	1.82	1.18	2.48	3.05	2.16	1.81	1.24	1.61	23.01	1
40 Chacon	8,500	1.11	0.78	1.07	1.22	1.82	1.46	2.97	3.73	1.75	1.29	0.90	0.91	19.01	2
41 Wolf Canyon	8,135	1.64	1.77	1.90	1.50	1.45	1.04	2.91	3.28	2.14	1.62	1.16	1.51	21.92	2
42 Elk Cabin	8,500	1.21	1.37	1.70	1.47	1.46	1.42	3.49	3.61	1.61	1.54	1.24	1.42	21.54	1
43 Sandia Crest	10,680	1.74	1.72	2.26	1.23	0.92	0.96	3.19	3.40	1.73	2.06	1.34	2.17	22.72	1
44 Cloudcroft	8,827	1.59	1.69	1.44	0.80	1.11	1.61	4.56	4.77	2.78	1.48	1.30	1.45	24.58	3
ARIZONA															
45 Jacob Lake	7,920	1.45	1.01	2.07	1.48	1.06	0.79	2.38	2.47	1.10	1.87	1.34	2.01	19.03	3
46 Fort Valley	7,347	2.32	2.27	1.92	1.52	0.69	0.76	2.65	3.65	1.83	1.52	1.14	2.07	22.34	2
47 Maverick Fork	9,050	2.52	2.26	2.30	1.53	0.82	1.16	4.80	4.31	2.20	2.75	1.82	3.49	29.96	1
48 Alpine	8,020	1.60	1.38	1.24	0.78	0.54	0.80	3.10	3.87	2.10	1.61	0.92	1.27	19.21	1
49 Rustlers Park	8,400	3.05	1.80	2.06	0.77	0.43	1.10	6.45	6.34	2.62	1.96	1.74	2.03	30.35	3

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[1] *These data come from several sources; most are from the National Weather Service and its predecessors under the U.S. Department of Commerce, the U.S. Department of Agriculture and the U.S. Army.*

[2] *Class 1 = aspen type is prominent in locale;*
Class 2 = a fair amount of aspen;
Class 3 = some aspen, may be largely mixed with conifers.

[3] *Also known as Sapinero 9W.*

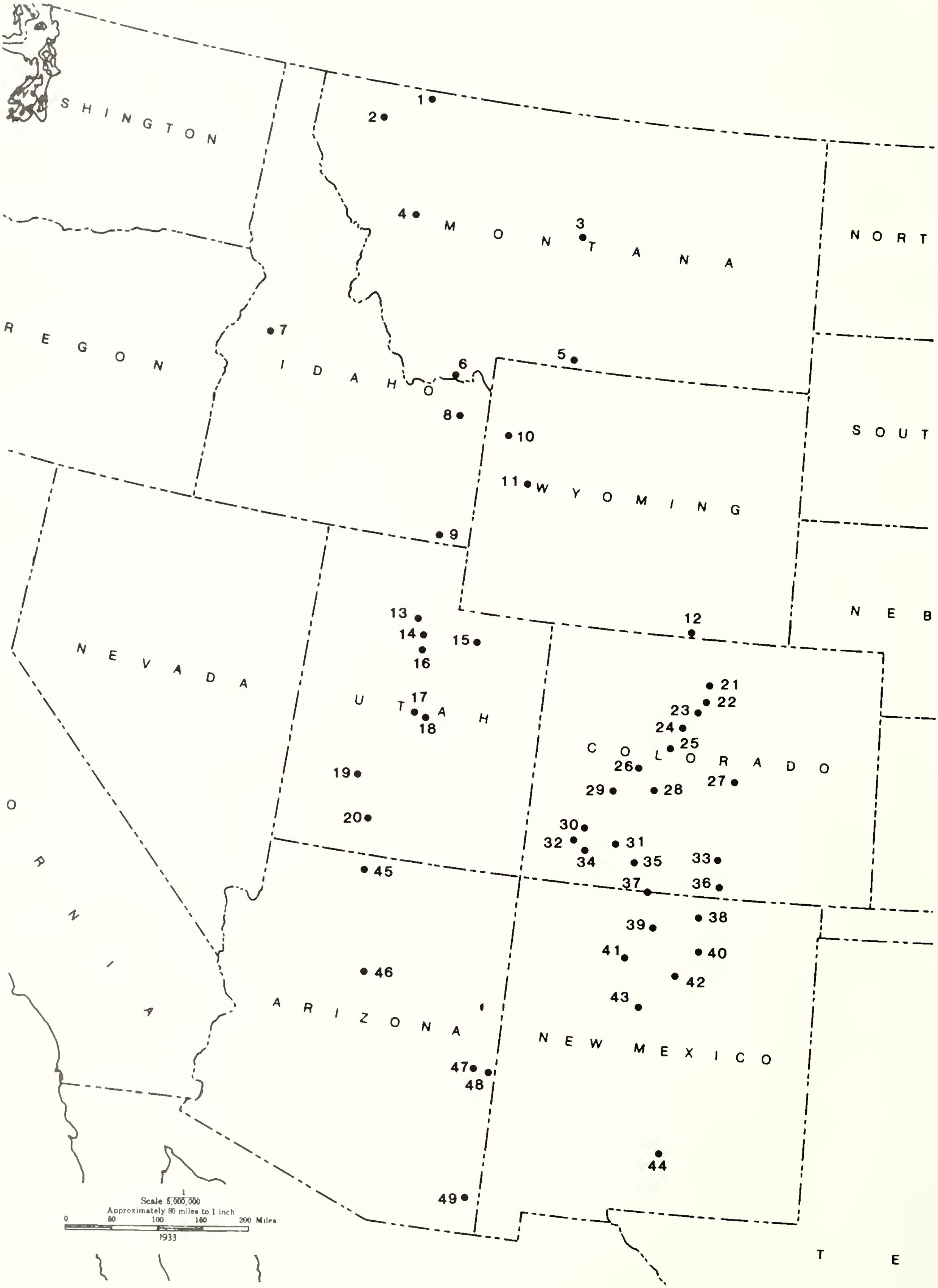

Figure 1.—Precipitation stations listed in table 1.

The temperatures listed are average maximums for each month, not the average monthly temperatures commonly reported. Most weather stations at aspen elevations are in valley bottoms and are not representative of aspen terrain. These valley locations commonly have severe temperature inversions at night, with much lower minimum temperatures than those on the nearby slopes that are covered with aspen. Daily high temperatures are affected less by the topography than are the minimums or the daily averages.

The temperatures in table 2 have little relationship to aspen growth and development (see the EFFECTS OF WATER AND TEMPERATURE chapter). Usually the limiting temperatures are the extreme minimums at the actual aspen site. The values listed should be used for comparative purposes only in terms of general climate.

Winter temperatures within the zone of aspen forest, as expected, decrease northward from southern New Mexico to Wyoming or Montana. Perhaps more important is the decline of spring (April-June) temperatures northward (fig. 4), because these determine when aspen begins its annual growth. The longer growing season in the Southwest may contribute to the large sizes attained by aspen in that region. By contrast, July and August temperatures are not very different in aspen forests from Wyoming to Arizona.

Summer temperatures at the intermediate- and low-elevation aspen sites in the north are often higher than on typical aspen sites further south. For example, Lyon (1971) described the climate at two stations in south-central Idaho, at about 6,500 feet (2,000 m) elevation, where patches of aspen were often associated with mesic microsites. Precipitation at the two stations was 14 and 17 inches (36 cm and 43 cm) per year, and summer temperatures reached or exceeded 90°F (32°C) on 7 and 15 days per year, which is appreciably warmer than the higher elevation sites in Utah described by Price and Evans (1937).


Figure 2.—Rime on aspen crowns, Sangre de Cristo Mountains, New Mexico (Gary 1972).

Other aspects of climate related to temperatures at a given site are length of the frost-free period and temperature extremes. Throughout much of the range of western aspen, particularly from Wyoming southward, 90°F (32°C) air temperatures are rare; therefore, critically high temperatures seldom are reached. Conversely, 0°F (−18°C) is common in winter, the period of dormancy when the aspens are most hardy. Extreme temperatures tend to be greater in aspen areas of the northern Rockies. South of Canada, one of the coldest temperatures experienced by aspen now living was near Rogers Pass, Montana where it dropped to −70°F (−57°C) on January 20, 1954. At the same latitude, aspen near Lewistown, Mont. have experienced summer air temperatures of 105°F (41°C).

Marr (1961) provided an example of an extreme climate in which aspen can grow in the West. He collected temperature data in a scrub stand, in the forest-tundra transition of northern Colorado, probably above 11,000 feet (3,350 m) in elevation. Although the data were collected for only 1 year, the most striking feature was the late beginning of the growing season. In May, temperatures fell below freezing every day but one; and the mean daily high was only 39°F (4°C). In July, the warmest month, the average daily high temperature was 61°F (16°C); the warmest temperature recorded during the year was only 70°F (21°C).

The length of the freeze-free season is especially influenced by topography. The weather station at Fort Valley, Arizona is in the forest, on a plain at 7,347 feet (2,250 m). At night, cold air flows down the slopes of the adjacent San Francisco Mountains and spreads across the plain, causing rapid cooling. Aspen there have experienced air temperatures as low as −37°F (−38°C). The average frost-free season lasts only 61 days. Fraser, Colo., at 8,560 feet (2,600 m) in the cold-air trap of a high mountain valley, has an average of only 24 days (June 24 to July 18) between 28°F (−2°C) air temperatures. In contrast, the Cloudcroft Ranger Station in New Mexico lies at 8,650 feet (2,650 m), with no high mountains nearby to intensify nocturnal cooling. The coldest temperature recorded there has been −15°F (−26°C), with a frost-free season of 147 days, more than twice as long as at Fort Valley and six times longer than at Fraser.

Aspen forest affects the microclimate. Miller (1967) studied temperature profiles within an aspen sapling stand in which the trees were large enough that a foliage-free "bole space" had developed beneath the canopy. On a sunny day, leaf temperatures measured near the top and bottom of the canopy did not get warmer than about 4°F to 7°F (2°C to 4°C) above air temperature. Within the central part of the canopy, temperatures of individual leaves generally were within 8°F (4°C) of air temperature. On a partly cloudy day, leaf temperatures responded somewhat to temporary shade from clouds. When the sun dropped behind the ridge in late afternoon, leaves sharply cooled to below air temperature. Because this typical aspen canopy was not dense, cold air settled through from the radiating surfaces of the upper canopy at night, so that the lowest night temperatures were at the top of the canopy and at ground level. On an August night with frost in the adjacent meadow, however, there was no frost beneath the aspen.

Gary (1968) compared soil temperatures beneath aspen and Douglas-fir in northern New Mexico. The soils froze earlier and deeper and stayed frozen longer under Douglas-fir (fig. 5). The difference was especially great on south slopes, where the snow under aspen received much more sunlight than under Douglas-fir. The upper few inches of aspen soils there were as warm in April as Douglas-fir soils were in June. At 1 to 2 feet (31 cm to 61 cm), south-slope aspen soils warmed about 1 month before Douglas-fir soils.

Table 2.—Mean daily high temperatures (°F) at some stations with aspen nearby at a similar elevation. Stations are listed in north-south order within states and are number-coded to map locations (fig. 3).[1]

	Elev.						Months							
Station[2]	(feet)	J	F	M	A	M	J	J	A	S	O	N	D	Class[3]
MONTANA														
1 Babb 6NE	4,300	31.4	32.7	38.6	51.7	61.1	66.1	76.8	75.0	65.7	56.0	43.0	35.6	1
2 Lewistown AP	4.132	32.1	34.9	40.6	55.7	65.5	71.0	82.9	80.5	70.3	59.9	44.6	36.7	2
3 Ovando 1SW	4,109	27.0	33.1	41.1	57.0	65.5	71.3	82.2	80.6	71.1	60.0	41.2	30.8	3
4 Red Lodge	5,575	32.3	34.4	39.4	51.7	60.9	67.3	78.4	76.6	66.8	56.7	43.0	36.7	2
5 Lakeview	6,800	19.3	26.3	31.9	47.3	58.2	63.9	75.8	75.7	66.4	52.9	33.8	23.8	3
IDAHO														
6 McCall	5,025	28.6	33.7	40.2	50.6	61.6	68.1	80.7	79.3	69.4	56.9	40.1	31.5	2
7 Ashton 1S	5,100	27.6	33.0	39.5	55.3	67.9	73.8	83.4	81.9	73.4	61.3	41.6	31.9	2
WYOMING														
8 Moran	6,740	24.5	30.2	36.4	47.8	58.9	62.0	77.1	75.3	66.8	54.9	37.3	28.3	1
9 Kendall	7,645	25.0	28.4	33.9	45.8	57.3	65.6	74.7	73.5	66.0	54.7	37.6	28.4	1
10 Pole Mt. Nursery	8,530	27.4	29.6	34.5	44.6	55.7	67.2	75.1	73.0	64.9	51.8	37.1	30.9	2
11 Foxpark	9,065	26.4	28.9	33.6	43.3	52.8	63.6	72.5	71.4	63.2	51.4	36.7	29.5	3
UTAH														
12 Silver Lake Brighton	8,740	29.9	32.2	36.1	45.1	53.6	62.1	71.7	70.6	63.8	51.8	39.9	33.5	2
13 Moon Lake	8,150	30.8	32.3	37.6	48.9	59.3	66.9	76.0	74.2	66.8	54.7	41.3	33.7	3
14 Bryce Canyon NP	8,213	34.2	38.9	43.7	55.1	64.8	73.1	80.8	78.0	73.3	59.9	44.8	36.9	1
COLORADO														
15 Longs Peak	8,956	32.7	33.2	36.6	45.8	55.0	65.8	72.4	70.8	63.5	53.8	41.0	36.5	3
16 Dillon	9,065	31.8	35.0	39.6	49.4	60.0	69.4	74.7	73.4	68.4	57.6	42.0	34.8	3
17 Leadville	10,200	30.7	33.2	36.7	45.8	56.1	67.0	73.3	71.4	65.2	54.2	39.9	32.9	2
18 Crested Butte	8,800	28.9	32.5	38.1	49.1	60.8	71.2	77.7	76.2	69.4	59.5	42.4	32.5	1
19 Fremont Exp. Stn.	8,900	35.5	36.5	39.8	46.4	53.4	66.3	71.8	68.1	63.1	54.4	43.8	37.6	2
20 Knott Ranch[4]	9,300	29.4	33.2	40.0	48.1	58.4	67.6	73.7	71.8	65.1	54.3	41.4	33.3	1
21 Silverton 2NE	9,400	32.9	35.6	39.2	47.7	57.0	66.4	72.4	70.4	64.9	54.8	42.8	35.6	1
22 Cumbres Pass	10,000	28.3	29.8	32.3	43.6	53.0	63.7	68.7	67.1	62.3	51.5	38.2	31.6	1
NEW MEXICO														
23 Red River	8,676	35.6	37.9	43.3	53.7	62.2	72.5	76.8	75.0	69.8	59.4	45.6	38.4	2
24 Lee Ranch	8,691	34.1	37.3	42.6	52.5	62.1	72.1	75.5	73.2	65.9	56.6	45.1	38.0	2
25 Cloudcroft 1	8,650	40.9	42.9	48.0	56.1	64.5	72.6	72.5	71.3	67.6	59.7	50.8	44.3	3
ARIZONA														
26 Bright Angel RS	8,400	36.2	38.3	43.6	52.3	63.0	72.8	77.9	75.3	70.9	58.3	47.1	39.7	1
27 Fort Valley	7,397	40.1	42.0	48.0	56.9	66.2	75.8	80.5	77.5	73.0	62.5	51.0	43.4	2
28 Alpine	8,000	44.9	46.3	50.4	60.9	68.8	77.2	78.6	75.8	72.8	64.9	55.2	47.5	1

[1] *These data come from several sources; most are from the National Weather Service and its predecessors under the U.S. Department of Commerce, the U.S. Department of Agriculture, and the U.S. Army.*

[2] *Some of these stations are at slightly different locations from stations in table 1 that have the same or similar names.*

[3] *Class 1 = aspen type is prominent in locale;*
Class 2 = a fair amount of aspen;
Class 3 = some aspen, may be largely mixed with conifers.

[4] *Also known as Sapinero 9W.*

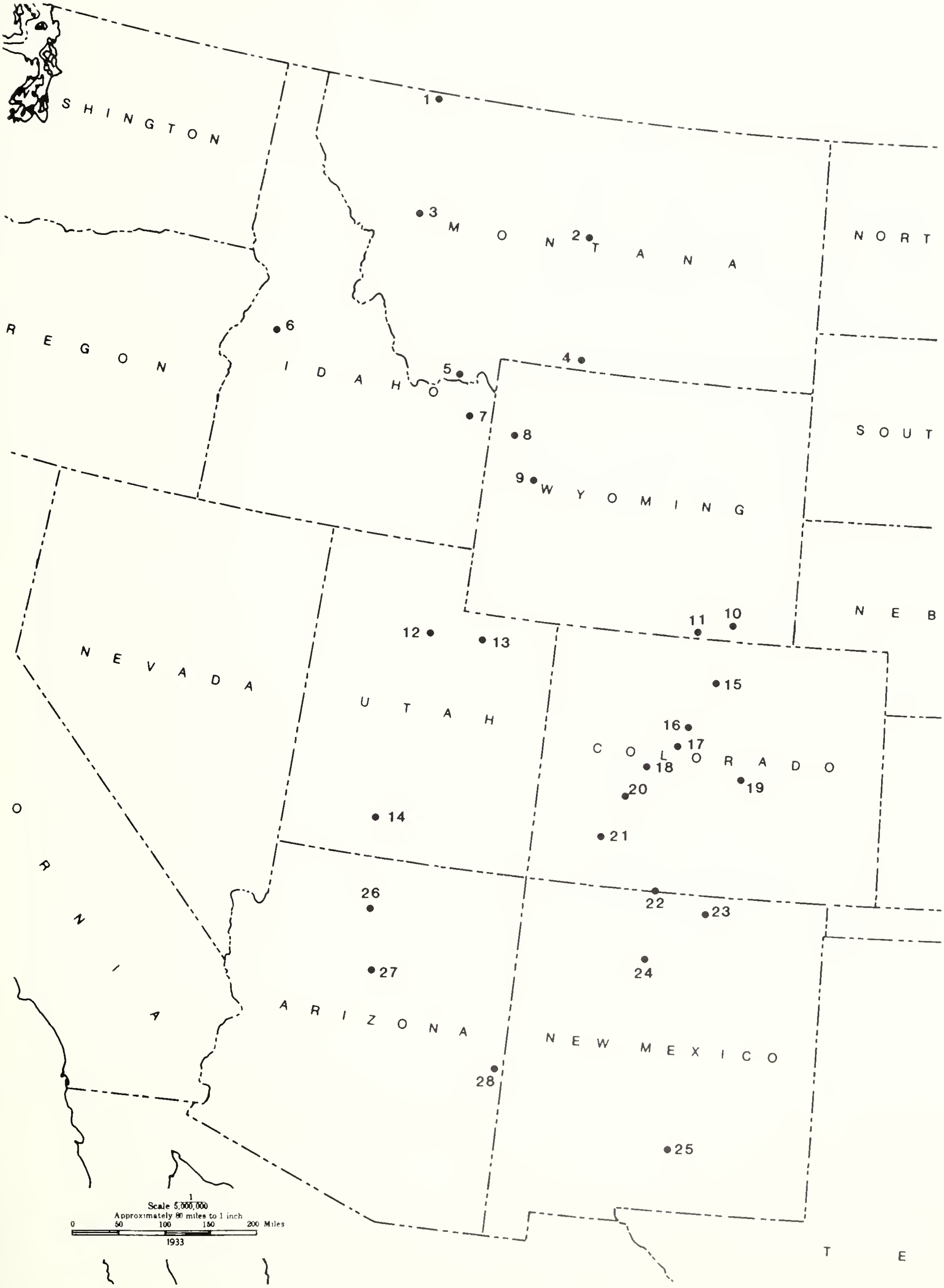

Figure 3.—Temperature stations listed in table 2.

Summary

Where there is adequate water, as in the eastern portion of its range, it appears that the southern boundary of aspen is near the 75°F (24°C) mean July isotherm. In the central Rocky Mountains, the lower elevational limit roughly coincides with a mean annual temperature of 45°F (7°C). Such relationships may not have a physiological basis, but are related to isolines that can be drawn on maps.

The range of aspen in the interior West, where much of the climate is semiarid, appears to be limited by water availability to satisfy the heavy evapotranspirational demands of the species rather than by any discernible temperature extreme or average. An average annual water runoff isopleth of at least 1 inch (3 cm) best describes the lower boundary in the mountainous West just as it does the western limits of aspen on the Great Plains (Perala, in press). Another isoline, the upper boundary, probably is best described by a combination of factors that limit the length of the growing season (temperatures, snowpack depths, radiation, etc.) and by wind.

The range of aspen probably is limited by a combination of factors; and, at any given site, it likely is limited by one or two critical climatic factors. Limits of soil moisture and extreme temperatures should be investigated first, when determining climatic restrictions to expansion of the range.

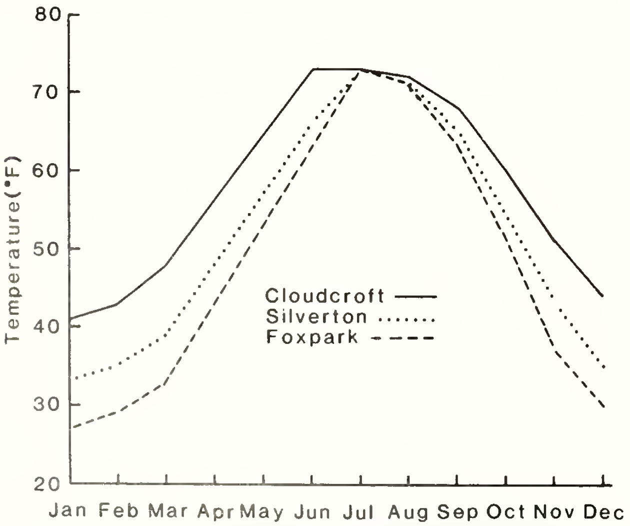

Figure 4.—Graph of average daily high temperatures for each month at stations at three different latitudes: Cloudcroft 1, New Mexico (32°58′N); Silverton 2 NE, Colorado (37°48′N); and Foxpark, Wyoming (41°05′N). The horizontal line at 56°F (13°C) is a hypothetical threshold temperature showing different lengths of growing seasons despite almost identical mid-summer temperatures.

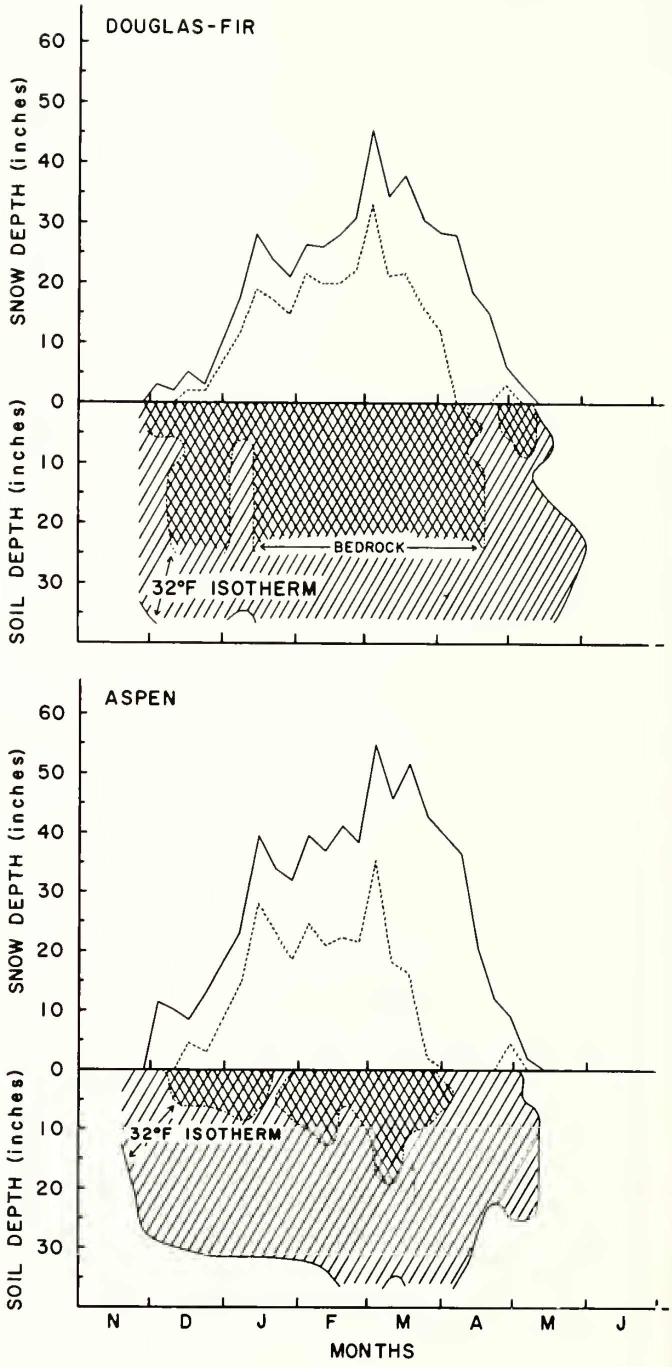

Figure 5.—Snow depth and 32°F (0°C) isotherms in the first 3 feet (1 m) of soil under aspen and Douglas-fir cover types on north and south aspects in northern New Mexico (Gary 1968).

SOILS

John R. Jones and Norbert V. DeByle

Edaphic and climatic characteristics of a site quite well define the quality of that site for plant growth. The importance of soil characteristics to the growth and well-being of aspen in the West is apparent from observations by many authors, from inferences resulting from work with other trees and agricultural crops, and from detailed study of aspen soils and site quality in the Lake States. However, there are not many descriptions of aspen-soil-site relations in the West. Only in recent years has enough soil survey information been collected from the forested areas of the West to define the soil series, and sometimes types and phases, upon which quaking aspen is found. Assessment of site quality is just beginning. For example, recent county soil surveys in Utah include information on forest productivity, including site indexes for aspen (Campbell and Lacey 1982, Carley et al. 1980).

The capacity of soils to hold water and make it available for plant growth is often their most important characteristic. This is discussed in the chapter EFFECTS OF WATER AND TEMPERATURE. Rooting behavior of plants partly depends upon the soils on which they grow; in turn, plant rooting characteristics affect soil properties. Aspen rooting characteristics are examined in the MORPHOLOGY chapter. Other aspects of soils are discussed in the WATER AND WATERSHED chapter.

Parent Rock

Parent rock types are extremely varied in the West; aspen grows on many of them. Berndt and Gibbons (1958) found aspen on soils derived from granite, sandstone, and limestone in Colorado. Severson and Thilenius (1976) found aspen stands on soils from calcareous sedimentaries, slates, quartzitic schists and "Tertiary igneous" parent rocks in the Black Hills and Bearlodge Mountains of South Dakota and Wyoming. Any given community type was likely to be found on soils from two or three different parent rocks. In southern Wyoming, Wirsing and Alexander (1975) reported the climax *Populus tremuloides*/*Carex geyeri* association on glacial outwash, loess, alluvium, gneiss, subsilicic igneous rock, shale, and limestone.

However, for growing aspen, the quality of soils from these different parent materials varies widely. Retzer[1] concluded that the best aspen in the Rocky Mountains and Great Basin grows on soils from subsilicic igneous rocks such as basalt, and from limestones and neutral or calcareous shales. He also noted that "some of the least vigorous and most diseased aspen" were found on soils derived from granite.

In the area of Crested Butte, Colo., all local parent rocks except igneous appeared to be favorable for aspen (Langenheim 1962). Aspen groves grew more frequently on limestones and shales than on associated conglomerates and sandstones. Limestone beds sometimes were outlined by aspen. Langenheim (1962) credited the correlation of parent rock and aspen distribution to the effects of parent material on succession. Soils that developed from granite, conglomerate, or siliceous sandstone generally had an open herbaceous cover that permitted conifer seedling establishment and, ultimately, replacement of the aspen by conifers.

In Big Cottonwood Canyon, near Salt Lake City, Utah, conspicuous bands of aspen grow along the contour, amidst large areas of mountain brush. Bedrock here is predominantly quartzite, with interbedded layers of more easily weathered limestone. Aspen is found on the soils derived from the limestone (Crowther and Harper 1965). Under the aspen, slopes are less steep, and the soil is deeper and less stony than under the brush.

Jones[2] described soils on many aspen plots—scattered mostly in western Colorado. Soil parent material on those plots included most of the rock types found in the Southern Rocky Mountain Physiographic Province and adjacent plateaus (table 1). No strong differences were observed in soils from these different parent materials. Even the calcium content in soils from calcareous sedimentaries was no higher than in some other soils. Aspen grew poorly or well on soils from almost any type of parent rock. Other environmental factors appeared to dominate aspen site quality in these locales.

The extensive research on aspen soil-site relations in the Lake States has yielded results that appear to be applicable, at least in principle, to the mountain West, particularly in areas that have experienced glaciation. Also, site quality differences between calcareous and non-calcareous parent materials appear to be similar in both areas of the country.

Soil parent materials in much of the Lake States were deposited by continental glaciers; some were later redeposited or modified by streams or lakes. Different glacial fronts deposited parent material of much different character. In northern Minnesota and Wisconsin, for example, parent materials can be classified as (1) Keewatin drift, which is gray, calcareous, and usually fine textured; (2) Cary drift, which is typically, red or brown, coarse-textured, and generally low in bases; and (3) Superior-lobe drift, which is reddish, intermediate in character between the other two, generally fine textured and containing more bases than the Cary drift (Voigt et al. 1957).

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[1] *John L. Retzer, unpublished review, 1949. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo.*

[2] *John R. Jones, unpublished data and notes, on file at Rocky Mountain Forest and Range Experiment Station's Forestry Sciences Laboratory, at Northern Arizona University, Flagstaff, Ariz.*

In very extensive sampling, Kittredge (1938) found that, on soils of the same textural class, aspen grew consistently and substantially better on the calcareous Keewatin drift. Stoeckeler (1948, 1960) found better height and volume growth and less decay on Keewatin drift. Voigt et al. (1957) found that volume growth per acre of aspen on Keewatin drift averaged about 2.6 times that on the Superior-lobe drift and 4.5 times that on the Cary drift. In a sample by Meyer (1956), 10 of 11 plots with site indexes higher than 70 feet (base age 50) were found on Keewatin drift. The difference in growth on different glacial drifts, and their textural and chemical differences, suggest that moisture and nutrient regimes are very important to aspen growth.

Land Form

In the area of Jackson Hole, Wyo., Reed (1952) found aspen on dry mountainsides as well as on alluvial terraces above the streamside belt of narrowleaf cottonwood and balsam poplar. In the southern Rocky Mountains, Jones[2] examined aspen on almost the full spectrum of land forms. Groves grew on the bottoms of draws and on ridge crests. Extensive stands were found on mountainsides and on the tops of mesas and plateaus. Aspen occurred on a gley soil next to a cattail marsh, and on a 73% slope of an old avalanche track, as well as on old talus with a very thin stony soil. In Wyoming's Wind River Range, Reed (1971) commented that all aspen observed above about 10,200 feet (3,100 m) were on talus slopes with little soil.

Table 1.—Site index (in feet) and oldest stands (in years) on different parent rock types on 53 plots in the southern Rocky Mountains.[1]

Rock types	Number of plots	Average site index at 80 years	Oldest stand
Sedimentaries, noncalcareous	16	58 ± 18	173
Sedimentaries, calcareous	5	53 ± 10	164
Igneous, silicic (acidic)	18	60 ± 15	151
Igneous, mesosilicic	6	54 ± 11	141
Igneous subsilicic (basic)	3	59 ± 5	144
Metamorphic	5	47 ± 10	170

[1] *John R. Jones, unpublished data and notes, on file at Rocky Mountain Forest and Range Experiment Station's Forestry Sciences Laboratory, at Northern Arizona University, Flagstaff, Ariz.*

Figure 1.—Rapidly growing aspen on a deep-soiled flat at the foot of a slope. Dominants averaged 87 feet (27 m) tall at age 79. San Juan National Forest, Colorado.

Aspen commonly grows larger and faster at the foot of slopes (fig. 1) than on their sides, and on benches rather than on the slopes above and below the benches. Topographic concavities, which tend to concentrate moisture, are likely to grow larger aspen than surrounding non-concave situations. According to Baker (1925), aspen grows best on rich, deep-soiled flats with plentiful moisture. It also tends to persist on those sites, especially on fine-textured soils, where thick herbaceous growth inhibits conifer seedlings. Hayward (1945) wrote that the best aspen stands in Utah's Wasatch Range were on benchlands, where the soil was deep and no snowslides occurred. He reported a heavy growth of forbs on those sites. The deep, dark surface mineral horizon (A_1) and the large decaying trunks of old fallen aspen on these benchlands suggested long aspen dominance.

Kittredge (1938) and Fralish and Loucks (1967) sorted growth data in the northern Lake States by parent material types--lake bed clay, outwash sands, and till, among others. They, too, found that growth differed considerably by type, even when soil textures were similar.

Soil Profiles

The soil forming factors of climate, parent material, topography, organisms, and time (Jenny 1941) act in concert to produce soils. Soil texture, structure, color, depth, and other physical and chemical characteristics reflect these factors. With the passage of time, layers or horizons develop in the soil, forming a soil profile. Horizons in some soils are easy to distinguish by visual examination; in others, including many soil profiles under aspen, chemical and physical tests are necessary to clearly delineate the horizons.

The nomenclature used throughout the remainder of this chapter follows the Soil Survey Manual (USDA 1951, with 1962 supplement) and Soil Taxonomy (USDA 1975).

Surface Organic Horizons (O_1 and O_2)

The surface organic horizons consist mostly of plant remains lying on top of the mineral soil. In the absence of a well-developed conifer component, the organic layer under aspen is thin and somewhat ephemeral. These organic layers seldom are thicker than 1 to 1.5 inches (3 cm to 4 cm) (Jones,[2] Reed 1971).

Bartos and DeByle (1981) found that about 1,600 pounds per acre (1,800 kg per ha) of aspen leaves and twigs dropped each year from stands in Utah with basal areas of 75 to 110 square feet per acre (17 m^2 to 25 m^2 per ha). Well stocked, young stands may produce 1 ton of litter per acre (2,250 kg per ha) (Jones and Trujillo 1975a, Zavitkovski 1971). This material, as well as litter from the herbaceous understory, decays rapidly (Hayward 1945, Hoff 1957, Lutz 1956). Van Cleve (1971) found aspen litter weight loss at an Alaskan site had a half time of 651 days. In Alberta, Lousier and Parkinson (1976, 1978) concluded that 99% of the litter crop would decay in 24 years. Bartos and DeByle (1981) reported a 42% weight loss during the first winter on a Utah mountain site. In addition to rapid decay of this litter, animal activity (notably that of pocket gophers) mixes much of the annual litter crop into the surface layers of mineral soil. Thus, by the end of summer, much of the previous year's litter has disappeared from many pure stands of aspen in the West.

Mineral Horizons—A, B, and C

The upper mineral soil horizons (A and B) that are affected by organisms and climate are collectively known as "the solum." Interactions between vegetation and soil are graphically reflected in the characteristics of the solum, particularly if a specific vegetation type occupies a site for a long time.

Under aspen, the thin surface organic horizon is typically underlain by a thick dark A_1 horizon, a mollic epipedon—high in organic matter content and available nutrients and of granular structure (fig. 2). This black or dark brown horizon under the better aspen stands in the Intermountain West is frequently up to 2 feet (61 cm) thick.[3] Morgan (1969) found organically enriched layers 10 to 23 inches (25 cm to 58 cm) thick in Gunnison County, Colorado. Jones[2] found an organically enriched solum 16 ± 8 inches (41 ± 20 cm) thick on 53 plots in the southern Rocky Mountains; the greatest was 35 inches (89 cm). He and Tew (1968) found that humified organic matter usually constituted 10% or more of the upper few inches of mineral soil, decreasing downward. Bliss[4] classified aspen soils in central Utah with mollic epipedons 10-16 inches (25-41 cm) thick in the "Typic" subgroup, and those more than 16 inches (41 cm) thick in the "Pachic" subgroup.

Aspen forest differs from associated vegetation types in character, distribution, and amount of organic matter and nutrients in the solum. As examples, Hoff (1957) found the A_1 horizon under aspen in northern Colorado was darker and contained considerably more organic matter than under adjacent coniferous stands. Tew (1968) discovered that the upper 6 inches (15 cm) of mineral soil under aspen in northern Utah differed from that under adjacent stands of shrubs and herbaceous vegetation by having 4% more organic matter, higher water holding capacity, slightly higher pH, and more available phosphorus.

Aspen are efficient nutrient pumps that enrich the surface soil horizons (Lutz and Chandler 1946, Stoeckeler 1961). Aspen leaves typically have a higher nutrient content than does foliage of associated coniferous trees (Daubenmire 1953, Troth et al. 1976, Young and Carpenter 1967). The rapid decay of aspen leaves provides a relatively quick return of nutrients to the soil (Bartos and DeByle 1981, Daubenmire and Prusso 1963, Hayward 1945).

In addition, herbaceous undergrowth usually is much heavier under aspen than under conifers in the West (Daubenmire 1943, Hayward 1945, Morgan 1969, Potter and Krenetsky 1967, Reed 1971). In extreme cases, herbs may stand 6 feet (2 m) tall (fig. 3). Herbage production approaches that of associated meadows (Ellison and Houston 1958, Houston 1952, Paulsen 1969). Potter and Krenetsky (1967) found that, in northern New Mexico, grasses, with their extensive fibrous root systems and litter of neutral pH, contributed greatly to organic matter in soil beneath aspen. This, in turn, improved soil water-holding capacity, percentage of base saturation, soil structure, and permeability.

The C horizon underlies the solum. It is a layer of unconsolidated material that has not been appreciably modified by soil forming factors, especially by vegetation. C horizons reflect very strongly the characteristics of the material from which they were derived. Usually the C horizon lacks structure, being either single grained or massive. Jones[2] found both types under aspen stands in the southern Rocky Mountains. He described

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[3] *Aspen Committee, unpublished report, 13 p. 1965. "Guidelines for coordination of uses in aspen areas." USDA Forest Service, Intermountain Region, Ogden, Utah.*

[4] *Personal communication from Timothy M. Bliss, Soil Scientist, USDA Forest Service, Fishlake National Forest, Richfield, Utah.*

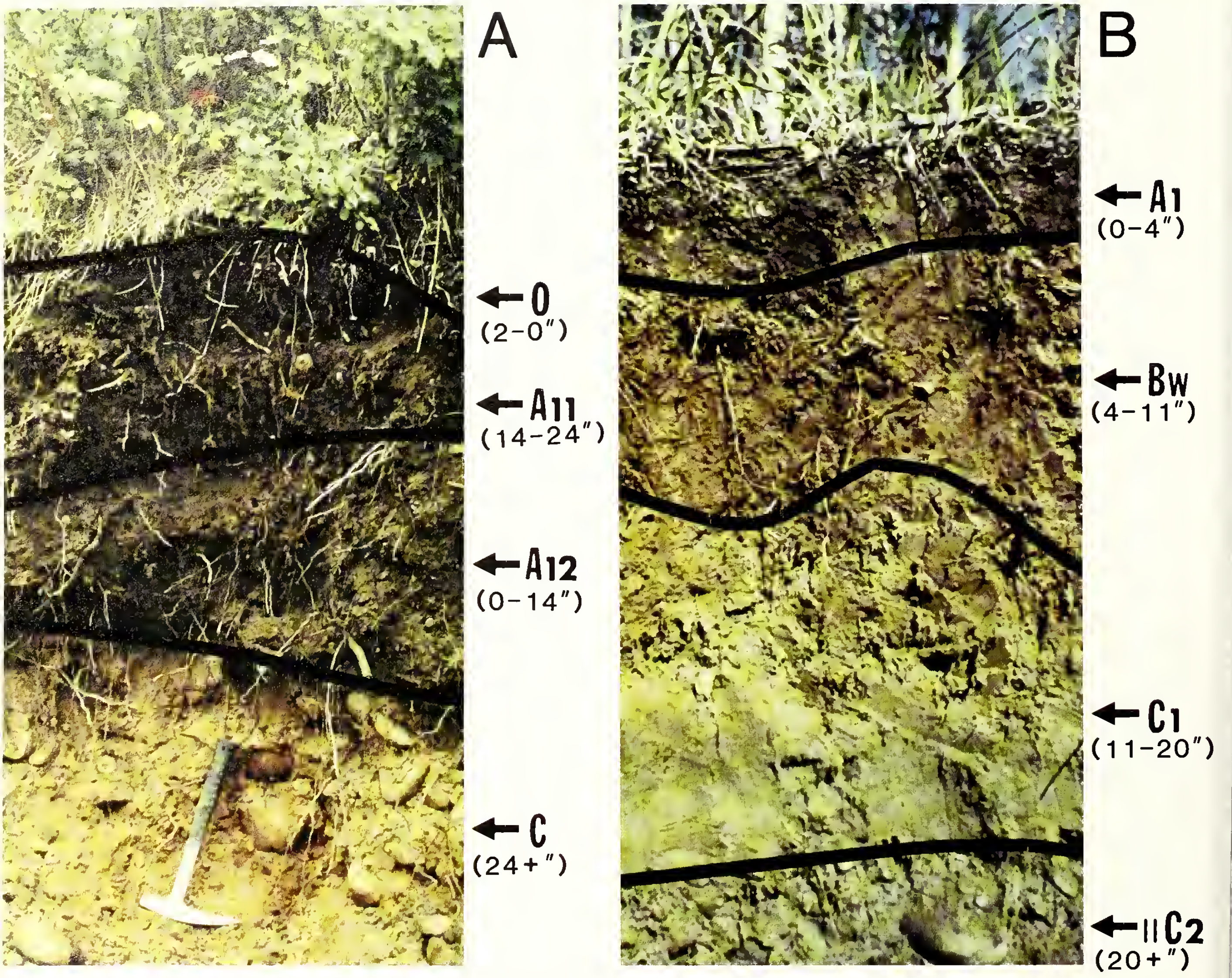

Figure 2.—(A) A mollisol, typical of soil profiles under stable aspen in Utah. A Cumulic Haploboroll with about 2 feet of dark A_1 horizon. (B) A Typic Cryumbrebt profile on a stream terrace in Alaska. Aspen occupies this site, but here is probably seral, and has not been the primary soil-forming factor over a long time span.

massive layers that extended clear to bedrock on a number of plots. The C horizons contained aspen roots, but the massive layers were penetrated only by sinker roots and contained few or no horizontal roots. In contrast, massive layers have not been described in soils mapped beneath aspen by others in the Rocky Mountain Region of the Forest Service.[5]

Jones discovered some sites with no C horizon.[2] Some very shallow aspen soils consisted of the organically enriched A horizon on fractured colluvial rock. In those cases, defining where the soil ended and the underlying rock began was arbitrary, because the organically enriched soil material, with roots, continued downward in the openings between the rocks.

In the Intermountain West, C horizons with strongly calcareous layers have been reported on some aspen sites.[3] A strongly calcareous layer contains considerable free calcium carbonate in unconsolidated material, as distinguished from calcium carbonate in stones; it reflects low precipitation as well as calcareous parent material. Where such a horizon was found within 4 feet (1.2 m) of the surface, aspen growth was very poor. Where it was found within 2 feet (61 cm) of the surface, aspen were not taller than 25 feet (8 m) at age 100.

Soils Under Seral Versus Stable Aspen Stands

If aspen occupies a site for several generations, a typical aspen soil develops. But, if it is seral, particularly to conifers, the solum reflects influences of the vegetation that occupied the site for the longest period of time. Even one generation of conifers can result in a leached, often light colored A_2 horizon underlain by an enriched B horizon. Perhaps the seral nature of aspen on some of the sites reported by Jones[2] accounts for the unusual soil

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[5] *Personal communication from F. A. Dorrell, USDA Forest Service, Rocky Mountain Region, Denver, Colo.*

profiles he found in parts of a 120-year-old aspen/forb stand, in which pale A_2 horizons had become thin and discontinuous beneath dark A_1 horizons that were several inches thick. He also found what was probably a gray-wooded soil (no A_1 and a pinkish A_2 that was 15 inches (38 cm) thick) beneath a 170-year-old aspen canopy, with a well-stocked spruce-fir understory, at 10,300 feet (3,150 m) elevation. This indicated long periods of conifer dominance with brief intervening periods of aspen/forb dominance on the site.

On the Fishlake National Forest, in central Utah,[4] the climax or stable aspen stands usually have a black or dark brown A_1 horizon from 16 to 24 inches (41 cm to 61 cm) thick. Common soil subgroups include Lithic, Pachic, and Argic Pachic Cryoborolls. Eroded sites or transition soils between seral and climax aspen stands are Typic or Argic Cryoborolls. In contrast, soils of seral aspen stands on the Fishlake National Forest typically have an A_1-A_2-B_{2t}t or A_2-B_{2t} horizon sequence, commonly with mixed A and B horizons. The upper boundary of the A_2 horizon seldom is deeper than 12 inches (30 cm) below the surface. Soils with thicker A_1 horizons usually show greater aspen dominance. Common soil subgroups under seral aspen include Typic and Mollic Cryoboralfs, and Boralfic Cryoborolls. Similar soil textures are found under both seral and stable aspen.

Figure 3.—Dense herbaceous undergrowth dominated by larkspur 6 feet (2 m) tall, at the foot of a slope. The mollic epipedon was 35 inches (89 cm) thick. San Juan National Forest, Colorado.

Texture and Stoniness

Soil texture has a major influence on several factors that presumably affect aspen: cation-exchange capacity, water-holding capacity, and permeability to water, roots, and air. For example, in Michigan, Day (1944) found that roots of young aspen penetrated deeply in fine sand, with many sinker roots deeper than 6 feet (2 m); but on a dense lakebed clay, only occasional roots penetrated deeper than 1 foot (30 cm); and, in soil with a dense hardpan, all penetration of the hardpan was through old root channels.

Jones found aspen on essentially the full range of soil textures available in Colorado and northern New Mexico.[2] Sandy loams were most frequent, although loams also were common. Loamy sands, sandy clay loams, and clay loams were occasional. Texture usually did not change much with depth on Jones' plots. Others,[5] however, reported medium-textured surface soils with clay loam or clay subsoils to be common beneath aspen in the central Rocky Mountains.

Stoniness and/or rockiness varies widely, too. Among Hoff's (1957) paired stands, soil beneath aspen was "invariably deeper and less rocky" than beneath conifers. Jones[2], however, found no notable difference in stoniness of soils beneath quaking aspen and Engelmann spruce (*Picea engelmannii*) in the southern Rocky Mountains.

Several studies in the Lake States showed that aspen site index and soil texture were related significantly (Kittredge 1938; Meyer 1956; Stoeckeler 1948, 1960; Voigt et al. 1957). Aspen height growth was strongly correlated to the combined content of silt and clay (Stoeckeler 1960). Stoeckeler (1960) concluded that the optimum texture is about 60-70% silt and clay on sites not having a shallow water table. Meyer (1956) and Voigt et al. (1957) found that aspen grew fastest where silt and clay content was 80% or higher. Strothmann (1960) considered that if 30% or more of the soil volume was occupied by stone or gravel, aspen growth would be reduced. Stoeckeler (1960) also considered a high stone and gravel content deleterious to aspen growth. The extent to which these Lake States findings apply in the mountainous West has not been adequately tested.

Drainage

Probably because of a preponderance of well-drained soils on the western mountainous landscape, the problems of too much water or lack of soil drainage have not been studied for aspen in the West. Nonetheless, aspen occurrence and growth are affected by too much water on some western sites and by too little on most others. The following findings from the Lake States should apply to the West.

Lake-bed clays, despite their high silt and clay content, tend to be very poor aspen sites in both Minnesota and Wisconsin (Fralish and Loucks 1967, Kittredge 1938). They are poorly drained internally as well as externally. Apparently it is drainage in the upper 2 or 3 feet (0.6 m to 1 m) that is critical. Growth is good on many soils with poor drainage at greater depths. The presence of ground water—either as a permanent or an intermittent water table—as near to the surface as 2 feet (61 cm), tends to improve aspen growth in the Lake States. The effect is largest on coarse-textured soils, and trends toward no effect on fine-textured soils (Fralish 1972, Fralish and Loucks 1967, Kittredge 1938, Stoeckeler 1960, Strothmann 1960, Wilde and Pronin 1949). Roe (1935) reported reasonably good aspen growth in swamps on wet mineral soils but poor growth on organic soils (Histosols).

Soil Fauna

Hoff (1957) presented data on invertebrates inhabiting the organic and surface mineral layers under aspen stands and nearby coniferous stands. Invertebrate populations were larger under aspen in 14 of the 15 comparisons, and much larger in 9 of the 15. Though not usually encountered, earthworms were found more frequently under aspen.

Hayward (1945) reported the soil turning activities of pocket gophers and ground squirrels to be much more prevalent in aspen forests than in coniferous forests of the Wasatch and Uinta Mountains of Utah. McDonough (1974) determined that the average pocket gopher mound in a Utah aspen stand was 15 × 18 inches (38 cm × 46 cm) across and 3.5 inches (9 cm) deep. Over a 4-year period, 40% of his 1-meter-square quadrats had one or more new mounds. The mound soil was similar to undisturbed topsoil, but was less compact and more friable. In a subalpine aspen stand in Colorado, Brown and Thompson (1965) found that pocket gopher activity had destroyed the upper part of the B horizon, mixing it with the thick dark A horizon.

Nutrients

As noted earlier, aspen and associated species are excellent nutrient pumps. They effectively withdraw large quantities of available nutrients from the entire rooting depth (more than 6 feet (2 m) on deep, well-drained soils), incorporate those nutrients in biomass, and return a large proportion of that biomass (nearly 2 tons per acre (4,500 kg per ha)) to the soil surface as litter each year. Rapid decay of that litter, combined with animal activity, returns those nutrients to the surface mineral soil. Mollic epipedons often develop. It is not surprising that the A_1 horizon under aspen usually contains greater concentrations of available nutrients than lower horizons. Jones[2] found more of each nutrient, especially potassium, in the A_1 horizon than in the C horizon of his many aspen plots in the southern Rocky Mountains. An average of 30 milliequivalents of extractable calcium per 100 grams of soil was found in the A_1 versus 14 in the C. In contrast, in Engelmann spruce he found an average of only 7 milliequivalents of calcium in each of these horizons.

The higher pH typical of surface mineral soils under aspen implies a greater base saturation of the exchange complex than that found in soils under nearby vegetation types (Jones,[2] Tew 1968).[2] Southard (1958) found a base saturation greater than 80% in the surface horizons under aspen in northern Utah. In central Utah[4], both seral and climax aspen stands growing on soil derived from igneous rock had base saturations of 65-80% in the surface horizon and 80-90% in the subsoil.

In many aspen stands in the West, legumes are prominent or even predominant. Legumes or alder, with their symbiotic nitrogen-fixing root bacteria, significantly improve the nitrogen supply in some forest types (Sprent and Silvester 1973, Tarrant and Miller 1963). Tew (1968) reported slightly greater nitrate production from soils under nearby shrub stands than from aspen in Utah—but it was still good in both cases. Beetle (1974) stated that heavy nitrate fertilization of a Wyoming stand greatly stimulated the grasses; but aspen height growth was not affected, implying that there was sufficient nitrogen for the aspen even before fertilization.

Jones[2] found some mature aspen in the southern Rocky Mountains with good to excellent height growth on soil with medium to low nutrient levels. While adequate nutrient levels are necessary for good growth, apparently the levels below which aspen height growth is retarded are not often encountered in the West. Poor height growth here seems to be caused by other factors. Fertilizing may increase basal area and volume growth, however, even where height growth is not affected (Cochran 1975, Einspahr et al. 1972).

The effect of soil nutrient levels on aspen growth has been much more extensively studied outside the mountain West. In the northern Lake States, the difference in aspen growth on different parent materials, especially its very superior performance on the nutrient-rich Keewatin drift, suggests that soil nutrient content is deficient for good aspen growth on many soils. Stoeckeler (1960) and Voigt et al. (1957) found the site index of aspen there to be significantly correlated with available nitrogen, calcium, magnesium, and potassium in the soil. Einspahr et al. (1972) fertilized a sandy loam soil in Wisconsin with nitrogen, phosphorus, potassium, calcium, and magnesium; this substantially increased volume growth but not height growth. Fertilizing an impoverished soil in Alaska dramatically increased both height and diameter growth (Van Cleve 1973).

In contrast, Fralish (1972) concluded that soil nutrient levels had very little effect on aspen growth in northern Wisconsin. These apparently contradictory results probably came from sampling different extremes or ranges of nutrient levels. However, on very nutrient-poor lake bed sands in the Lake States, the soil nutrient status improved with long periods of humus accumulation; and more nutrients were accompanied by better aspen growth on these moist sites (Wilde and Paul 1950, Wilde and Pronin 1949).

EFFECTS OF WATER AND TEMPERATURE

John R. Jones, Merrill R. Kaufmann, and E. Arlo Richardson

Distribution

Aspen's geographic and elevational ranges indicate a species that tolerates severe cold but does not tolerate sustained high temperatures, or semiarid or even dry, subhumid conditions. Much can be inferred from observation of the sites on which quaking aspen grows in the West. Aspen's distribution is related to its regeneration characteristics, its pathology, and its relations with other plants. Water and temperature, to some degree, affects each of these relationships.

Where the northern grasslands approach the foothill and boreal forests, groves of aspen grow in depressions and on north-facing slopes (Brown 1935, Lynch 1955, Moss 1932), where concentration of soil moisture or reduction of evapotranspiration compensates somewhat for inadequate or marginal precipitation. In the central and southern Rockies, aspen reaches its lowest elevations along stream bottoms in the ponderosa pine, mountain brush, sagebrush or even pinyon-juniper climax zones (Baker 1925, Russo 1964, Vestal 1917). This implies a minimum moisture requirement for aspen that is greater than that of prairie, ponderosa pine forest, mountain brush species, or sagebrush.

Despite available or even abundant groundwater, however, aspen is not found along streams in relatively hot deserts. This indicates intolerance of high temperature effects—either direct effects or indirect effects such as sustained high atmospheric moisture stress.

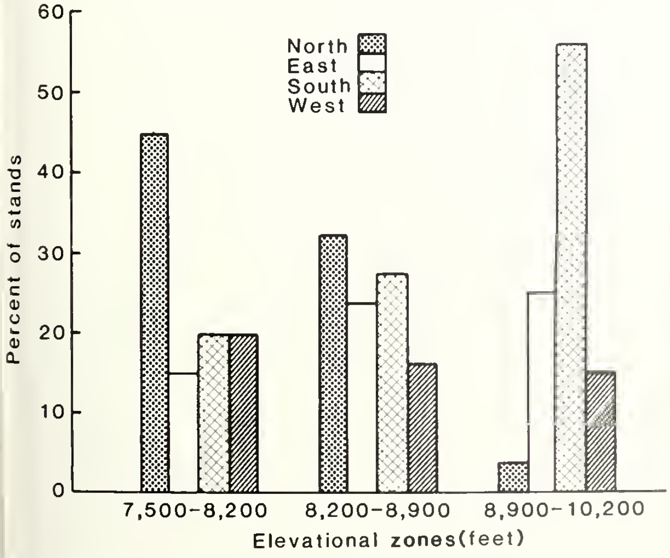

Figure 1.—Percentage of aspen stands on different slope directions, at different elevations, in the Wind River Range, Wyoming (Reed 1971).

In the Interior West, even within the elevational zone where it is prominent, aspen favors certain slope aspects (Baker 1925, Choate 1965, Dixon 1935, Langenheim 1962, Marr 1961, Reed 1952, Reed 1971), as diagrammed in figure 1 for the Wind River Range in Wyoming. In the lower part of that elevational zone, it is most abundant on north-facing slopes (fig. 2), and in the upper part on south-facing slopes. At lower elevations, which are drier and warmer, aspen survives best on the cooler, wetter, north-facing slopes. At higher elevations, because of the shorter growing season and colder temperatures, aspen survives best on south-facing slopes. At intermediate elevations, it shows less definite preferences (Langenheim 1962, Reed 1971).

On the Kamas Ranger District (Wasatch National Forest, Utah), Richardson[1] found the elevation of greatest prevalence of aspen between 8,500 and 9,000 feet (2,600 m and 2,750 m), but some clones were found near the 7,000-foot (2,150-m) level and others to near 10,000 feet (3,050 m). At the lower elevations, most of the aspen were found on north-facing slopes. As elevation increased, the dominant area of aspen dropped into the canyon bottoms and level plateaus. At higher elevations, the south-facing slopes became the most important aspen habitat.

Aspen forest is not prominent in the Black Hills of South Dakota (Green and Setzer 1974), which are mostly within the ponderosa pine climax zone. Severson and Thilenius (1976) found the aspen stands there almost exclusively on north-facing slopes—the slightly wetter and cooler sites. In interior Alaska, in contrast, aspen grows mainly on south-facing slopes (Zasada and Schier 1973)—the slightly warmer sites. In the cool, wet climate of Newfoundland, aspen is virtually absent from the wettest districts and areas with the coldest summers (Page 1972).

The scarcity of aspen in the upper subalpine zone in the West probably is not caused by cold summers or late-lying snow, because it is found even higher, frequently at timberline (Cox 1933, Jones and Markstrom 1973, Marr 1961), where summers are quite cold, and snow collects and persists late in patches of scrub. Instead, aspen scarcity in the upper subalpine probably reflects the relative infrequency of fires and competition from heavy invasion of Engelmann spruce and subalpine fir or corkbark fir (fig. 3).

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[1] *Information compiled by E. Arlo Richardson, Utah State University, Logan.*

Figure 2.—Effects of slope direction on vegetation type in Utah. The photo, taken facing east, shows (A) aspen forest and (B) Douglas-fir forest on northerly slopes, and mountain brush on south-facing slopes. Manti-Lasal National Forest (Choate 1965).

Drought Resistance and Avoidance

Kaufmann (1982b) found that leaf conductance of quaking aspen decreased by more than 50% when xylem pressure potential decreased from −16 bars to −23 bars. In contrast, needle conductance was unaffected by xylem pressure potentials as low as −22 bars in Engelmann spruce (*Picea engelmannii*), −19 bars in subalpine fir (*Abies lasiocarpa*), and −18 bars in lodgepole pine (*Pinus contorta*). Somewhat in contrast, Tobiessen and Kana (1974) found that quaking aspen in New York continued to transpire rapidly when leaf water potential was as low as −60 bars. In comparison, they noted water loss from associated bigtooth aspen and white ash decreased sharply at −30 and −20 bars of leaf water potential, respectively. This suggests that the stomata of quaking aspen leaves in the eastern United States do not close effectively under water stress.

Recent unpublished work by Kaufmann indicates that the annual transpiration of aspen trees is less than that of Engelmann spruce, subalpine fir, and lodgepole pine, although the understory evapotranspiration may be greater beneath aspen. This work suggests that aspen sites often are wetter than conifer sites simply because the aspen trees extract less soil water. Lower annual transpiration by aspen results from low leaf area index, evaporative cooling of leaves, and shorter growing season, factors which offset the higher foliage conductances of aspen than those of conifers (Kaufmann 1982a, Kaufmann et al. 1982).

Differences in environmental conditions can result in differences in aspen stomatal responses in the West versus the East. Full aspen canopies in the West are more open than eastern hardwood canopies, resulting in more air mixing and more uniform temperature and humidity profiles. In West Virginia, Lee and Sypolt (1974) found deciduous forest canopy temperatures on a 20% south-facing slope were about 9°F (5°C) warmer at midday than on a 20% north-facing slope. Therefore, in those forests, vapor pressure gradients would be much greater on the south slope, and water loss would either be greater or stomata would close earlier in the day. For aspen forests in the West, this might be true for small aspen trees near the ground but probably not for full aspen canopies. Small aspen trees in the West may experience more temperature difference between north and south slopes because of irradiance effects in these canopies, which have poorly mixed air. For large trees, however, canopy temperatures of subalpine forests generally are not influenced by irradiance differences associated with slope and aspect (Kaufmann 1984). In fact, unpublished data collected by Kaufmann indicates that aspen leaf temperature is as much as 9°F (5°C) cooler than air temperature in full sunlight, not warmer. This probably is the result of evaporative cooling associated with high transpiration rates.

The wood of living aspen has a rather high water content—the weight of water in a block of green aspen wood is about equal to the weight of the oven-dried wood itself. Water stored in boles and branches may provide a small reserve from which transpiring leaves can draw during the day—a reserve replaced to some degree during the night by translocation from the roots. Aspen trunks shrink notably in diameter during droughts (Kozlowski and Winget 1962a), and contain consistently and substantially more water during dormancy than when the leaves are on (Bendtsen and Rees 1962, Lothner et al. 1974).

Perhaps most important, aspen regeneration from existing mature root systems, and the fast initial growth that results, is a superb system for avoiding drought during the seedling stage. It is a mechanism that gives aspen strong competitive advantage over other western forest species, and a mechanism which largely defines its role in the western landscape.

Seedlings

Explicit information on the moisture and temperature needs for germination and seedling establishment has been presented by Barth (1942), Benson and Dubey (1972), Borset (1954), Faust (1936), McDonough (1979), Moss (1938), and Strain (1964). Seedlings can germinate over a wide range of temperatures, from as low as 32°F (0°C) to at least as high as 98°F (37°C); however, temperature extremes are detrimental. Seedling establishment requires continually favorable moisture. Once wetted, the seed germinates within a few hours or at most a few days, even if submerged. Once the seed has germinated, the seedling will be killed by even superficial soil drying during at least the first week and apparently the first 2 weeks or longer; the period probably depends to some degree on temperatures. (See the SEXUAL REPRODUCTION, SEEDS, AND SEEDLINGS chapter.)

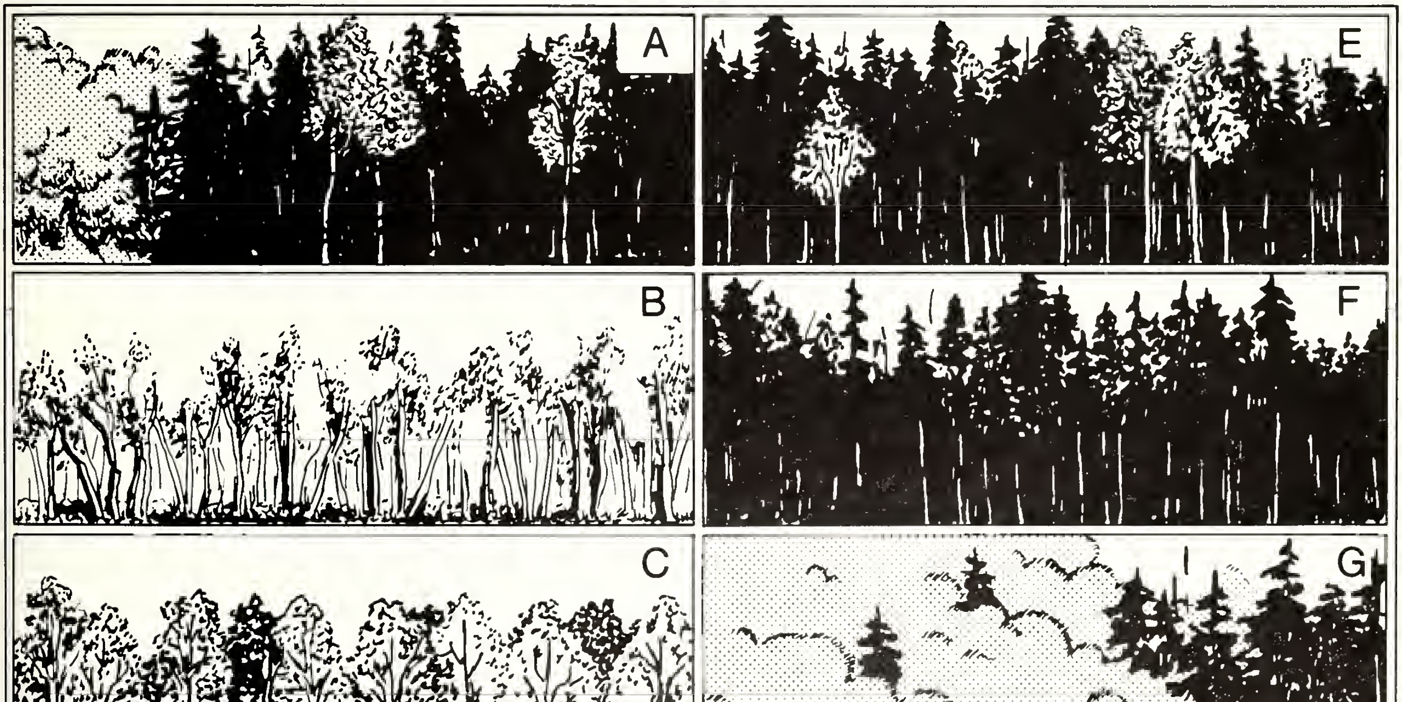

Figure 3.—Hypothetical sequence of events on a 10,600-foot Colorado site, with cold, wet summers, late-lying spring snow, and early autumn snow cover. The climate favors rapid invasion of aspen stands by conifers and long intervals between fires. (A) Fire destroys a 180-year-old mixed forest; (B) 5 years later aspen are 6 feet tall; (C) 30 years later; (D) 80 years later aspen are 60 feet tall with Engelmann spruce and subalpine fir understory; (E) 200 years later; (F) 300 years later aspen are gone; (G) after 350 years extreme drought and fire coincide; (H) after 400 years site is subalpine meadow.

Dixon (1935) reported aspen seedlings on spring banks in south-central Utah. Faust (1936) and Larson (1944) described a stand of aspen established from seed on the drawdown shore of Strawberry Reservoir in Utah, on what had been sagebrush land before the dam was built. In both cases, the moisture regimes were exceptionally favorable.

However, aspen stands, which must have originated with a seedling at some time, can be found in rather dry habitats as well as on sites where moisture is relatively abundant. The explanation seems to lie in the variability of weather and microsites, combined with vegetative regeneration. One or a few protected microsites in a habitat, temporarily free of competition, and having at least a few good seeds, need only have coincided with one suitable summer 1,000, or even 5,000 years before. One such summer could establish many aspen seedlings in a region, scattered about on a variety of habitats, expanding and perpetuating themselves by root suckers. Over centuries or millenia, events would then reduce the number and types of sites occupied, until another extraordinary summer renewed the cycle.

Suckers

Successful suckering requires less ideal moisture conditions than does seedling establishment. The shallow sections of roots from which the suckers arise are supplied with water from greater depths. Gifford (1964) concluded that enough water to support growth of sprouts was translocated through the parent root from moist soil to regions of high moisture stress.

The promptness of suckering, as well as the number and initial growth of suckers on root cuttings, varies with temperature but is satisfactory over a considerable range (Maini 1968, Maini and Horton 1966b, Zasada and Schier 1973). However, there were fewer suckers, and sucker growth was slower, at the cool day/night temperature regime of 68°F/50°F (20°C/10°C) than at warmer regimes (Zasada and Schier 1973); these cooler temperatures are similar to the day/night midsummer air temperatures in the shade of subalpine forests in the Rocky Mountains.

Unusually low temperatures can be disastrous. In the late spring and summer, when sucker and shoot growth are active and succulent, frost can cause serious injury (Baker 1925, Sampson 1919).

Growth

Recent unpublished studies by E. Arlo Richardson indicated that aspen clones in the mountains above Logan, Utah have the following cardinal temperatures for growth and development: base temperature, below which no appreciable growth will occur, is 39°F (4°C); optimum temperature, at which the maximum rate of growth will occur, is 77°F (22°C); critical temperature, above which little or no growth will occur, is about 97°F (36°C). These cardinal temperatures are preliminary, because they are based on very limited information. There probably are differences among clones, especially those that grow in markedly different climatic regimes.

Richardson's studies also indicate that aspen requires a limited amount of winter chilling before growth can begin in the spring. By applying the chill unit model for fruit trees developed by Richardson et al. (1974), he found that aspen required about 300 chill units to complete their winter dormancy. (A chill unit is 1 hour at 43°F or its equivalent.) The required energy accumulation between the end of rest and bud swell was a little more than 1,600 growing degree hours (°F) using the asymmetric model developed by Richardson and Leonard (1981). Accumulations for other phenological stages have not been determined. The rate of growth of aspens may be estimated from how the actual temperature regime relates to the cardinal temperatures for this species.

Height Growth

The start of aspen height growth in spring is related to temperature. Allowing for considerable variation in the temperature responses of different genotypes, growth starts earliest at the lower elevations. Although aspen phytosynthesis seems to be affected relatively little by high leaf moisture stress during the day, overall height growth is influenced quite strongly by the moisture regime—the balance of moisture supply and evapotranspiration.

Bate and Canvin (1971) found that well-established second-year Ontario seedlings grew better at day/night temperatures of 59°F/50°F (15°C/10°C) and 59°F/59°F (15°C/15°C) than at warmer temperatures. This agrees with observations in the West which indicate that aspen height growth is best in the upper montane and lower subalpine zones—roughly from about the elevation where Engelmann spruce first enters the forest, up to a point perhaps 1,200 feet (350 m) higher. However, in the upper 500–1,000 feet (150–300 m) of the spruce-fir zone, aspen normally is more or less stunted (fig. 4).

The zone of best aspen height growth seems to be defined by the temperature regime. Available moisture determines where, within that optimum temperature zone, the best growth takes place. For example, where aspen occurs on exceptionally moist sites within the ponderosa pine climax zone, its height growth is not especially good, and is usually poorer than in the cooler temperatures found 1,000–2,000 feet (300–600 m) higher.

The amount of available water is directly reflected in height and volume growth. Stoeckeler (1960) pointed out that aspen grows 15–25 feet (5–8 m) taller in north central Minnesota than on comparable soils in the Turtle Mountains of North Dakota, where the temperatures are quite similar but precipitation is less. On a sandy loam soil in Wisconsin, regular irrigation of sapling plots produced volume growth 63% greater than that on unwatered plots, mostly by its effect on height growth (Einspahr et al. 1972).

The available water held in the soil (conventionally that held between 1/3 and 15 bars tension) moves downhill in significant quantities at slow, sustained rates (Hewlett 1961, Hewlett and Hibbert 1963). As a result, it responds to topographic features—more soil water is available in deeper soils in and below concavities, and less soil water is available in shallower soil in and below convexities. Usually, the heights of aspen on those sites directly reflect these differences.

In the Lake States, soil characteristics which contribute to more than ordinary supplies of available water normally are associated with superior aspen height growth; and those with less have poor growth (Kittredge 1938; Stoeckeler 1947, 1960; Voigt et al. 1957). That same basic relationship presumably is true in the West. In the West, topographic and climatic variations are larger and more complex within small geographic areas. Therefore, the relationship of aspen height growth to the soil's capacity to provide water is obscured.

Jones (1971a) tried to integrate monthly precipitation and temperature values, topographic variables, and soil variables into a model that would simulate the moisture regime in its effect on aspen height growth. Other data were separately integrated to simulate the growing season temperature regime. Height growth was significantly related to both the moisture regime and the temperature regime; but only about 30% of the site index variance was accounted for. That probably was a result of the shortcomings of the model and the genetic variability among aspen clones.

Figure 4.—The dominants in this even-aged aspen stand are nearly 100 feet (30 m) tall at the lower end and scrubby saplings near the crest, 1,000 feet (300 m) higher. Temperature effects are probably confounded by soil and terrain differences. Fishlake National Forest, Utah (Choate 1965).

Diameter Growth

Except in dendrochronology, diameter growth has been used much less than height as a barometer of environmental effects. Diameter is more influenced by stand density than is height; therefore, site relations are confounded. Much less has been published about moisture and temperature effects on diameter growth than on height growth.

Because the beginning of diameter growth in spring is keyed to temperature, diameter growth begins earlier at lower elevations (Covington 1975, Strain 1964). With ideal conditions for producing photosynthate (adequate water and nutrients, moderate temperatures, and little insect or disease damage to the foliage), the longer growing season at lower elevations should permit diameter growth to continue later there, too. Such conditions seldom occur.

Duncan and Hodson (1958), in an extensive Minnesota survey, found that aspen diameter growth increased, at a declining rate, with increased April–June precipitation. On a sandy loam in Wisconsin, irrigation alone did not increase diameter growth appreciably in a sapling stand; fertilization without watering caused a modest increase; irrigation and fertilization together caused a large increase in diameter growth (Einspahr et al. 1972).

Frost Damage, Insects, and Diseases

Freezing damage to aspen occurs mainly when warm spring days are followed by a severe freeze. That sequence is most likely in nocturnal cold-air sinks at relatively low elevations. Perhaps mature leaves are less susceptible to freeze damage than new or immature leaves. Strain (1964) reported that immature aspen leaves in California were severely damaged by a 26°F (−3°C) temperature on June 3. Marr (1947) reported similar damage by an early June freeze in Colorado.

Aspen shoots are believed to become susceptible to frost damage when the cambial cells become filled with sap in the spring. This begins just below the leaf buds when they begin to swell. Egeberg (1963) reported twigs killed by 6 days of severe freezing in April, in Colorado. Cayford et al. (1959) reported similar frost damage in Canada following 7 days of unseasonably warm April weather which had caused leaf buds to swell. The most severe freeze damage reported was in Utah in 1919 (Korstian 1921). After an exceptionally warm spring, many aspen had fully expanded leaves. On May 30 and 31 temperatures dropped to 15°F (−9°C). All the leaves and much of the previous year's shoot growth was killed. For several weeks, the aspen looked entirely dead. Strain (1966) found that mature aspen with June frost damage grew much less in diameter that summer than adjacent, undamaged aspen.

There is limited evidence that aspen may suffer fewer severe insect and disease attacks on its cold uppermost fringe sites than at lower elevations where it is relatively common and grows much faster. At least it appears to live longer near timberline (Greene 1971, Strain 1964). Observation suggests that at its warm lower fringe, aspen is particularly prone to attacks by insects and disease.

Hofer (1920) reported that, in the Pikes Peak region of Colorado, the poplar borer was prevalent in aspen only below 8,000 feet (2,450 m) and was not found at all above 9,000 feet (2,750 m). It was most frequent on dry sites. However, another damaging borer, *Xylotrechus obliteratus*, replaced the poplar borer at higher elevations. This suggests that the temperature or moisture effects of elevation may have been mainly on the insect rather than on host susceptibility.

After severe drought in Canada's aspen grovelands, aspen lost vigor; and while in a state of severe decline, they were heavily attacked by the poplar borer and by a fungus, *Cytospora chrysoperma* (Riley and Hildahl 1963).

In Utah, epidemics of aspen leaf blight, caused by *Marssonina populi*, seem to coincide with wet summers (Harniss and Nelson 1984, Mielke 1957). Spores of *Venturia tremulae* (*Polaccia radiosum*), which causes shepherd's crook in young sucker stands, are released only on rainy days (Dance 1961). In Canada, decay in aspen is more common on very wet or very dry sites than sites in between those extremes (Basham 1958, Thomas et al. 1960).

The incidence of insect and disease damage in aspen is largely controlled by the climatic variables that control insect or pathogen populations. The impact of this damage to the well-being of the western aspen stands appears to be greatest on the dry marginal sites.

FIRE

John R. Jones and Norbert V. DeByle

Role of Fire

In some areas, many aspen stands are all the same age, dating from a single great fire or a year of widespread fires (fig. 1). The 1879 fire in the Jackson Hole region of Wyoming (Loope and Gruell 1973) and the 1904 fires in Arizona's White Mountains (Kallander 1969) are examples. Choate (1966) found that almost all aspen stands in New Mexico were even-aged, many of them originating after fires dating since the mid-1800s.

Some authors (Fetherolf 1917, Langenheim 1962, Marr 1961, Reed 1971), considered aspen to be climax in some habitats. Others, notably Baker (1925), felt that all aspen forests are successional and fire-dependent in the Interior West, and, if not burned, that they would be replaced by conifers (see the VEGETATION ASSOCIATIONS chapter). Baker (1925) attributed the apparent aspen climax in some areas to the virtual absence of coniferous seed sources. However, he considered aspen to be a minor codominant species in some coniferous climaxes.

Charcoal from old fires is commonly found in the soil under aspen. Morgan (1969) cited charcoal on the sites he studied as evidence that aspen is successional. However, fire would also leave charcoal on sites where aspen is climax. The presence of coniferous charcoal would be much more meaningful. In some aspen stands, investigators have not found charcoal or other evidence of past fire (Reed 1971, Wirsing and Alexander 1975), unless the presence of aspen itself is taken as such evidence.

It is clear that many aspen stands, in the absence of fire, are replaced by grass, forbs, shrubs, or conifers (Beetle 1974, DeByle 1976, Krebill 1972, Schier 1975a). Also, almost all even-aged aspen stands in the West appear to be the result of severe fire, whether or not the aspen type is climax on the site. The development of uneven-aged aspen stands, on sites where fires have been light or absent for a long time, is discussed in the MORPHOLOGY chapter.

Even a mere scattering of aspen in a coniferous stand commonly will restock the area with a new aspen forest after a severe fire (Jones and Trujillo 1975a, Patton and Avant 1970, Pearson 1914, Stahelin 1943) (fig. 2). Perhaps many existing even-aged aspen forests developed after fire burned coniferous forests with a substantial aspen component (fig. 3). Descriptions of the development of aspen on some conifer burns state or imply that suckers formed scattered clumps during the first post-fire years and took over the burned site only after a period of about 5 to 20 years (Clements 1910, Ives 1941b, Loope and Gruell 1973, Stahelin 1943). This suggests that aspen had been very thinly scattered in those forests before they burned.

It is clear that fire is responsible for the abundance of aspen in the West and for the even-aged structure of so many stands.

Fire Occurrence and Behavior

Aspen forest does not readily burn. Mutch (1970) pointed out that many vegetation types favored by fire have evolved characteristics which make them especially flammable. He considered aspen to be a low-flammability exception.

Fechner and Barrows (1976) proposed that existing aspen stands might be maintained and new stands

Figure 1.—Pure even-aged aspen that probably originated from fire about 90 years ago. This excellent quality commercial aspen is on a good site in southwestern Colorado.

Figure 2.—Fire that kills the overstory in mixed aspen-conifer stands results in prolific aspen root suckering. Aspen often dominates sites such as this for perhaps a century after burning.

established as fuel breaks in critical areas. Their proposal was based on the infrequence, slow spread, low intensity, and ease of control of fires in aspen forests.

During a 14-year period on national forests in Colorado, an average of only 0.28% of the aspen acreage burned annually—a rate of less than 3% in a century (Ryan 1976). Aspen stands commonly will not burn at all. Crown fires running through coniferous forest drop to the ground when they come to an aspen stand and may even extinguish after burning into the aspen only a few yards. Fires sometimes bypass stands of aspen enclosed within coniferous forest. However, fuel conditions and flammability of aspen vary considerably among stands and times (Barrows et al. 1976).

Dated fire scars, historical records, and other evidence indicate that, before and during the mid-19th century, much larger acreages of aspen burned than have burned since. In the area of Jackson Hole, Wyo., the aspen stands date from fires between 1850 and 1890; significant fires burned in aspen forests there about every 6 years (Loope and Gruell 1973). In the Ephraim Canyon area of central Utah, Baker (1925) and Meinecke (1929) found very few aspens fire-scarred later than 1885. Earlier fire scars were common, indicating that fires burned in aspen there at intervals of 7 to 10 years. Extensive sampling of aspen in Colorado found few aspen fire scars dating later than about 1880 (Davidson et al. 1959).

Clearly, there has been a great reduction in the rate of fire rejuvenation of aspen in the West. This has resulted in a major and continuing change in the ages and structures of aspen stands. Green and Setzer (1974) showed that a heavy preponderance of western aspen acreage is dominated by pole and sawtimber-sized trees, which, for this species, means mature and overmature timber. Young stands are not common.

Factors Influencing Fires in Aspen

During a sampled 14-year period on national forests in Colorado, most fires in aspen were found to be caused by people. Only 16% were started by lightning, compared to 57% of fires started by lightning in coniferous forests. October was the month with the most fires in aspen (Ryan 1976). In Colorado, not only are the weather and fuel often dry in October, it is also the month with the most hunting.

Houston (1973) briefly reviewed human factors that he believed were important in reducing burning late in the 19th century, in the Yellowstone National Park area. Although recently expanded use of the area has the potential to increase burning, current fire prevention campaigns and sophisticated suppression programs generally keep fire to a minimum.

When conditions are dry enough in aspen stands with a dense understory of conifers or shrubs, the abundance, chemistry, and vertical distribution of the fuel may favor a hot fire with rapid spread (fig. 4). In most aspen stands, however, the stocking of young conifers or shrubs is absent to moderate. In these stands, fuel largely consists of dead herbaceous material, fallen leaves,

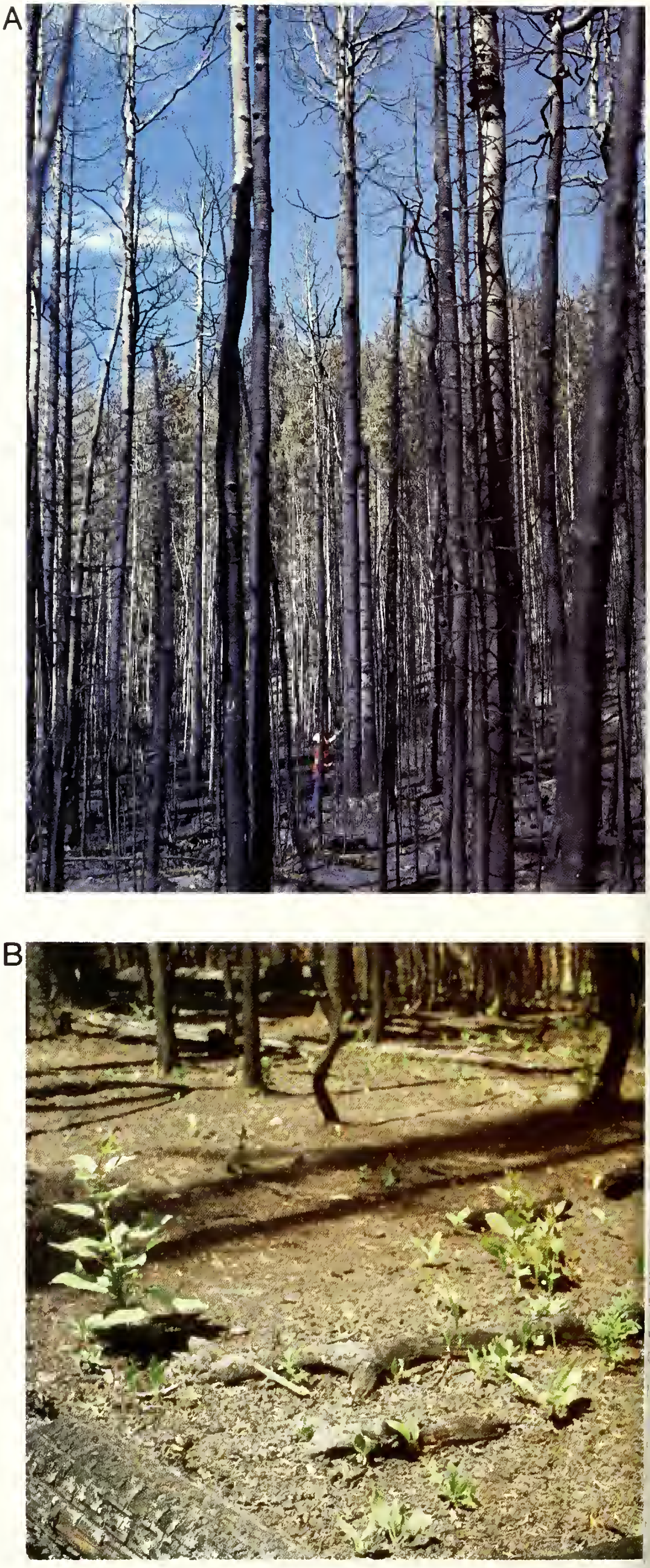

Figure 3.—(A) A wildfire in June killed this mixed forest of aspen, lodgepole pine, and other conifers. (B) The scattered aspen trees in this forest produced enough aspen suckers by the end of that growing season to largely restock the site.

downed timber, and any shrubs or conifers that may be present. These fuels often are not abundant, and usually are not in a condition to burn. Under suitable conditions, fires in them may spread fairly rapidly but are not as intense as is common in coniferous forests.

Baker (1925) credited livestock use with major fuel reductions under aspen in the late 19th and early 20th centuries, when fire suppression was much less effective than it is today. Overgrazing by sheep was widespread, and by late summer there were little herbaceous fuels left beneath the aspen.

However, sheep grazing has become less common and less intense in aspen forests. Since about 1940, cattle have replaced sheep on many acres of western range. Where grassland is available, cattle do not use the nearby aspen stands as heavily as sheep once did. Heavy herbaceous stands are more common beneath aspen canopies. However, grazing still annually reduces the supply of fine fuels in most of the western aspen forest land (fig. 5). Without these fine herbaceous fuels, fire seldom burns through the aspen forest.

The combination of dry weather and cured fuels in the aspen forest does not occur every year. Most frequently, it occurs in the autumn, sometimes in late summer, and occasionally in spring. Late September and October can be wet, but often have periods of dry, sunny weather. By then, the herbaceous understory is frozen and dead, is still largely upright, and can burn readily. Also, the aspen canopy loses its leaves in late September and October. If conditions are dry, a continuous layer of loosely packed, fine fuels develops, making the aspen forest most flammable in this season. In most years, however, aspen leaf-fall and the first heavy, wet snowfall of autumn coincide in much of the aspen range, particularly in the north. The fall fire season ends when the winter snows come. These normally cover the ground from late October or November until April or May.

In much of the West, May and June are normally moist or wet. In Arizona and New Mexico, however, west of the Sangre de Cristo crest, May and June constitute the major fire season in coniferous forests. The weather is sunny, dry, and windy. However, in aspen stands without a coniferous understory, conditions then are much less favorable than is common in autumn. The previous year's dead forbs, grass, and fallen leaves form a low matted layer (fig. 6); and in the shade of June's new foliage, a fresh green herbaceous layer begins to develop that is essentially nonflammable. The May-June dry season is followed by the summer monsoon of July and August, with high humidities, frequent showers, and few fires.

Beneath aspen in the West, the litter layer from the previous autumn largely decays by mid-July. In the absence of a coniferous understory, there is little that will burn until the herbaceous undergrowth dies and dries in the late summer or autumn.

In the subalpine zone, coniferous understories are common beneath aspen; but the climate is not conducive to fires. Drying is slow. Snow may cover the ground in September or October, and may remain far into May or later. After the late snowmelt, green-up is very rapid.

Figure 4.—(A) An intense prescribed fire in September killed all the aspen in this pure stand with a shrub understory. Most trees were crown-killed as well as girdled. More than 50% of the fine fuels and 66% of the forest floor were consumed. Bare soil exposure increased from 3% to 35%. (B) One year later, this site had almost a complete cover of herbaceous plants. At the end of this first postburn growing season, there were about 1,250 pounds per acre (1,400 kg/ha) of grasses and forbs.

Even in Minnesota and Ontario, where a substantial layer of duff commonly is present for fuel (Alway and Kittredge 1933), conditions suitable for fire in aspen are infrequent (Buckman and Blankenship 1965, Horton and Hopkins 1965, Perala 1974b).

Aspen Response to Fire

Although aspen forests do not burn readily, aspen trees are extremely sensitive to fire. Baker (1925) noted that very light fires kill aspen, because its bark is thin and green, with no protecting corky layers (fig. 7). He also stated that basal scars, which lead to destructive heart rot, are made on good-sized trees by the lightest of fires. Davidson et al. (1959) and Meinecke (1929) also pointed out the seriousness of fire scars as a cause of rot in aspen.

Despite the difficulty of getting fire to burn through aspen stands, the very sensitivity of the species, especially that of young trees, apparently would make repeated prescribed fires a viable tool for eliminating aspen from a site. For example, Buckman and Blankenship (1965) found that reburning sucker stands in Minnesota markedly reduced the abundance and vigor of suckering. Two spring burns reduced sucker populations 68%, three burns 86%, and four burns 94% from the number found after only one spring burn. However, Perala (1974b) concluded that repeated dormant season burning was a poor tool for converting aspen to conifers, largely because fire was so undependable. He found that a spring burn killed only 42% of 21,000 2-year-old suckers per acre (52,000 per ha). A more effective burn in the autumn killed all the woody vegetation; but suckering was substantial 1 year later.

Bailey and Anderson (1979) tried to control aspen on sandy rangelands in Alberta, using a combination of fire and herbicides. Despite marginal success, they recommended burning as a desirable option if applied at about 4-year intervals. In a later article, Anderson and Bailey (1980) reported that 24 years of annual spring burning checked the invasion of aspen into grassland, reduced shrub and forest cover, but actually increased the numbers and cover of aspen suckers on the area.

A fire intense enough to kill the aspen overstory will stimulate abundant suckering (fig. 8); but some suckers will arise after any fire. For example, Maini and Horton (1966b) reported substantial suckering on burned plots whether or not the aspen canopy was removed. They suggested soil heating as the cause. However, the vigor of suckers growing under a live overstory is likely to be poor, as Barmore (1968) found in Yellowstone National Park after a light fire that killed existing suckers, the understory conifers, but few of the overstory aspen.

A severe fire removes the insulating duff, blackens the soil surface, and permits more solar radiation to effectively warm the mineral soil. A very severe fire also may kill roots in the surface 0.75-1 inch (2-3 cm) of soil (Horton and Hopkins 1965). Either or both of these effects may have contributed to the findings of Schier and Campbell (1978a), who reported an average suckering depth of 4 inches (10 cm) under a severe burn (more than 90% of the litter and duff consumed) as compared to 2.5-3 inches (6-7 cm) under a moderate burn in Wyoming. Removal of all organic debris and exposure of bare mineral soil by fire also provides an ideal seedbed for the possibility of aspen seedling establishment.

Figure 5.—Grazing by cattle or sheep reduces fine fuels in the aspen understory, which, in turn, reduces the flammability of the aspen forest.

Figure 6.—As illustrated in this vertical view, the matted forest floor in a typical aspen stand just after snowmelt in spring does not carry fire, especially after rapid greenup begins.

Figure 7.—A surface fire that burns around the base of aspen trees girdles and kills this thin-barked species.

Severe or repeated fires may have a detrimental effect on site quality. Stoeckeler (1948) attributed a 6- to 25-foot reduction in site index and reduced understory production to repeated burns in Lake States aspen. Horton and Hopkins (1965) and Perala (1974a), also reported poorer sucker growth on severely burned sites in Ontario and Minnesota, respectively. Severely burned sites in Wyoming produced the most suckers 2 years after the fire, as compared to 1 year after on the moderately to lightly burned sites (Bartos 1979, Bartos and Mueggler 1979). Most authors reported about equal numbers of suckers on both moderate and severe burns; but vigor and quality may be affected.

It appears that a moderate intensity fire that kills most or all the overstory will stimulate very adequate suckering and will have the least effect on subsequent sucker growth. From 12,100 to 60,700 suckers per acre (30,000 to 150,000 per ha) were produced after burning

Figure 8.—A dense sucker stand 3 years after fire killed the pure aspen overstory.

Figure 9.—Fire on this relatively dry site in western Wyoming rejuvenated this derelict stand of aspen. There were about 12,000 suckers per acre and about 3,200 pounds per acre of understory production in this second postburn year.

several sites in western Wyoming (Bartos 1979), certainly enough to adequately regenerate aspen on those sites (fig. 9).Also, after an initial decline during the first postburn year, Bartos (1979) and Bartos and Mueggler (1979) measured an increase in herbage production for several years on these burned sites.

If fire occurs at infrequent intervals (e.g., 50 years) (Baker 1925) and is moderately intense enough to kill most or all of the aspen and competing conifers, most aspen sites in the West will retain viable stands of aspen. More frequent fires may adversely affect site quality for aspen. Complete fire protection, however, will permit coniferous species to take over the majority of sites. In summary, fire is a natural feature in much of the aspen ecosystem of western North America. It is responsible for the abundance of aspen in the West and for the even-aged structure of most stands. Without human intervention, fire appears to be necessary for the continued well-being of aspen on most sites where aspen is seral.

OTHER PHYSICAL FACTORS

John R. Jones and Norbert V. DeByle

Light

Aspen has been recognized for many years as being very intolerant of shade (Baker 1918a, Clements 1910, Weigle and Frothingham 1911, Zon and Graves 1911). In dense stands, vigorous aspen trees are confined to the dominant and codominant crown classes. Regardless of size, when they are overtopped by larger trees, aspen trees deteriorate and eventually die. Many well-stocked, even-aged aspen stands have virtually no aspen regeneration beneath them, even in the form of small ephemeral suckers (Beetle 1974, Jones 1974b). In contrast, healthy coniferous seedlings may be plentiful under the densest aspen canopies. Paucity of suckers in an aspen stand, however, is only partly a result of reduced light; it also is partly a matter of apical dominance and of low temperatures in the shaded soils. (See the VEGETATIVE REGENERATION chapter for a fuller discussion of suckering physiology.)

Light Intensity

Often, well-stocked even-aged stands have many ephemeral suckers. These arise, reach heights of a few inches, die, and are replaced (Baker 1918a), often without being noticed. Some suckers may arise annually; but sufficient light is needed for successful development of viable saplings. Strain (1964) found maximum photosynthetic rates in two California clones at about 10,000 foot-candles—equivalent to a bright sunny day near sea level. At 6,000 foot-candles, photosynthesis was 80-95%; at 2,000 foot-candles it was still about 50% of maximum. Development of independent roots on suckers was found to be greater with increasing light intensity from 25% to 100% of full sunlight (Sandberg 1951, Sandberg and Schneider 1953). Under more open canopies, suckers persist longer and grow larger. Under old aspen stands in advanced stages of deterioration, canopies have as much gaps as crowns, and many suckers reach large sapling size. (See the stand structure discussion in the MORPHOLOGY chapter for more details.)

The number of suckers that regenerate after partial cutting of an aspen stand varies with degree of overstory removal. In Maine, Weigle and Frothingham (1911) followed the development of suckers that came in after timber cuttings that reduced the canopy to different densities. Light cutting produced a few suckers; these soon died. Moderate cutting produced abundant suckers; these subsequently dwindled and died, too. Only when almost the entire canopy was removed and the suckers were given nearly full light was a uniform and vigorous sucker stand produced. Suckers under residual canopy trees do not do well, even where stands are heavily cut. Baker (1925) counted suckers in different light regimes in Utah. At 50% of full sunlight, there were only about 6% as many suckers per acre as on a clearcut, and they were much smaller.

After a fire or clearcut, most of the suckers which start in full sunlight are subsequently overtopped by more vigorous neighbors (Jones 1975, Jones and Trujillo 1975a, Pollard 1971). These overtopped and suppressed suckers progressively decline and finally die.

Photoperiods

Light can have other effects on aspen besides providing the primary energy source for photosynthesis. Using seedlings from two sources grown under uniform temperatures and near-optimum moisture, Vaartaja (1960) found that photoperiod differences were accompanied by differences in growth, with seedlings from the two sources differing greatly in response. Bate and Canvin (1971) induced dormancy in Ontario seedlings with 4 to 6 weeks of 8-hour light period. In the forest, however, dormancy would be induced in the autumn by lower temperatures before the period of daylight shortened to 8 hours.

Sunscald

Mature aspen trunks are likely to sunscald if they are exposed abruptly to a large increase in sunlight. Stems on the north side of clearcuts, those remaining after heavy thinning (Hubbard 1972), and those exposed by construction of campsites and roads (Hinds 1976) are likely candidates. Strain (1964) suggested that susceptibility to sunscald may vary with the amount of loose waxy periderm cells ("bloom") on the surface of the bark. The reflectivity of aspen bark differs with the amount, and probably the color, of that bloom. The amount and color of bloom differs among genotypes. On most clones, the amount also varies somewhat with the time of year. Covington (1975) felt that production of bloom was a function of temperature, and pointed out that it was greater on the south sides of trunks than on the north. He reported that it was increased by increased exposure to sunlight.

Wind

Aspen Blowdown

Occasionally, wind can have somewhat the same impact as a severe forest fire. For example, in 1958, an exceptional storm blew down 1,300 acres (500 ha) of mixed spruce, fir, and aspen forest on the Kaibab Plateau, in northern Arizona. After usable timber had been salvaged and the debris disposed of, aspen suckers came up over much of the area (Russo 1964).

Ordinarily, however, aspen is relatively windfirm. Trees with root rot or heartrot usually are the ones blown down (Baker 1925). Most blowdown of aspen in the West is windthrow—the trees tip over instead of breaking off above the ground. At least in Colorado, most trees that blow down have butts and roots rotted by *Ganoderma applanatum (Fomes applanatus)* (Davidson et al. 1959, Landis and Evans 1974).

Resistance to blowdown is largely a matter of mutual protection. An old, heavily stocked, mixed conifer stand in Arizona, with scattered large old aspen, was cut very heavily in summer (fig. 1) (Gottfried and Jones 1975). The aspen were left. Most of the large aspen blew down during a series of storms in October. On adjacent unlogged areas, few aspen blew down despite decay, wind, and saturated soils.

Other Effects of Wind

Wind has other effects on aspen besides blowing trees down. Basham (1958) suggested that trees swaying in storms may break small aspen roots, thereby providing entrances for root diseases. Fralish (1972) wrote: "Exposure to wind is nearly as important in influencing aspen growth as soil water-holding capacity and water table depth. Isolated stands and stands located on ridge tops have lower site indices because of higher internal wind velocities. In general, protected stands, whether in valleys, between ridges, or surrounded by forest, have higher site indices than unprotected stands, other factors being equal."

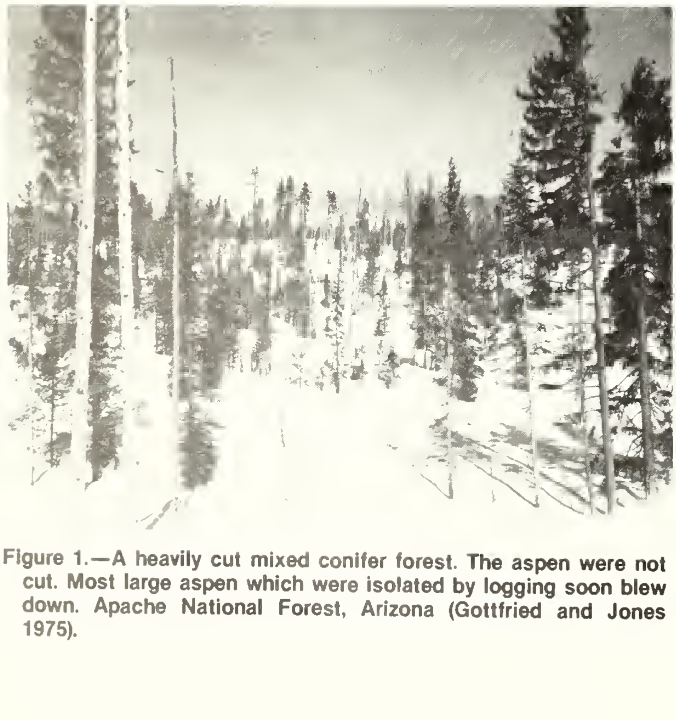

Figure 1.—A heavily cut mixed conifer forest. The aspen were not cut. Most large aspen which were isolated by logging soon blew down. Apache National Forest, Arizona (Gottfried and Jones 1975).

Beetle (1974) wrote that, in Wyoming, aspen height growth was strongly inhibited where the trees were exposed to wind. "On sheltered sites [aspen] trees grow much taller than on similar, neighboring unsheltered sites. The formation of doghair stands suggests that climatic suppression causes hormonal stimulation similar to that caused by browsing of the terminal shoot."

Despite the observations by Fralish (1972) and Beetle (1974), which seem reasonable, there are no known data concerning wind effects on the growth or behavior of standing aspen. Where an aspen stand is isolated on an open, windswept area, there may be reasons other than wind for the openness of the area and the small size of the aspen.

In the foothills of southern Alberta, aspen often is damaged by warm dry Chinook (fohn) winds in winter. When the trees break dormancy the next spring, the leaves cluster at the tips of the branches; all the buds on older parts of the trees are dead.[1]

Branches sometimes are broken by wind. These may scar the trunks and provide infection points for pathogens (Hinds and Krebill 1975).

Air Movement Within Stands

Wind conditions inside a stand are much different than those outside. Marston (1956) reported total air movement in a stunted Utah stand of aspen was only 21% as much as in an adjacent meadow. High velocities were reduced the most. In October, after leaf fall, air movement increased, but still was markedly less in the aspen stand than in the meadow. In two Wyoming stands, Turlo (1963) reported that summer windspeeds averaged only 7% and 16% of those in adjacent openings. Rauner (1958) reported on winds above and within a well-stocked, 55-foot (17-m) tall, two-storied stand of aspen and birch in Russia. When the wind was 5.5 mph (8.8 km per hour) at twice the canopy height, it was 2.2 mph (3.5 km per hour) at the canopy top, and zero at 26 feet (8 m) and 5 feet (1.5 m) above the ground. When 21.5 mph (34.6 km per hour) at twice canopy height, it was 11.2 mph (18 km per hour) at the top of the canopy, 2.7 mph (4.3 km per hour) at 26 feet (8 m), and 1.3 mph (2.1 km per hour) at 5 feet (1.5 m).

Snow Damage

Snowstorms are infrequent when aspen are in full leaf. Extensive damage may result if the snow is wet and clings to aspen crowns. Limbs often break. Whole trees of sapling to pole size may be broken off, bent to the

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[1] *Personal communication from A. K. Hellum, University of Alberta.*

Figure 2.—Approximately 1 foot (30 cm) of wet snow on September 17-18, 1978 damaged aspen stands throughout northern Utah and southeastern Idaho. This photo was taken 2 weeks later, on the Caribou national Forest, near Preston, Idaho.

Figure 3.—Several years after the September 1978 snowstorm, damage to many aspen stands still was very evident, as illustrated in this 1981 photo.

ground, and sometimes partially uprooted. Such bending is permanent in the larger trees. Snowstorms in early September, before formation of a leaf abscission layer, most frequently cause such damage. Late spring storms are likely causes, too. A storm in the Wasatch Mountains of northern Utah and southern Idaho in September 1978 illustrated this impact (fig. 2). Several inches of wet snow weighed down, broke, and bent over aspen throughout these mountains. Some stands were devastated; the damage was still very evident 3 years later (fig. 3). In contrast, during dormancy large aspen are relatively immune from such damage. For example, freezing rain in winter in Manitoba deposited a heavy layer of ice on tree branches. About 12 inches (30 cm) of snow fell just after that. Many conifers were bent and broken; but aspen, bare of leaves at the time, suffered only minor damage (Cayford and Haig 1961).

Snow damage to seedling-size aspen is more common and more insidious than damage to large trees in the West. Usually any aspen trees shorter than 4 to 8 feet (1 m to 2 m) become entirely buried as deep snowpacks develop during a typical winter on mountain slopes. As the snowpacks creep downhill, they frequently bend these small stems to the ground, producing the characteristic pistol butt on aspen growing on mountain slopes (fig. 4). Even on level terrain, settling of the snowpack, particularly if ice lenses have formed in it, breaks branches and sometimes stems (fig. 5).

Figure 4.—Aspen on mountain slopes in the West are commonly pistol butted because of flattening by snow creep during their youth.

Figure 5.—Burial of aspen suckers under deep snowpacks, even on relatively level terrain, sometimes can be disastrous when the pack settles. These suckers were sampled from a clearcut on the Wasatch National Forest, in northern Utah.

Hail and Lightning

Riley (1953) described an aspen stand in Saskatchewan in which the crowns had been heavily damaged by a severe hail storm. Some trees were killed. Survivors suffered many bark bruises on the upwind side, marked by black callus overgrowths, which led to increased insect and fungal attacks. Severe hail damage to aspen also has been reported from the Great Lakes region (Basham 1953, Thomas 1956). However, hail damage in the western mountains appears to be rare; such storms are very unusual there.

Meinecke (1929) reported that in Utah, lightning scars were "negligible" on live aspen. Hinds and Krebill (1975) stated that aspen struck by lightning usually were killed. They felt that lightning should be suspected when groups of aspen die suddenly, especially if one of the group has a lightning scar.

DISEASES

Thomas E. Hinds

Although many diseases attack aspen, relatively few kill or seriously injure living trees. The common leaf diseases, in general, are widely distributed throughout the range of aspen, whereas there are subtle differences in distribution between the important decay fungi, and apparently entirely different areas of distribution of major canker-causing organisms. However, there still are large gaps in knowledge of the disease organisms and their influence on natural and regenerated stands.

Foliage Diseases

Fungus Diseases

Many fungi are capable of attacking aspen leaves, from juvenile growth to senescence. However, only a few may be of local significance; and even then, their damage is of consequence only when they cause moderate to severe defoliation. Small trees suffer the most damage, and may be killed by repeated infections. Clonal susceptibility to individual foliage diseases is common (fig. 1); but under certain conditions, whole stands can become infected. Because these fungi kill small to large areas of leaves and often cause premature defoliation, their damage is usually confined to reduced tree growth of severely infected trees. Therefore, in most areas, these diseases are not important in aspen management (Christensen et al. 1951).

Although control of leaf diseases in forest stands has not been attempted because of their slight impact upon growth, suitable protective fungicides are available which allow a certain measure of control for more valuable trees in nurseries, plantations, and urban areas. Because some aspen clones are highly susceptible to foliage diseases, cuttings or root sprouts to be used for propagation should be taken from the less susceptible or apparently immune clones.

Black leaf spot.—This disease, caused by *Marssonina populi* (Lib.) Magn., is the most common leaf disease of quaking aspen in the West. Small brownish spots appear on the infected leaves in late July and early August. The spots later enlarge and turn blackish, and are of various sizes and irregular in outline, with a yellowish to golden border (fig. 2A). The leaves often are smaller than normal, and fall prematurely. Infection is usually more severe on smaller trees and in the lower crowns of larger trees. Light infection is common in many western stands, and clonal susceptibility to intense leaf spot is very noticeable. Epidemic conditions are intensified by abundant rainfall in the spring and summer, possibly followed by warm temperatures for about 1 week. Infection sometimes is widespread, covering several hundred acres (Harniss and Nelson 1984, Mielke 1957). Twig and branch mortality after two severe infection years has been reported (Harniss and Nelson 1984, Mielke 1957). These epidemic situations may kill trees. However, the effect of leaf spot on overall aspen mortality is assumed

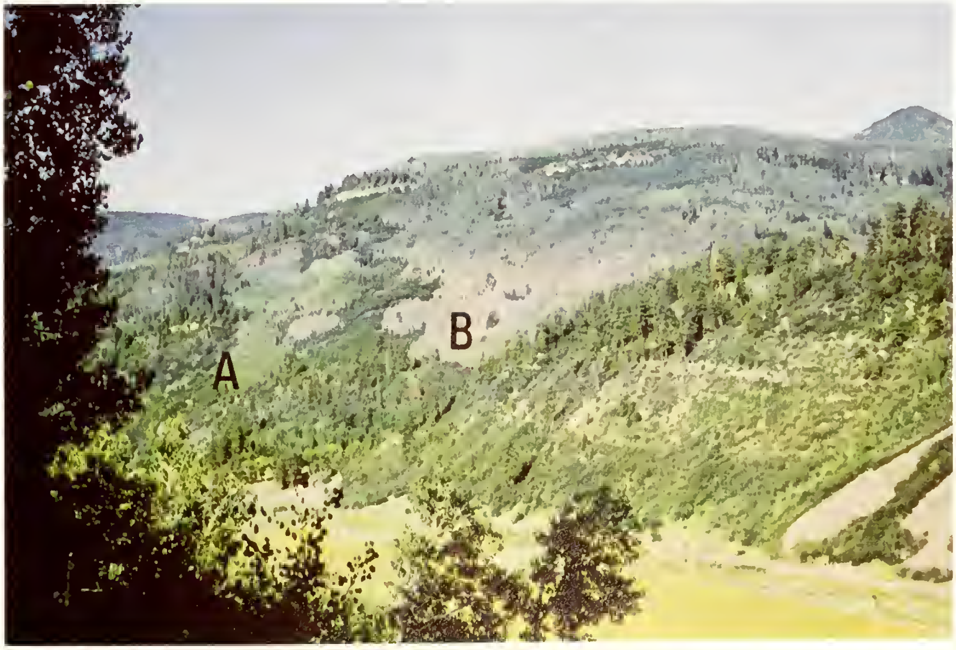

Figure 1.—Aspen stands in August, exhibiting various degrees of clonal susceptibility to infection by *Ciborinia whetzelii*. (A) Resistant clone with green leaves. (B) Heavily infected clones with brownish infected areas.

to be of little consequence, because successive epidemic years are unusual, and even then, mortality appears to be light. In most years, the annual infection repeats only in the lower crown, and usually late in the growing season.

Ink spot.—This disease is caused by two or more species of *Ciborinia* (Groves and Bowerman 1955). *Ciborinia whetzelii* (Seaver) Seaver (*Sclerotina bifrons*), the most common, is found throughout the West, where it occasionally kills 50% of the foliage over extensive areas (Baranyay and Hiratsuka 1967, Ehrlich 1942, Hartley and Hahn 1920). Leaves are infected in the spring by ascospores produced on apothecia that have developed on overwintering sclerotia on the ground. By midsummer, the infected leaves turn brown, and the black sclerotia, called ink spots (fig. 2B), which are circular to ellipsoid in shape and up to several millimeters across, begin to drop from the leaves, leaving holes. Early defoliation follows; however, it is not unusual for the dead leaves bearing sclerotia and holes to persist until autumn. The disease is more severe on smaller trees and in the lower crowns of larger trees. Some clones appear to be more susceptible than others.

Shepherds crook.—*Pollaccia radiosa* (Lib.) Bald. & Cif., the imperfect stage of *Venturia macularis* (Fr.) E. Muller and Von Arx (*V. tremulae*, Barr 1968), most frequently is associated with the leaf and twig blight commonly called "shepherd's crook" (fig. 2C). Primary infections initiated by conidia, and ascospores from perithecia which occasionally develop on old blighted shoots, appear as small black spots in mid-May. The spots enlarge until the fungus kills the leaf, and it then spreads down the petiole causing dieback, curling, and blackening new terminal shoots (Dance 1961). Secondary infections appear late in May on other shoots and leaves, multiplying rapidly, until most shoots and leaves of terminal growth are infected. Seedlings and suckers are severely attacked, killing or deforming their terminal growth. The disease can be controlled by applying the fungicide benomyl (methyl 1-[butyl-carbamoyl]-2-benzimidazole carbamate) at 2- to 3-week intervals during the growing season (Anderson and Anderson 1980).

Leaf rusts.—These occur sporadically throughout the forests; the conifer-aspen rust *Melampsora medusae* Thuem. (*M. albertensis*) is the most common (Ziller 1965). The rust does not survive on aspen leaves; it must have a conifer alternate host, such as larch, Douglas-fir, pine, true fir, spruce, or hemlock, to complete its life cycle (Ziller 1974). In the spring, germinating teliospores that have overwintered in the dead aspen leaves on the

Figure 2.—(A) Black leaf spot caused by *Marssonia populi*, with yellowish golden border. (B) Ink spot of aspen with black sclerotia of the fungus formed in the leaves. (C) "Shepherds crook" (*Pollaccia radiosa*) associated with terminal leaf and stem necrosis.

ground, release basidiospores that infect the alternate host. Wind-disseminated aeciospores produced on the alternate host then infect aspen leaves in the summer, causing yellow spots and the formation of orange-yellow urediospores, which, in turn, reinfect more leaves. Late in the summer, masses of teliospores are produced on the underside of the leaf beneath the yellow spots. Premature defoliation may or may not occur (Hartley and Hahn 1920, Ziller 1974), and, although the leaf tissue dies, damage in aspen stands is not considered serious.

Powdery mildew.—This disease, caused by *Erysiphe cichoracearum* DC. ex Merat and *Uncinula salicis* (DC. ex Merat) Wint., is often found on lower leaves of small trees and sprouts after periods of high moisture. Although the fungi are widespread (Meinecke 1929, Shaw 1973, USDA 1960), they appear to act as saprophytes on debilitated leaves and are normally considered to be of minor importance.

Roadside Salt Damage

Although foliar damage to aspen caused by winter road salting is not considered a disease in the strictest sense, it is included here, because the symptoms of chloride toxicity may appear to be caused by disease. Symptoms of salt damage to aspen along roads begin to show up in late August. By mid-September, the leaves in the lower crowns of the larger trees appear smaller than normal, with their margins somewhat curled and discolored reddish-brown (fig. 3A). The discoloration may encompass up to two-thirds of the leaf area. Smaller trees are more affected, and their entire crowns appear reddish. Tree decline or mortality associated with aspen salt damage has not been studied.

Shortle and Rich (1970) considered quaking aspen in southeastern New Hampshire to be relatively salt-tolerant. There, uninjured roadside trees had leaves containing a chloride content (dry weight) of 0.78% in comparison to 0.12% in healthy woodlot trees. In New Mexico, Gosz found that aspen trees along a roadside showed symptoms in September, when the chloride content of some trees reached a maximum of 2.9% (dry weight).[1] However, values as low as 0.6% were found in some trees exhibiting stress symptoms. Leaves of trees alongside an unsalted road contained only 0.14% chloride. Damage differences were found between individual locations and within groups of trees in a single area, which indicated a possible genetic difference in susceptibility. Various road and site characteristics influence the road salt distribution into forested areas and the accumulation of chloride by leaves (Gosz,[1] Piatt and Krause 1974).

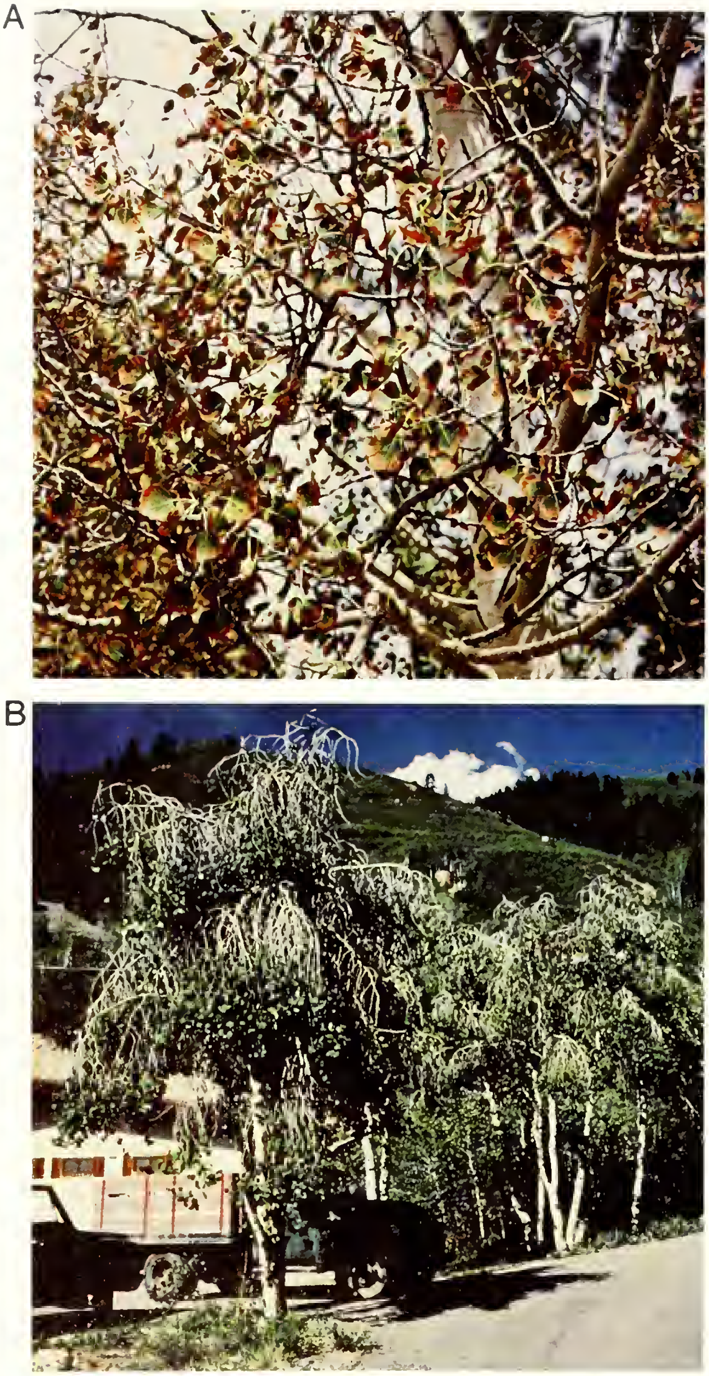

Figure 3.—(A) Bronze foliage damage of roadside aspen caused by chloride toxicity resulting from using a sand-salt mixture on the road during the winter. (B) "Droopy aspen." The symptoms of pendulous branches and lack of lateral growth existed before road construction.

Virus and Virus-like Diseases

Viruses and systemic pathogens (mycoplasms, rickettsia, flagellates) are the least understood in aspen pathology. Because they are far more difficult to recover from trees than from herbaceous plants and the research on them is more difficult and time-consuming than is research on ordinary pathogens, very few tree

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[1] *Gosz, James R. 1974. Effects of road surfacing and salting on roadside vegetation in New Mexico mountain areas. 32 p. Research Agreement 16-361-CA, Eisenhower Consortium for Western Environmental Forestry Research. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo.*

pathologists have studied these diseases and their effects upon forest trees. However, because the importance of virus and virus-like diseases in the intensive culture of hybrid aspen and other poplars is becoming more significant in plantations established for the production of wood fiber, more research on their recognition and diagnosis might be expected in the future.

Boyer (1962) reported a necrotic leaf spot disease of hybrid and native aspen in Ontario, transmitted by grafting and by insects under conditions that suggested it may be caused by a virus. Although a further study did not determine the infectious agent (Boyer and Navratil 1970), it has been speculated that the disease very likely is present and widespread in the United States (Berbee et al. 1976). Navratil (1979) later observed virus and virus-like diseases of poplar in Ontario and Saskatchewan between 1972 and 1976. The necrotic leaf spot was not found; however, he reported poplar mosaic virus (PMV) on various hybrids, and, although it was suspicious on aspen, it was not confirmed. A vein mottling of aspen leaves also recognized as a virus-like disorder was found in locations associated with human activities and believed to have been introduced into those areas.

Although the Canadian virus and virus-like disorders have not been reported in the United States, virus-like decline symptoms in aspen clones and in Aigeiros (cottonwoods) are being investigated. An apparently new poplar virus belonging to the potato virus Y group was recovered from five different Aigeiros clones in Wisconsin, and an isolate that may be identical, was recovered from a deteriorating aspen clone (Berbee et al. 1976).

Martin et al. (1982) isolated a virus in the potyvirus group from *Populus* spp. and four declining, native aspen clones in Wisconsin. The decline symptoms included necrotic leaf spots early in the growing season, with leaf bronzing symptoms scattered throughout the crown in late July and August. Branches with bronzed leaves died the next year. The symptoms were observed throughout Wisconsin. Transmission trials established that the virus was a pathogen of poplars, including *P. tremuloides*. Similar leaf bronzing symptoms have been observed on aspen at Fallen Leaf Lake, south of Lake Tahoe, California.

The role of viruses in deterioration of aspen clones in the West, characterized by trees with low vigor, poor form, increased mortality, and scarce regeneration, has received some attention (Schier 1975a). Foliar symptoms of infection include chlorotic spots, line patterns, and abnormalities in size, color, and shape. Hibben et al. (1979) isolated a tobacco necrosis virus (TNV-A) from 5 of 33 clones with symptoms indicative of virus infection. Two additional isolates of TNV autigenically dissimilar to TNV-A and to each other also were recovered. The low rate of TNV recovery from the deteriorating clones was insufficient to implicate the virus as a cause of deterioration. The importance of virus or virus-like diseases in natural stands of aspen in the West is unknown. Other causal factors, such as site conditions, stand age, genotype, insects and diseases, browsing, and apical dominance, all contribute to clonal deterioration (Hibben et al. 1979) and overshadow the role of viruses.

Droopy Aspen

"Droopy aspen" is a fairly descriptive term for the symptoms of this disorder. Affected trees are characterized by flexuous-rubbery, pendulous branches throughout the crowns of small trees; in larger trees, the secondary branches are symptomatic (fig. 3B). The affected branches have shortened internodes and enlarged nodes, a lack of lateral twig growth and foliage for the preceding 5 to 20 or more years, and larger than usual terminal leaves. After 20 or more years, the pendant branches die, and, depending upon the severity of infection and tree size, the entire tree succumbs. Although these abnormal trees usually are seen along roadsides, in campgrounds, and as transplants in urban areas and mountain communities, single trees and small groups are found in forest areas not associated with human activities.

The symptoms do not appear to be clonal in nature. Droopy aspen have been observed in Colorado, New Mexico, and Utah, but not in Alaska or Wisconsin, suggesting that this malady may be unique to the southern Rocky Mountain region (Hinds and Laurent 1978, Livingston et al. 1979). Preliminary studies failed to reveal any virus particles or mycoplasma-like bodies associated with the symptoms; the cause or causal agents of droopy aspen remain unknown (Livingston et al. 1979).

Aspen Decay

Tree decay has long been recognized as important to aspen management (Baker 1925, Weigle and Frothingham 1911). Essentially, merchantable volume lost to decay increases with age; but this age factor varies between the Northeast and the West.

While trees grow faster in the Great Lakes area, they also deteriorate and decay earlier. The mean annual growth of aspen stands in northern Minnesota, on average sites, culminates in about 50 years, which indicates a pathological rotation of from 40 to 50 years for production of mass products (Schmitz and Jackson 1927). Volume lost to decay amounted to 4.8% at 30 years, 7.8% at 40 years, 11.4% at 50 years, and 15.7% at 60 years. To minimize losses to insects and diseases, recommended rotations for aspen stands there now range from about 30 years on poor sites to 50 or 60 years on good sites (Brinkman and Roe 1975).

In the Upper Pic region of Ontario, Basham (1958 found decay in 69% of the trees on 47 plots. Merchantable volume loss was 13.1%. Trees with heart rot in the merchantable portion of the bole increased steadily from 26.7% in stands at age class 41-60 to 100% in stand age class 161-180. Two types of stain were recorded: a red-mottled stain, which occupied approximately 2% of the total tree volume at all ages, and a brown stain, which increased from about 10% in stands 41-60 years old to more than 20% in stands older than 120 years. A later comparison between gross and net volumes per acre showed that, whereas the gross merchantable volume per acre was greater at 100 years, the net merchantable volume was at a maximum at 90 years (Basham 1960). The mean annual increment reached a peak value at 60 years for both gross and net volumes.

The results of a more comprehensive cull study covering a larger area in Ontario showed there was a marked uniformity in the percentages of the total merchantable volume defective at similar age classes in the two studies, although there was a lower rot/stain ratio in the Upper Pic sample. Variations in the extent of decay on four sites, based mainly on the availability of soil moisture, were not pronounced, although stands on deep, sandy silts or loams, or on shallow, sandy loams over impervious material, generally were less defective than stands on drier or wetter sites. Similar conclusions were made earlier regarding aspen stands in Wisconsin and Minnesota (Stoeckeler 1948).

In Alberta, slightly more decay is present on wet than dry sites because of the increased activity of *Fomes igniarius* on the wet areas (Thomas et al. 1960). During a study of 835 living aspen (Thomas et al. 1960), an overall volume loss of 25% was found in 73% of the trees with decay. Butt infections accounted for 31.5% of the infections (10.8% of the rot volume), and trunk infections for 68.5% (89.2% of the rot volume).

In the West, Baker (1925) recommended a pathological rotation age of about 110 years for aspen growing on the better sites in central Utah, based on the net maximum volume. Meinecke (1929), however, from the same study data, recommended a rotation age of about 80-90 years, on the basis of net volume production and net increment. In Meinecke's study, decay accounted for 6% of the gross volume in the age class 61-70, 18% in the class 101-110 age and from 10% to 41% in the older age classes. Decay amounted to 18% of the gross merchantable volume.

In a broader study of decay in typical commercial aspen forests, Davidson et al. (1959) found decay in 53% of the trees (8.4% of the gross volume) dissected on 35 plots, in five national forests, in Colorado. Although there was little relationship between decay and site class for the younger stands, the differences were marked in stands more than 100 years old. In 100-year-old stands, cubic foot decay averaged 4% on site 1 (the better site), 8% on site 2, and 13% on site 3. The incidence of decay was lower than that reported by Meinecke (1929) for Utah. Decay volumes in the older age classes varied from 7% to 27%.

The merchantability of aspen on a board foot basis was analyzed later from the Colorado study (Hinds and Wengert 1977). Incidence of decay and cull, based on Baker's (1925) site quality classes, plotted as a function of 10-year age classes, showed linear relationships. Tree infection increased with age, and the percentage of cull at tree age 100 amounted to 21% and 25% on sites 1 and 2, respectively. The variation of cull in trees on site 3 was too large to obtain a significant relationship. It was concluded that, before decay data can be applied to stands, the age distribution of the merchantable trees must be known.

Aspen is extremely susceptible to attacks by fungi; however, most wood-destroying fungi are only capable of infecting a wound to the wood. Because it is often difficult to determine the exact mode of entrance of a fungus causing heart rot, the association of external indicators with decay frequently is based upon general observations. Although some are reasonably accurate, definite figures for the frequency of infection often are questionable.

As early as the 1920s, infection was associated with fire scars, branch scars, insect injuries, and grazing (Hofer 1920, Schmitz and Jackson 1927). Basham (1958) suggested that most of the fungi responsible for butt rots probably enter through roots, and that only a minority originate from basal wounds, such as fire scars, frost cracks, and branch stubs. Approximately 90% of the trunk rots in his study were traced to dead, broken branch stubs; a few entered in forked crowns, frost cracks, and mechanical injuries. Extensive heart rot was associated with 84% of the pronounced trunk wounds, indicating that they were fairly reliable indicators of heart rot. Basham (1958) also suggested that "preliminary fungi," not generally associated with advanced decay, invade and colonize the heartwood before the "principal fungi" causing advanced decay become established.

Meinecke (1929) analyzed 255 open and closed wounds and found 126 decay infections. Incidence of infection was fire scars, 88%; bruises, 33%; dead and broken tops, 19%; ingrown stubs, 60%; frost cracks, 17%; and undetermined wounds, 20%.

Etheridge (1961) studied the cause of infection in living and dead branches of aspen to obtain information regarding the time and conditions under which dead branches might serve as entrance points for heart rot fungi. He found that a higher incidence of branch infections were on wet sites; young branches were more prone to infection than old branches; and there were at least three successive stages of infection by different organisms before heart rot fungi became established (8 to 12 years after branch mortality). Because *F. igniarius* appeared only rarely in the succession, and then as lateral extensions of heartwood infections after 19 years, it was suggested that bark wounding constituted its main avenue of infection into the heartwood of aspen.

The most reliable external indication of decay in aspen is the appearance of *Phellinus tremulae* (*Fomes igniarius*) fruiting bodies (fig. 4A), often called sporophores or conks, which usually project from branch stubs or old wounds. Basham (1958) found conks on 86% of the infected trees. Hinds and Wengert (1977) reported 75% of the merchantable size trees with scalable cull attributed to the fungus had these external indicators of decay. Cull averaged 82% of the gross tree volume when conks were present, whereas infected trees without conks averaged 40% cull. The extent of decay as indicated by the presence of conks has been reported for Ontario (Riley and Bier 1936), Minnesota (Horton and Hendee 1934), and Colorado, where the average length of decay above and below the highest and lowest conk was 12.0 ± 0.7 feet (3.7 m ± 21 cm) (Hinds 1963). A system for predicting the amount of *P. tremulae* trunk rot in 45- to 50-year-old stands in the Lake States has been developed. Aspen stands older than about 40 years there are subject to breakup because of the decay (Anderson and Schipper 1978). This early stand breakup has not been reported in the West.

Cull resulting from decay varies greatly in unmanaged aspen stands in the West. The tree age difference in many uneven-aged stands accounts for much of the cull variation. Decay is usually more prevalent in the older trees; the greater the proportion is of older trees in a stand, the greater are the decay losses.

The fungi causing cull in the older stands are likely to be found in the younger stands, also. However, their impact on volume losses should not be as great in the regenerated stands, and their relative importance may change when even-aged stands become more prevalent.

Decay Fungi

More than 250 species of wood-decaying basidiomycetes have been recorded on aspen in North America (Lindsey and Gilbertson 1978). However, only about 25 species are considered important in the decay of dead standing or fallen trees, and a dozen or more in the decay in living trees. Much of the following information was derived from the only broadly based, quantitative decay study of live aspen in the West (Davidson et al. 1959).

Trunk Rots

Since 1909, *Phellinus tremulae* (Bond.) Bond. et Borris (*Fomes igniarius* var. *populinus*) has been recognized as the predominant aspen trunk rot fungus in North America (Schrenk and Spaulding 1909). Although the decay is usually considered a white trunk rot or white heart rot (fig. 4B), it frequently occurs in the basal portion of a tree but seldom, if ever, in the root system (Schmitz and Jackson 1927, Ross 1976a). The false tinder fungus is essentially a wound parasite; infection takes place through wounds to the sapwood and heartwood (Etheridge 1961, Manion and French 1968, Riley 1952). Numerous other fungi are associated with the decay, and many are assumed to be precursors of *P. tremulae* (Good and Nelson 1962, Shigo 1963).

In the West, *P. tremulae* is also the major cause of volume loss. Meinecke (1929) considered it the most important individual factor causing the 18% decay cull in his Utah study; however, he did not give specific information on the decay fungi. Although the incidence of trunk infection by *Peniophora polygonia* (Pers. ex Fr.) Bourd. et Galz. was greater (28%) than that of *Phellinus tremulae* (26%) in a Colorado decay study (Davidson et al. 1959), *P. tremulae* was responsible for 59.1% of the

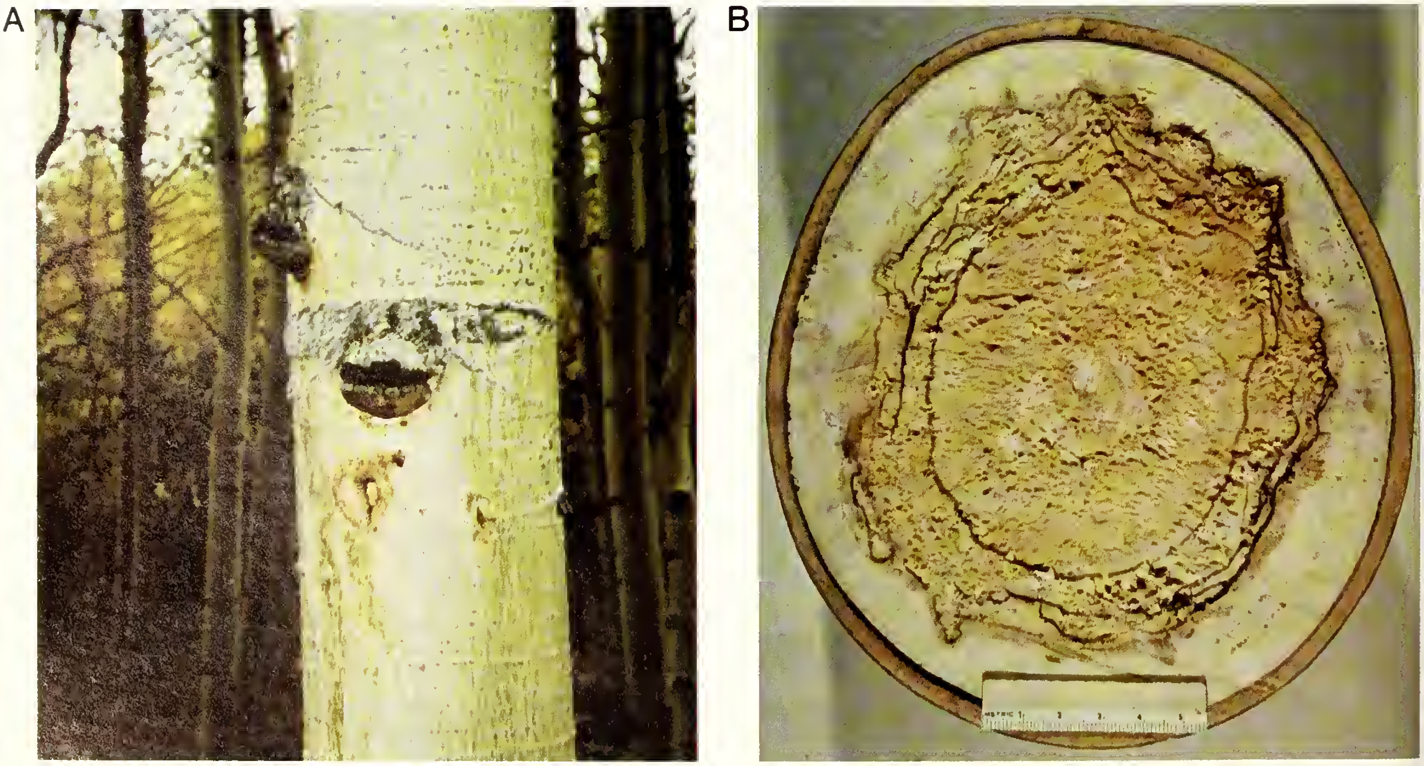

Figure 4.—(A) Conks of the false tinder fungus on the trunk indicate extensive trunk rot. (B) Cross section of a live 7-inch (17-cm) diameter aspen with *Phellinus tremulae* trunk rot.

cubic foot decay volume, compared to 9.6% for *Peniophora polygonia*. On a linear volume basis, *P. tremulae* loss amounted to 10.2% of the gross volume (33.8% of the rot volume) and was found in 15% of the trees larger than 8 inches (20 cm) d.b.h. (Hinds and Wengert 1977). Trees infected with the fungus had an average of 70% cull.

There is no apparent relationship between site and cubic foot volume of *P. tremulae* decay, although the incidence and amount of decay increases with stand age (Riley 1952) and may vary among clones (Wall 1969). In one area of Ontario, 28-69% of the trees in stands 60-70 years old were infected (Riley 1952), whereas 42% of the trees 41-180 years old in the Upper Pic region were infected (Basham 1958). Decay attributed to this fungus has amounted to 75% of the decay volume in Ontario (Basham 1958) and 35% in Alberta (Thomas et al. 1960), in contrast to 59% in Colorado. Total cubic foot volume losses attributed to *P. tremulae* in stands 41-180 years old range from 6.4% in Ontario to 3.6% in Colorado.

Peniophora polygonia (Pers. ex Fr.) Bourd. et Galz. (*Cryptochaete polygonia, Corticium polygonium*) usually is associated with a brown stain with a reddish-brown margin suggestive of an incipient stage of decay, which later develops into a yellow, stringy decay in older trees (fig. 5A). The stain, or incipient stage, is common in young trees 30-50 years of age (Basham 1958, LaFlamme and Lortie 1973), and, while rarely encountered in trees older than 120 years in Ontario (Basham and Morawski 1964, Thomas et al. 1960), it is common in older trees in Colorado.

The fungus enters through branch stubs or wounds (Fritz 1954), occurs more frequently on wet than on dry sites, and is one of the earliest decayers to colonize dead branches (Etheridge 1961). The incidence of tree infection is sometimes greater than that of *Phellinus tremulae* (Basham and Morawski 1964, Davidson et al. 1959, Thomas et al. 1960) but seldom causes extensive decay losses. In Alberta, the fungus was associated with 18.9% of the decay infections but only 14.3% of the decay volume (Thomas et al. 1960). It was the most common trunk rot encountered in Colorado aspen, where it accounted for 28.3% of the decay infections but only 9.6% of the decay volume (Davidson et al. 1959). Because the incipient stage of decay is more common, and when sawn lengthwise does not fall out, it is usually considered stain, and the cull is much less than that scaled (Hinds and Wengert 1977).

The third most common trunk rot of quaking aspen in the West is probably that caused by *Libertella* sp. Only recently has the asexual form of this Deuteromycete been associated with its sexual form, *Cryptosphaeria populina* (Pers.) Sacc., the canker fungus (Hinds 1981). *Libertella* sp. has been consistently associated with stain, discoloration, and decay of aspen and other poplars (Basham 1958, 1960; Fritz 1954; Thomas et al. 1960). The fungus has been implicated as an early colonizer of dead branches preceding the wood-destroying basidiomycetes (Etheridge 1961) and one of many fungi associated with *P. tremulae* decay (Good and Nelson 1962, Shigo 1963). The fungus was associated with a red-mottled stain in Ontario aspen (Basham 1958), where it was the main defect in many mature and overmature trees. The stain occupied approximately 2% of the total tree volume. Although Basham (1958) did not find advanced decay associated with *Libertella*, and Thomas et al. (1960) questioned the decay status of the fungus, other studies by Fritz (1954), Hinds (1981), and Ross (1976a) clearly indicate the ability of the fungus to cause decay.

Various hues of gray, brown, yellow, orange, and even pink are associated with the white-mottled trunk rot of *Libertella* sp. (fig. 5B). Decay was found in 7.8% of 449 trees sampled in Colorado, where it amounted to 0.8% of the gross cubic foot tree volume (Hinds 1981). Sixty-one percent of the infections were associated with dead or broken tops, living and dead branches, and trunk wounds mainly in the midtrunk and upper trunk areas. The fungus has also been associated with advanced root decay (Ross 1976a). Tree infection decreases from the best to the poorest sites, and increases with tree diameter size. It is speculated that infection takes longer to kill trees by cankers in the larger trees on good sites, whereas smaller trees on poorer sites succumb to the disease faster.

Other trunk decay fungi reported to cause cull in live aspen in the West are *Antrodia serialis* (Fr.) Donk (*Tremetes serialis*), *Daldinia concentrica* (Fr.) Cs. & De Not., *Inonotus rheades* (Pers.) Bond. et Sing. (*Polyporus dryophilus* var. *vulpinus*), and *Sistotrema brinkmannii* (Bres.) J. Erikss. (*Trechispora brinkmannii*). Because these fungi cause only slight amounts of cull, they are considered to be of little consequence (Hinds and Wengert 1977).

Root and Butt Rots

More species of decay fungi are associated with root and butt decay than with trunk decay; however, the amount of decay involved usually is much less. Although basal decay may amount to only 11-24% of the total decay volume in aspen (Davidson et al. 1959, Thomas et al. 1960), some of the fungi involved cause extensive decay of the roots, predisposing trees to early mortality and windthrow.

Flammulina velutipes (Curt. ex Fr.) Sing. (*Collybia velutipes*) causes the most frequently encountered butt rot in aspen in Colorado, and is responsible for the most butt cull (Hinds and Wengert 1977). It causes a brown-mottled white rot, which frequently is associated with basal wounds. Decay columns may extend above 16 feet (5 m) in older trees; however, the average length was 10 feet (3 m).

Ganoderma applanatum (Pers. ex Wallr.) Pat. (*Fomes applanatus*) is found in almost all aspen stands but is more common on moist sites with deep soils (Hedgcock 1914, Ross 1976a). Infection occurs at wounds; the fungus attacks sapwood, heartwood, and cambium. The white-mottled rot usually is concentrated in the large roots and basal part of the stem; however, it often extends up into the trunk for several feet (fig. 5C). Fruiting

Figure 5.—(A) *Peniophora polygonia* trunk rot in cross section. (B) *Libertella* discoloration and decay associated with large branch stub (scale is cm). (C) *Ganoderma applanatum* causing extensive butt rot with the artist conk fruiting at the base of the live tree (scale is 1 foot (30 cm)). (D) Windthrown aspen with broken roots decayed by *G. applanatum*.

bodies of the fungus, frequently found at the base of an infected tree, indicate extensive butt rot. Root rot is restricted to roots larger than 2.5 inches (6 cm) in diameter, indicating that only large roots might act as avenues of spread to new hosts (Ross 1976b). Because of this, rot centers may occur more frequently on good sites, because large roots there are further from infected trees.

Ganoderma applanatum eventually rots entire cross sections of larger roots, and windthrow is common in mature aspen stands in the Rocky Mountains (fig. 5D). Trees in infection centers on good sites often blow down in groups, whereas single, isolated trees go down on medium and poor sites (Ross 1976a). Although the loss caused by decay may be small—it amounted to 6.3% of the cubic foot decay volume in Colorado (Davidson et al. 1959)—windthrow losses may be considerably greater. Windthrow in overstory aspen 100-120 years old, caused by a windstorm in the San Juan Mountains of southwestern Colorado, resulted in a loss of 2.3% of the bolewood biomass of the stand (Landis and Evans 1974). Sporophores of the fungus were found on 86% of the downed trees that were larger than 6 inches (15 cm) d.b.h., but were only on 5.2% of the remaining standing trees, indicating a relationship between windthrow and occurrence of the fungus.

While of secondary importance, *Pholiota squarrosa* (Fr.) Kumm., *Pleurotus ostreatus* Fr., and *Sistotrema raduloides* (Karst.) Donk. (*Trechispora raduloides*) cause basal white rots that often extend into the larger roots (Davidson et al. 1959). Although *Pholiota squarrosa* appears to be more common, the amount of decay they all cause is about equal, and none appear to be as parasitic as *G. applanatum*. Other white rot fungi associated with minor amounts of butt rot in living trees include *Armillariella mellea* (Vahl ex Fr.) Karst. (*Armillaria mellea*), *Bjerkandera adusta* (Willd. ex Fr.) Karst. (*Polyporus adustus*), *Hirschioporus pargamenus* (Fr.) Bond. et Sing. (*Polyporus pargamenus*), *Radulodon americanus* Ryv. (*Radulum casearium*), and *Pleurotus elongatipes* Pk. (*Tricholoma unifactum*). One or more species of *Coniophora* are associated with brown butt rots, which are fairly common, and *Coprinus atramentarius* (Fr.) Fr. with brown cubical root and butt rot (Ross 1976a). Sporophores of the various root and butt fungi, although not numerous, often are found at the base or on the ground at the base of an infected tree, indicating butt rot.

Armillariella mellea, the "shoe-string" or "honey mushroom" fungus, is one of the most consistently reported root and butt decays of aspen in North America. Although numerous infections are usually associated with only minor amounts of decay (Davidson et al. 1959, LaFlamme and Lortie 1973, Ross 1976a, Thomas et al. 1960), Basham (1958) considered it one of the two principal causes of butt rot in northern Ontario aspen. The fungus is widespread on many species of forest trees, usually as a saprophyte; but it is capable of killing trees of subnormal vigor by destroying the roots. Diseased trees may appear in groups that increase in size as more trees are attacked, or as individuals scattered throughout a stand. Its effect in aspen stands has not been studied; but observations indicate that its effects may be similar. Ives et al. (1974) reported that approximately 50% of the mature aspen at the campsite in Crimson Lake Provincial Park, in the Prairies Region of Canada, had been killed by the fungus; and Hinds and Laurent (1978) noted that *A. mellea* and insect borers were associated with the extensive mortality of saplings covering several acres on a poor site, at the Bonanza Creek Experimental Forest, in interior Alaska. Observations by Hinds in the southern Rocky Mountains indicate that the fact that some stand openings have no reproduction may be attributed to this root disease. Large dead and live trees surrounding such openings are infected with *A. mellea*. As the disease spreads outward, somewhat in a circular manner, the root systems are killed; sprouts are not formed or are too weak to grow; and peripheral trees eventually die or are windthrown.

Other fungi that have been associated with root diseases of aspen in Wyoming include an *Ascocoryne* sp., *Phialophora* sp., *Talaromyces vermiculatus* (Dang.) C. R. Benjamin, and *Satorya fumigata* Vuill. (Ross 1976a).

Stain or Discoloration

Estimates of the amount of stain, or discoloration, in quaking aspen in the West are not available; however, studies in Ontario indicate it could be considerable, and of more importance in regenerated stands than presently acknowledged (Basham and Navratil 1975). In Ontario, 76% of the stems on a 5-year-old cutover were affected by a light-to-dark brown stain (Smith 1973); and the incidence of stain in 23-year-old cutover stands amounted to 84% for a defect of 1.4% (Kemperman et al. 1976). The volume of stain within the merchantable portion of trees in a 41- to 60-year age class, in uncut stands in the same general area, was earlier found to amount to 12.6% of the volume, and increased to 24.6% in trees in a 161- to 180-year age class (Basham 1958).

Stain discolorations include hues of black, brown, red, yellow, and green in both heartwood and sapwood. Because stain normally affects lumber quality rather than quantity, cull usually is not deducted when the stain is firm and light in color.[2] Many hymenomycetes (decay fungi), ascomycetes, fungi imperfecti, bacteria, and yeast are associated with the various discolorations (Basham 1958, Etheridge 1961, Good and Nelson 1962, Kemperman et al. 1976, LaFlamme and Lortie 1973, Shigo 1963); yet, trees can discolor at wounds even without microorganisms (Sucoff et al. 1967).

The role of microorganisms in discolored aspen is not completely understood. A succession of organisms takes place in the discoloration and decay in living trees (Shigo 1967). Etheridge (1961) provided a good account of the succession in branch infections in aspen. Shigo and Larson (1969) expanded the concept to other hardwoods. Basically, a tree reacts to wounding by chemical changes taking place in the wounded tissues, resulting in discoloration; bacteria and nondecay fungi then become active before the decay fungi.

Wetwood

The term "wetwood" usually is applied to a water-soaked condition of wood in living trees. It is found in many tree species and is common in aspen and other *Populus* species (Hartley et al. 1961, Ward and Pong 1980). Wetwood zones in aspen can be in the heartwood or sapwood, or extend into both, but usually are limited to the inner growth rings between heartwood and sapwood. Wetwood also is found in roots (Sachs et al. 1974). Wetwood areas usually are somewhat darker than the surrounding tissues; they often have a fermentation odor; and the high moisture content makes it easier to

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[2] *U.S. Department of Agriculture, Forest Service. 1970. National Forest log scaling handbook. Forest Service Handbook FSH-2409.11. 193 p. Washington, D.C.*

detect them on freshly cut cross sections. Trees with wetwood are common in some aspen stands, while they are rare in others. While the discolored zones usually are not associated with decay columns, they have been associated with wood borer tunnels, frost cracks, and wounds in which decay was present (Davidson et al. 1959).

The moisture content, pH, and mineral content of wetwood is considerably higher than that of normal heartwood and sapwood (Clausen et al. 1949, Hartley et al. 1961). Phycomycetes, yeasts, and numerous bacterial species consistently have been isolated from wetwood; however, because bacteria are also found in the wood of normal aspen, their role in the formation of wetwood is not clear (Bacon and Mead 1971, Etheridge 1961, Knutson 1973, Sachs et al. 1974, Seliskar 1952).

More recently, Sachs et al. (1974), using a scanning electron microscope (SEM), compared observations with cultures of wetwood from bigtooth aspen (*Populus grandidentata*), white poplar (*Populus alba*), and cottonwood (*Populus* spp.). Although bacterial populations were isolated from the inner sapwood, they were not as numerous or as diverse as those from wetwood. The SEM supplied information not easily obtained by the culture techniques, and showed that the bacteria invaded the vessel lumina of aging sapwood and selectively attacked the vessel-to-ray pit membranes. Their observations suggested that wetwood occurs after invasion of sapwood by bacteria, presumably from initial root infections, and can be characterized under the SEM as a bacterial degradation of the pit membranes.

The mechanical properties of wetwood differ from that of normal wood. In addition to having a higher moisture content, the wood is lower in specific gravity, in toughness, and in compression strength, and is impervious to the passage of air and water (Clausen and Kaufert 1952, Clausen et al. 1949, Haygreen and Wong 1966). Because the wetwood zones are weaker than normal sapwood, collapse at the zone between heartwood and sapwood in aspen lumber during kiln-drying can cause serious defect. Collapse in air-seasoned lumber is not as serious.

Disease symptoms are associated with wetwood in Lombardy poplar (*Populus nigra* var. *italica*) and cottonwoods (Hartley et al. 1961). They include branch dieback and crown wilting, usually in August and particularly during dry summers, often resulting in premature death. Wounds and dead bark with underlying wetwood also bleed. In such cases, wetwood is found in large branches and in most of the lower part of the trunk, including portions of the current year's growth. These symptoms have not been associated with aspen decline or mortality.

Cankers

Trunk canker is the most obvious disease problem of aspen in the West. Because the bark is soft and living, the tree is extremely susceptible to damage and subsequent attacks by canker-causing fungi. Perennial cankers are the most important, because they gradually enlarge until they girdle and kill the tree. Although some cankers may never girdle the infected trunk, it becomes so deformed that it is useless for commercial purposes. As early as 1920, Hartley and Hahn considered trunk lesions and cankers to be the most serious damage to aspen in the Pike's Peak area, even though they were unable to identify them (Hartley and Hahn 1920).

Two studies in Colorado (Hinds 1964, Juzwik et al. 1978) were made to determine the distribution and abundance of the different aspen cankers in western stands. Based on 30 sites (two 0.04-ha plots each) within nine national forests, canker frequency on a site basis was sooty-bark, 93%; Cryptosphaeria, 83%; and Ceratocystis, 80%. Canker incidence on 2,873 live trees was sooty-bark, 1.1%; Cryptosphaeria, 1.1%; and Ceratocystis, 4.4%. More than one-half (55%) of the 13% tree mortality found during the survey was attributed to sooty-bark canker and one-fourth (26%) to Cryptosphaeria canker. Ceratocystis canker was found on only 8.9% of the dead trees, but was not considered responsible for tree mortality in every case. Hypoxylon canker was not on the sites examined. However, it was observed in one forest. This is not too surprising, because it was found only on 13% of the plots, on 0.2% of the living trees, and on 2% of the dead trees (Hinds 1964). Information on Cytospora canker was included by Hinds (1964); but, because it is so commonly associated with wounds, other cankers, and trees weakened by other causes, it was eliminated as a serious canker disease from the later survey by Juzwik et al. (1978).

Host records, observations, and collections made throughout the western United States indicate a general distribution of these aspen cankers, with the exception of Hypoxylon canker.

Canker infection resulting from wounding of live trees, and subsequent tree mortality can increase dramatically in managed stands. Walters et al. (1982) found a 19% mortality of residual live trees in partially cut stands, in New Mexico and Colorado, 5 to 7 years after harvest. Trunk cankers infecting logging wounds were one of the major causes of tree death. Forty percent of the remaining residual trees were infected by the various cankers, indicating that tree mortality would continue to increase.

Sooty-bark Canker

Sooty-bark canker, caused by *Cenangium singulare* (Rehm) Davidson and Cash, is the most lethal canker of aspen in the West (fig. 6A). The fungus was first collected in Colorado in 1888 (Ellis and Everhart 1888); but, it was not consistently associated with a canker until 1956 (Davidson and Cash 1956), and was not proven to be the causal agent until 1962 (Hinds 1962). The canker has been collected in all of the Rocky Mountain states from New Mexico (Andrews and Eslyn 1960) northward to Alaska (Hinds and Laurent 1978). It also has been found in Arizona, California, Nevada, Oregon, and in North Dakota and South Dakota eastward to Minnesota

Figure 6.—Sooty-bark canker. (A) Large aspen in center with typical elliptical shaped, 6-year-old canker, and smaller trees girdled within 3 years without typical canker symptoms. (B) Black, stringy, dead bark. (C) Black, net-like patterns where the fungus mats retain the dead bark to the sapwood for several years. (D) Apothecia (fruiting structures) of the fungus found on dead bark (scale is mm).

(Hinds and Anderson 1970), Michigan, and New Hampshire (Davidson and Cash 1956). In western Canada, it has been collected on aspen in Alberta, British Columbia (Tripp et al. 1975), and the Yukon Territory (Hinds and Laurent 1978).

Although the cankers sometimes start at points where there is no apparent injury (Davidson and Cash 1956), the fungus infects trunk wounds (Hinds 1976, Krebill 1972), penetrates the inner bark and cambium, and spreads rapidly. Cankers can extend to 40 inches (1 m) in length in 1 year, and 12 feet (4 m) in length by 29 inches (74 cm) in width in 4 years (Hinds 1962). Trees of all sizes are killed, usually within 3 to 10 years.

Young cankers first appear on aspen bark as slightly sunken oval areas with blackened inner bark. The fungus invades bark tissue so rapidly that a prominent callus formation is unusual. The bark area killed by the fungus can be seen each succeeding year by the expansion of the original sunken area. The dead bark epidermis begins to slough off after 2 or 3 years, exposing the blackened inner bark, which has become a uniform sooty black (fig. 6B). Because the epidermis sloughs off quicker in the central portions, the cankers assume a somewhat concentric zoned pattern. The thicker inner bark remains tightly attached to the wood for several years, even after the tree dies and falls. It eventually sloughs off in long stringy strips, revealing black netlike patterns on the trunk where fungus mats held the dead bark to the wood (fig. 6C).

The canker has been termed "sooty-bark canker," because the dead bark easily crumbles to a sooty-like residue when handled. The wood behind the canker tends to dry out and, consequently, usually is not decayed; however, wind breakage at the canker point is not unusual. The wood is light gray and exhibits various patterns of yellow fluorescence under ultraviolet light.

A phytotoxin has been implicated in causing canker. While working with a phytotoxin produced by the Hypoxylon canker fungus, Schipper (1978) also found a toxin produced by C. *singulare*. The toxin reactions of both fungi were similar, as measured by an aspen leaf bioassy; and the two toxins migrated in almost identical manner on thin-layer chromatography plates.

Apothecia (fruiting bodies) of the fungus usually appear on bark that has been dead for at least 1 year (fig. 6D). The light gray apothecia are about 1-2 mm in diameter, angular to hysteroid in shape, and open when they become wet. The spores formed on the surface are forcibly ejected and wind disseminated when moisture and temperature conditions are favorable.

Numerous fruiting primodia (pycnidia) are found penetrating through the epidermis around the perimeter of infection, in the spring, before apothecia form. The epidermis sloughs off during the summer, and the pycnidia disintegrate. Whether or not this form is the asexual stage of the fungus remains to be determined. Small insects often are present and may feed on these fruiting bodies (Davidson and Cash 1956).

Nematodes are common in the necrotic tissues of sooty-bark canker. Most are closely related to nematodes known to be insect associates. The nematodes probably are carried to the diseased trees by various species of *Epurea*, and may be a factor in the etiology or pathogenesis of the cankers (Massey and Hinds 1970).

Sooty-bark canker is found mainly on the larger dominant and codominant trees older than 60 years, in the middle elevational limits of aspen (Davidson and Cash 1956, Hinds 1964, Juzwik et al. 1978). Although it occurs on trees as small as 2 inches (5 cm) in diameter, the infection is atypical in that it girdles the stem in 1 or 2 years and the canker is not obvious; only the sooty-bark is present. Apothecia production is rare, possibly because of the thinner bark on the smaller trees. Cankers are more common in stands disturbed by partial cutting (Walters et al. 1982), construction (Hinds 1976), or animal damage (Krebill 1972).

Black Canker

Black canker, caused by *Ceratocystis fimbriata* Ell. & Halst., is the common name given to this canker (Boyce 1948), which was described by Long (1918), although he realized that it was not caused by *Cytospora chrysosperma* (Long 1918). Baker (1925) found similar cankers of unknown origin plentiful in areas throughout the Rocky Mountain region; Meinecke (1929) published the first photographs of them in 1929. Wood and French (1963) first reported that *Ceratocystis fimbriata* was associated with a similar canker on aspen in Minnesota and that the fungus was capable of attacking aspen sprouts and causing canker. Soon thereafter, the association was reported in Pennsylvania (Wood 1964), Colorado (Hinds 1964), and the Provinces of Quebec (Ouellette 1965), Manitoba, and Saskatchewan in Canada (Laut and Hildahl 1965).

With the exception of *Cytospora* infection, this is the most common canker of aspen throughout its range in the western United States. It is not uncommon to find that 50-75% of the trees in small areas have numerous cankers (figs 7A, 7B). Cankers are common in stands in Arizona, Colorado, New Mexico, Utah, and Wyoming (Hinds 1972a). Specimens also have been collected from California, Idaho, Nevada, Oregon, Montana, South Dakota, and from the Turtle Mountains in North Dakota eastward to Minnesota (Hinds and Anderson 1970) and north to British Columbia, the Yukon Territory, and Alaska (Hinds and Laurent 1978).

Ceratocystis fimbriata can infect through the epidermis of leaf blades, petioles, and young stems (Zalasky 1965); but trunk wounds are considered to be the primary places of infection (Hinds 1972a). Infection first appears as a circular necrotic area on the trunk around a fresh wound or branch junction. During cambial growth in the spring, the tree forms a callus at the margins of the canker, which temporarily walls off the infection. The fungus invades the new cambium and inner bark during the tree's next dormant season, and kills a new zone of tissue. This process is repeated each year until the canker, consisting of successive rings of dead bark and wood, is formed.

Figure 7.—Black canker. (A) A young stand heavily infected with canker. (B) An older stand with numerous older trunk cankers. (C) Cankers initiated at 12-year-old trunk injuries. (D) A young canker of about 24 years (bottom) and an old canker of about 59 years (top) on an 83-year-old aspen. (E) Old canker which originated along the sides of a basal wound.

Small cankers are young, are typically oval or elliptical, and appear "target shaped." The dead bark usually adheres to the wood for several years; then it begins to slough off, exposing successive rings of dead woody tissue (fig. 7C). The canker grows faster vertically than horizontally; and the height-width ratio increases with age. Because the tree generally grows in circumference faster than the canker enlarges, cankers seldom kill large trees, unless one or more coalesce. Infection is frequently callused off at various places on the canker margin. Older cankers typically have a central area of dead wood surrounded by a series of bark calluses. These callused areas may be concentric in outline, but usually are irregularly shaped and ragged in appearance because of the massive callus folds and flaring dead bark (fig. 7D). The canker face and dead bark tissue adjacent to the canker is usually black—therefore, the name "black canker."

Black perithecia of the fungus often are hard to find. They form along the canker perimeter in the spring, on wood or bark that has been dead for at least 1 year. Ascospores are forced out of the perithecia necks in a sticky mass and can be accidentally picked up by insects inhabiting the canker. Although perithecia frequently are consumed by insects, and some are disintegrated by sap flow and rain, remnants of perithecial bases can remain for several years. Perithecia of *C. alba* DeVay, Davidson, & Moller, *C. crassivaginata* Griffin, *C. populina* Hinds & Davidson, and *C. tremulo-aurea* Davidson & Hinds often coexist with those of *C. fimbriata* (Hinds 1972a). Past, unreported inoculation studies utilizing these other species of *Ceratocystis* revealed that they were incapable of causing perennial canker.

Insects burrow along the canker edges. Some pupate in the bark crevices, while others overwinter in cankers of all ages. The disease is thus transmitted by insects that visit new wounds. Nitidulid beetles (sap-feeding beetles) are considered to be the principal vectors (Hinds 1972b). However, *C. fimbriata* also can overwinter with beetle pupae in the soil, with the adults capable of spreading infection to new wounds in the spring, when they emerge.

The major impact of black canker is trunk deformity and cull (Meinecke 1929) not mortality, because infected trees survive for a long time (fig. 7E). Cankers 78 years old and older have been found on trees that were 103 years old (Hinds 1972a). A brown stain and wetwood extending into the heartwood above and below the canker's limit usually is present in the tree trunk. On older trees infected with wood decay fungi, sporophores are produced in the dead portion of the canker, and wood beneath such cankers is decayed.

Cryptosphaeria Canker

This canker is a relative newcomer to the list of aspen cankers. Although the fungus *Cryptosphaeria populina* was collected on dead aspen bark near Golden, Colo., by E. Bethel in 1897, it was not associated with a canker until 1969 (Hinds 1981). In northwestern Wyoming, Krebill (1972) found the canker on 2% of the sampled trees which had been damaged by big game in the Gros Ventre elk winter range. Examining trees wounded by campers, Hinds (1976) later found the canker on 2% of the live and 8% of the dead trees surrounding aspen campsites in Colorado. This incidence of infection in wounded trees was nearly double that found by Juzwik et al. (1978) in natural stands.

The canker has been found in the northern states of Coahuila and Chihuahua in Mexico (Hawksworth and Tovar 1983), northward in the Rocky Mountains from Arizona and New Mexico to Idaho, British Columbia, the Yukon Territory, and Alaska (Hinds and Laurent 1978). The fungus also has been reported in the Lake States area and on other poplar hosts (Hinds 1981).

The cankers, usually associated with trunk wounds, are long and narrow (fig. 8A). They may be only 2 to 4 inches (5 cm to 10 cm) wide, yet up to 10 feet (3 m) or more long, following the grain of the underlying wood. Annual lateral extension of the canker margin may be only several millimeters per year, but it may be several centimeters or more in the vertical direction. Small trees die several years after infection and before the trunk is girdled. Branch cankers often are found on large trees, where they girdle the branch and enlarge onto the trunk. *Cytospora chrysosperma* frequently is found along the canker perimeter, and is quick to colonize the remaining bark after tree death.

The infected bark around the perimeter of a canker is discolored light brown to orange. Annual callus formation by the host in an attempt to limit bark infection is obvious after 2 or more years. The dead bark adheres tightly to the sapwood. Bark that has been dead for more than 1 year is black, stringy, and sooty-like, similar to sooty-bark canker. However, they are easy to distinguish, because the dead bark contains small, lenticular, light-colored areas, varying from 0.5 to 2.0 mm in size (fig. 8B). Perithecia of the fungus are formed within an effused pseudostroma, beneath the dead bark periderm, in the central portion of the bark that has been dead for at least 1 year (fig. 8C). Light orange acervuli of the imperfect *Libertella* stage occasionally are found in the advanced portion of the canker.

The fungus infects fresh wounds in the inner bark and wood, colonizing sapwood and heartwood, and causing discoloration and decay before it penetrates the bark, causing canker (fig. 8D). Inoculation studies have shown that *Cryptosphaeria populina* is capable of killing branches and sprouts within 1 year; saplings in 2 years; and causing cankers ranging up to 3 inches by 13 inches (7 cm by 33 cm), with sapwood discoloration extending up to 13 feet (4 m) beneath the canker, after 4 years, in larger trees. This discoloration, in hues of gray, brown, yellow, orange, and even pink, usually extends up to 3 feet (1 m) or more beyond the vertical extent of the canker, and is associated with the *Libertella* stage of decay.

Figure 8.—Cryptosphaeria canker. (A) Elongate cankers at 5-year-old trunk wounds on 12-inch (30-cm) diameter aspens. (B) Lenticular light-colored areas in the dead, black bark. (C) Current year's perithecia formation under dead bark epidermis (left); epidermis removed (right) to show perithecia formed the previous year (scale is cm). (D) Sapwood discoloration with cambium and bark necrosis preceding canker formation. (E) Cross section through canker (right side) with discoloration and brown mottle trunk decay (scale is cm). (F) Fluorescence of cross section (B) under ultraviolet light.

Cytospora Canker

This canker, caused by *Valsa sordida* Nit., usually is referred to as Cytospora canker, because the imperfect stage of the fungus *Cytospora chrysosperma* (Pers.) Fr. is more commonly encountered (Christensen 1940). Long (1918) described the canker on poplar, and also found it on aspen in Arizona and New Mexico. It is the most common fungus found on aspen throughout its range. The fungus is considered a normal inhabitant of aspen bark microflora. It readily enters and parasitizes bark that has been injured or weakened by any cause (Hubert 1920, Long 1918, Povah 1921).

Infection takes place through bark wounds or dying twigs. The bark invaded by the fungus may be either regular or very irregular in outline. Infection can be so general on small branches, twigs, sprouts, and small trees that a definite canker is not formed (fig. 9A). Trunk cankers are formed by a gradual killing of the bark in a more or less circular area, over a period of several years (fig. 9B). Annual canker growth can be seen by the slight annual callus formation around the perimeter of infection, which usually is sunken. The diseased inner bark turns dark brown to black, and the sapwood beneath is stained light brown. The dead bark remains attached to the tree for 2 or 3 years. It then turns lighter brown in color and falls off in large pieces.

The fungus fruits readily in the dead outer bark, even when typical canker symptoms fail to develop. Pycnidia—small, black, fruiting bodies of the *Cytospora* stage—are the most common. Sticky pycniospores ooze out of the pycnidia in long, coiled, orange to dark red masses called spore tendrils, spore horns, or cirri (fig. 9C). During rains, the spores are partially washed away, leaving sticky masses of spores about the openings. They then dry to hard, hemispherical, colored masses. The *Valsa* stage also is common on aspen (fig. 9D). Flask-shaped perithecia are formed beneath and in a circle around the old pycnidia (Christensen 1940). Some ascospores are forcibly discharged; others

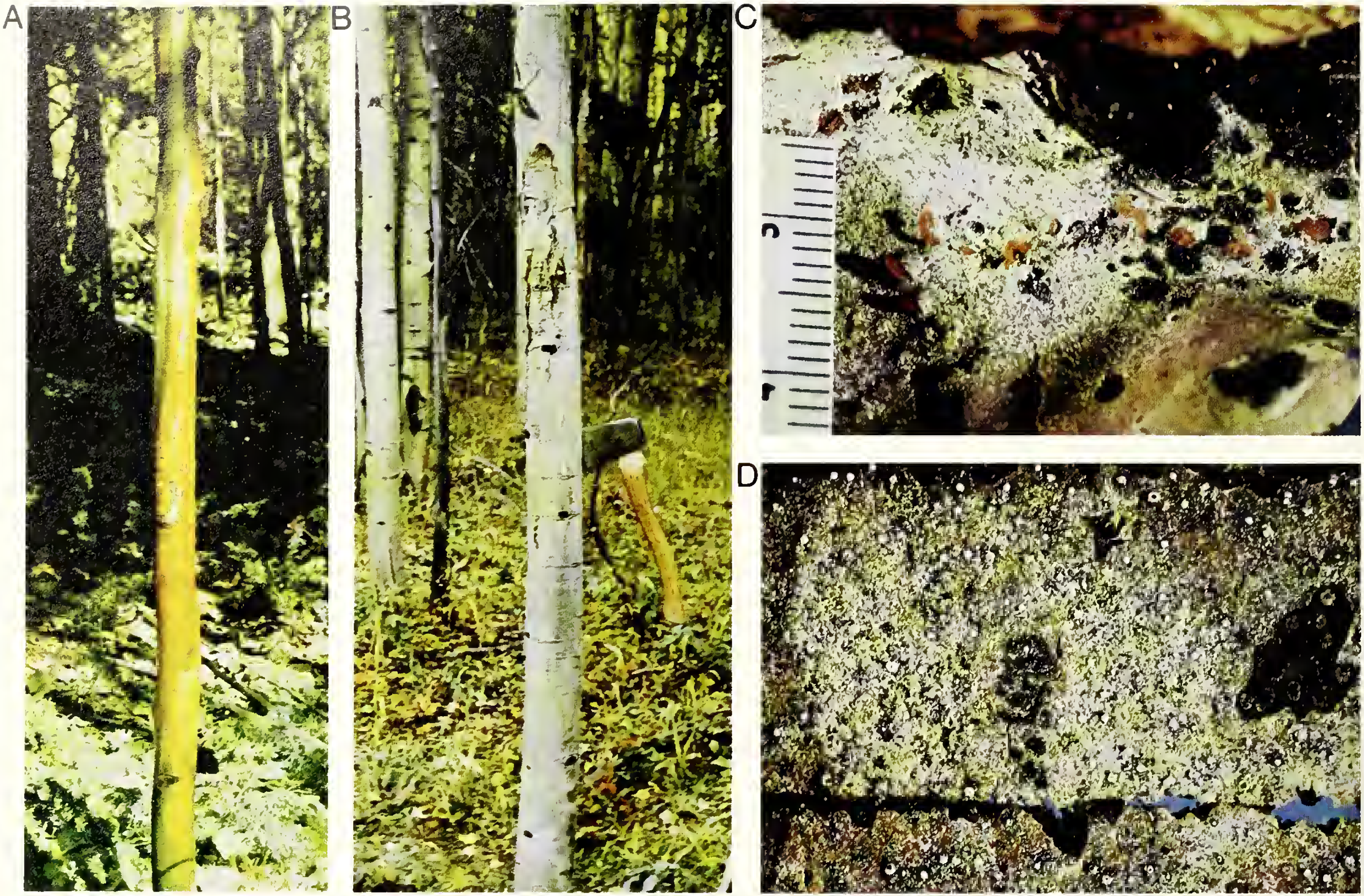

Figure 9.—Cytospora canker. (A) Extensive yellow-to-orange bark discoloration of a stressed or suppressed small tree in the spring often indicates a general trunk infection without canker formation. (B) Three-year-old canker with slight annual callus formation, which originated at a trunk wound. (C) Spore tendrils of the *Cytospora* stage emanating from pycnidia within the infected bark. (D) Whitish ascospore masses of the *Valsa* stage around perithecia ostiolar openings. Bark epidermis removed (right) to reveal the circular fashion of perithecia formation (scales are mm).

collect around the ostioles of the perithecia in sticky white masses on the dead bark.

Inoculation experiments indicate that the fungus is a facultative wound parasite, and that the degree of parasitism is more severe during the tree's dormant period, and is usually greatest on poorly growing trees and branches (Schreiner 1931). Large trees in healthy condition may successfully callus out an infection or severely limit canker growth. Although the fungus often is not responsible for the injury with which it is associated, *Cytospora* infection is associated with frost cracks and sunscald (Hinds 1964), elk feeding wounds (Krebill 1972, Packard 1942), partially cut stands (Martin 1965), tree vigor and slash fires (Hubert 1920), drought (Riley and Hildahl 1963, Schreiner 1931, Wright 1957), and as a secondary parasite with other cankers (Hinds 1981).

Factors influencing the development of the disease on poplars, such as bark and soil moisture content, temperature and humidity, and anatomy, have been studied to help understand the role of the host factors in the disease with a view toward selecting poplar varieties for disease resistance (Bloomberg 1962a, 1962b; Bloomberg and Farris 1963).

Hypoxylon Canker

Although Hypoxylon, caused by *Hypoxylon mammatum* (Wahl.) Miller, is the most important canker disease of aspen in the Lake States region (Anderson 1964, Bier 1940), it is less important in the West. *Hypoxylon pruinatum* (Klotz.) Cke. (a synonym of *H. mammatum*) was first reported in New York as a canker disease of aspen in 1924 (Povah 1924). It occurs throughout much of the range of aspen in the eastern United States (Anderson and Anderson 1969) and Canada (Conners 1967). In the West, the canker was first found in the Rocky Mountains in the interior of British Columbia in 1953 (Molnar 1954) and in Colorado in 1955 (Davidson and Hinds 1956). Since then, it also has been reported in Arizona, New Mexico, and Wyoming (Riffle and Hinds 1969).

Young infections appear as slightly sunken, irregular, yellowish-orange areas around wounds, branch stubs, or insect injury and galls (Anderson et al. 1979, Bier 1940, Manion 1975, Nord and Knight 1972). Although callus tissue develops at the margin of infection, the fungus invades new tissue each year, and the cankers elongate (fig. 10A). The diseased bark appears laminated or mottled black and yellowish white, and white mycelia fans are formed near the canker margin under the bark. About a year after infection, the fungus produces pillarlike structures between the bark cortex and periderm, causing blistered areas in the central portion of the canker. The periderm ruptures, exposing the grayish layer of hyphal pegs (fig. 10B), which are solidly covered by a layer of conidiophores and conidia of the asexual stage. The spores are wind disseminated and the conidial fructifications eventually disintegrate.

Cankers are easier to identify after 2 or 3 years, when perithecia are formed in small crustlike stroma up to several millimeters in diameter (fig. 10C). The young stroma are covered with a grayish bloom and are then formed annually on the dead black bark. They persist for several years. Ascospores are forcibly discharged from the perithecia; the most active discharge occurs immediately after rainfall (Bier 1940). The faded, dead bark in the center of older cankers begins to crack in a checkerboard fashion, and it sloughs off in small patches, revealing a checkering of the wood beneath (fig. 10D).

The fungus invades the sapwood (Bier 1940, Hubbs 1964) and trees often die before they are completely girdled. Sapwood decay beneath a trunk canker predisposes the tree to wind breakage, often before girdling is complete. Decay is more rapid in the Lake States area, where broken stems are common (Anderson and Anderson 1969), in contrast to the arid conditions in the Southwest, where breakage is not common. Cankers are found on saplings, which may be girdled in 4 or 5 years; yet, cankers on large trees in the Southwest may attain ages of 20 to 50 years before tree death. A live, 33-inch (84-cm) d.b.h. aspen in Arizona has been observed with a Hypoxylon canker extending from the ground to a height of about 39 feet (12 m), only half-girdling the tree.

Hypoxylon canker annually kills an estimated 1-2% of the standing aspen volume in the Lake States area (Anderson 1964). Because of this, most research on the

Figure 10.—Hypoxylon canker. (A) Canker approximately 20 years old originating at a dead leader. (B) Hyphal pegs formed beneath the blistered bark periderm (scale is mm). (C) Perithecia bearing stroma of the fungus as they appear on dead bark (scale is mm). (D) Checkerboard pattern of dead bark as it begins to slough off old cankers.

disease has been conducted in that area. While the disease causes serious mortality in localized areas in the Southwest, its overall importance there remains to be determined (Hinds and Krebill 1975); and only generalizations based on eastern studies can be made concerning the prevalence of infection and mortality.

Infection varies from one geographic area to another (Anderson 1964). There does appear to be a genetic relationship, because some clones are more infected than others (Copony and Barnes 1974). Low-density stands, mixed stands, and thinned stands appear to have more infection (Anderson 1953, Anderson and Anderson 1968, Day and Strong 1959), as do trees on the edges of, rather than within, stands (Anderson 1964). In the Lake States area, juvenile trees are more susceptible to infection (Anderson and Anderson 1969), with less infection found in older stands (Anderson 1964, Bier 1940, Gruenhagen 1945); new cankers usually occur on the upper bole or in the crown of older trees (Day and Strong 1959); severity apparently is greater on poorer sites (Anderson 1953, Gruenhagen 1945); and infection fluctuates substantially from year to year (Schmiege and Anderson 1960).

Observations in the Southwest do not confirm, nor dispute, these findings. As elsewhere, the disease is not uniformly distributed over the range of aspen in the West; and there does not appear to be a relationship between canker and site index (Anderson 1964).

Other Cankers

The occurrence and importance of the little-known fungus *Dothiora polyspora* Shear and Davidson in aspen regeneration should not be overlooked. It was described from the dead tips of living twigs of aspen and willow, and annual stem cankers of young aspen on Grand Mesa, Colorado (Shear and Davidson 1940). Shear and Davidson (1940) implied it might be a weak parasite capable of infecting frost-injured tissue. Although pathogenicity studies with this fungus have not been made, observations indicate that it is associated with a perennial canker and mortality of aspen regeneration throughout the West and Alaska. Stem wounds caused by browsing and trampling by domestic livestock, deer, and elk appear to be particularly susceptible to infection. These wounds usually are near the ground. The stem is girdled by the fungus in 2 or 3 years, and *Cytospora* colonizes the remaining live bark. Because the small canker near the ground is often overlooked, *Cytospora* or the wound is blamed for the mortality. Its frequency of occurrence has not been determined; but the amount of infection and mortality appears to be related to the amount of animal damage within a regenerating stand.

There have been reports of two other canker and dieback diseases of poplars occurring on aspen. Dothichiza canker, caused by *Dothichiza populae* Sacc. & Br., attacks numerous species of poplars and poplar hybrids in Europe, Canada, and the United States (Waterman 1957). Although it has been in this country since 1915 (Hedgcock and Hunt 1916), the only report of it on aspen was in Wisconsin, when Honey (1944) observed it on *Populus tremuloides* and *P. grandidentata* nursery stock.

Neofabraea canker, caused by *Neofabraea populi* Thom., was found mainly at the base of 3- to 6-year-old *Populus grandidentata*, *P. tremuloides*, and *P. balsamifera* Mill. trees smaller than 1.5 inches (4 cm) d.b.h., on Bear Island, Ontario (Thompson 1939). Six of seven inoculations on aspen sprouts proved it to be the causal agent. The canker has not been reported in the United States. Like Dothichiza canker, it probably is an aberration on aspen.

Canker Formation

How these fungi induce canker formation is not entirely clear; but the concept that they produce a toxin which results in cell death, bark collapse, and necrosis has been shown for Hypoxylon canker, and has been strongly suggested for others. Schreiner (1931) found a few hyphae among cells which apparently were not entirely dead, on the edge of *V. sordida* cankers. The wood was stained brown, and the mycelium was found in the vessels, the fibers, to some extent in the wood parenchyma, and also between the medullary ray cells; but they apparently penetrated into the medullary ray cells only when the cells were dead. A black line of demarcation always formed when different clones of the fungus were grown in culture. Schreiner (1931) suggested that an enzyme action preceded the advance of the mycelium, and that the nature or amount of the toxic substance was specific for the individual clone.

The mode of *H. mammatum* infection under natural conditions is unknown, because the bark of aspen contains fungitoxic compounds that strongly inhibit mycelia growth (Hubbes 1966). The fungus is a wound parasite of sapwood tissue that invades the bark from within (Bier 1940, Hubbes 1964, Schipper and Anderson 1971). The fungus produces a toxin, mammatoxin, that causes bark necrosis and collapse in advance of the fungus; consequently, the fungus is well established in the sapwood before canker symptoms appear in the bark (Schipper 1978). A mammatoxin assay has been developed to determine genetic and environmental predisposition of aspen to cankering (Bruck and Manion 1980).

Results of recent work with *Cryptosphaeria populina* indicate it is similar to *H. mammatum* (Hinds 1981). The fungus more readily infects sapwood wounds and penetrates the sapwood before the canker forms in the bark (fig. 8E). A water-extractive material produced by the fungus in culture is similar to that found in infected sapwood. The material is fluorescent under ultraviolet light (fig. 8F), like material produced by *H. mammatum*, which suggests that this material may be toxic to living cells and may be a precursor to the eventual discoloration and decay caused by the fungus.

Figure 11.—Aspen rough bark. (A) Extensive trunk infection by *Diplodia tumefaciens*. (B) Confined oval trunk infection typical of *Curcurbitaria staphula*. (C) Angular trunk infection by *Rhytidiella baranyayi*. (D) Old damage by rodents at the base of aspen. (E) Sunscald over many years on the south side of the trunk. (F) Common bark wounding by campers.

Canker Control

No control measures are known for these aspen cankers; and, as yet, they cannot be prevented, except by preventing wounds. If aspen stands are opened too quickly, the residuals will suffer from sunscald and canker, and the stand might deteriorate rapidly. Wound cankers on high-value trees sometimes can be excised by cutting away the infected bark and adjacent healthy tissue (Hinds and Krebill 1975).

Certain silvicultural techniques can minimize canker impact. Because canker diseases frequently increase with stand age, managing aspen in small even-aged groups on a short rotation of 80-100 years may be effective. Clearcutting, prescribed burning, and managed wildfires often are effective techniques (Hinds and Krebill 1975). Because Hypoxylon canker is favored by stand openings and poor stocking, maintaining fully stocked stands and a closed canopy without openings or poorly stocked patches will reduce its occurrence (Anderson and Anderson 1969, Schipper and Anderson 1976).

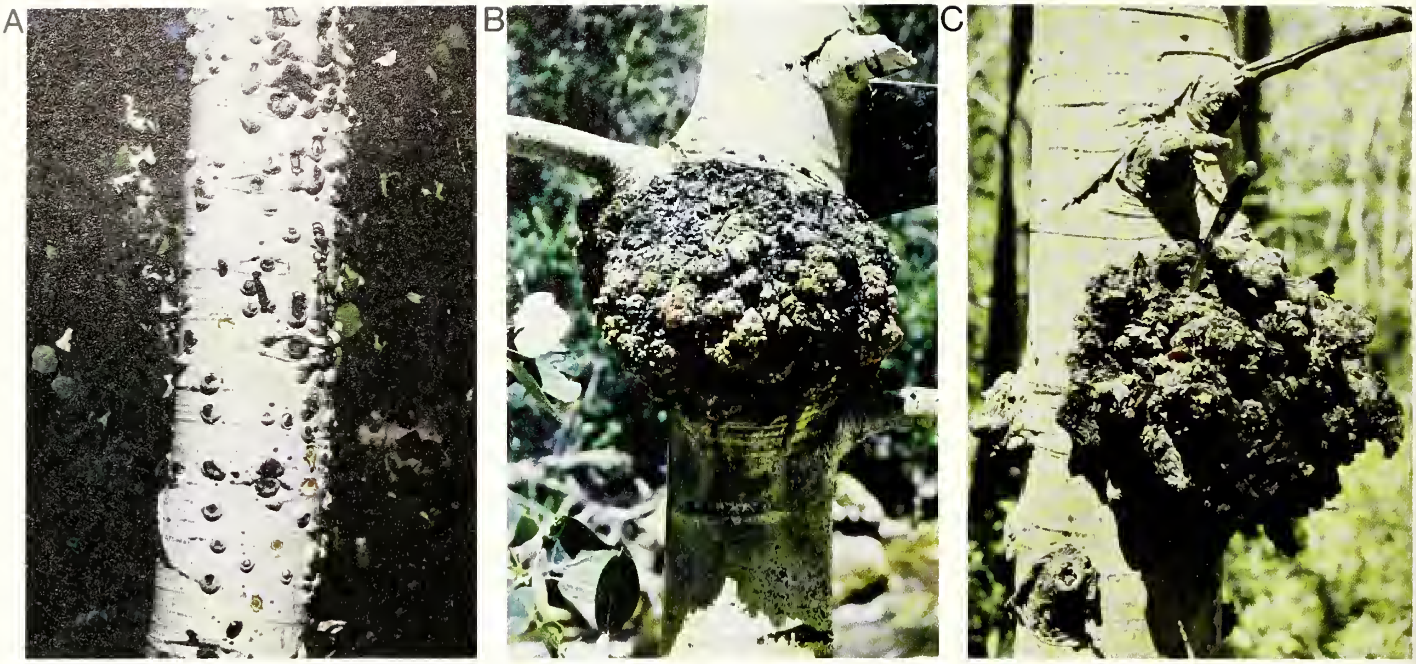

Figure 12.—Aspen bark abnormalities of unknown origin. (A) Small nodules. (B) Globose trunk gall presumed to be insect related. (C) Rough clinker-like trunk gall.

Aspen Rough Bark and Branch Galls

Branch galls and rough bark on the smooth stems of aspen in the West are widespread. Although the natural healing of wounds is often responsible for this condition, various fungi are associated with the rough oval spots and fissured bands of grayish-black, corky bark that often extends all or part way around the trunk or branches. The damage caused to the tree by rough bark is unknown but presumed to be unimportant, although some of the fungi affect the bark periderm, cortex, and phloem. Lichens and one or more fungi often are found fruiting on the corky ridges; consequently, a microscopic examination is necessary to identify them. The number of trees affected with this type of hypertrophy at any one location can vary from a few to 100 or more. In a recent survey of aspen in Colorado, rough bark attributed to fungi infection was found on 23.8% of the live trees (Juzwik et al. 1978).

Diplodia tumefaciens (Shear) Zalasky (*Macrophoma tumefaciens*) has been proven capable of producing galls on aspen (Kaufert 1937). Branch galls do not appear to be as numerous as the trunk rough bark (fig. 11A). The fungus gains entrance into the bark through lenticles but does not penetrate deeper than the outer layer of the cortex, because it apparently stimulates the formation of a protective periderm. As the fungus invades the layer of periderm, a new phellogen develops and a new layer of periderm forms. This fungus invasion and formation of a protective barrier against the pathogen continues for years, resulting in the formation of rough bark and branch galls. Zalasky (1964) reported fungus penetration of intact or broken cuticle and epidermis of aspen and black poplar (*Populus nigra*), and its occurrence on other poplars.

Curcurbitaria staphula Dearness often is associated with *D. tumefaciens* galls on aspen and balsam poplar (*Populus balsamifera*), and is speculated to be a secondary invader in the tissue of the galls initiated by *D. tumefaciens* (Arnold and Russell 1960). *C. staphula* frequently is the only fungus found fruiting on aspen rough bark (fig. 11B); however, its exact relation to the disorder of rough bark is unknown.

Rhytidiella baranyayi Funk and Zalasky is consistently associated with and considered the probable cause of another cork-bark disease of aspen in western Canada (Funk and Zalasky 1975). Observations in the West indicate it is widespread. The rough bark is more angular in shape without forming a band around the trunk (fig. 11C); and it frequently is initiated around branch stubs. *Parkerella populi* Funk has been found fruiting within the bark fissures produced by *R. baranyayi*; but it is suspected to be a secondary invader (Funk 1976).

Seimatosporium etheridgei Funk is associated with cushion-like swellings, more circular in outline and smaller than the other rough barks. The fungus affects only the cortical area of the bark. The central portion of the swelling later assumes a cork-bark appearance, with the fruiting bodies of the fungus near the surface, sometimes forming in roughly concentric rings (Funk 1978). *Leciographa gallicola* Funk is considered to be a putative parasite on *S. etheridgei* and *D. tumefaciens* galls (Funk 1979).

Other agents are responsible for aspen rough bark. Rodent damage, mainly voles, gnawing at the base during the winter months is very common (fig. 11D), sunscald on the south and southwest side of trees suddenly exposed to the sun (fig. 11E), and even mechanical wounds caused by various means (fig. 11F). (See the ANIMAL IMPACTS and the OTHER PHYSICAL FACTORS chapters.) There also are other bark abnormalities of unknown origin, such as bark nodules (fig. 12A) and trunk galls (fig. 12B, 12C), which may cause rough bark.

INSECTS AND OTHER INVERTEBRATES

John R. Jones, Norbert V. DeByle, and Diane M. Bowers

Quaking aspen throughout its range appears to be host to several insect and other invertebrate pests (fig. 1). It is a short-lived species that is palatable to a large variety of animals. Furniss and Carolin (1977) listed 33 insect species that use aspen as a food source. Some are quite damaging and may kill otherwise healthy stands of aspen; others feed on weakened or dying trees; and still others have incidental impacts (fig. 2).

Boss (1972) found that seven species of insects caused major damage to quaking aspen in Colorado: the western tent caterpillar, *Malacosoma californicum* (Packard); the poplar borer, *Saperda calcarata* Say; the poplar twig saperda, *Saperda moesta* Leconte; a flatheaded wood borer, *Poecilonota cyanipes* (Say); and three species of leafhoppers in the genus *Idiocerus* Lewis. Other families, genera, and species also were found associated with aspen during the 2-year survey, although none were found in epidemic numbers.

A more local survey in northern Utah[1] revealed a different array of insects. Most numerous were leafminers (Lepidoptera, Gracillariidae), sawflies (Hymenoptera, Tenthredinidae), and leafhoppers (Homoptera, Cicadellidae). Aphids (Homoptera, Aphididae), thrips (Thysanoptera, Thripidae) and parasites (Hymenoptera, Chalcidoidea) were moderately abundant. Generally, insect abundance varied inversely with tree height.

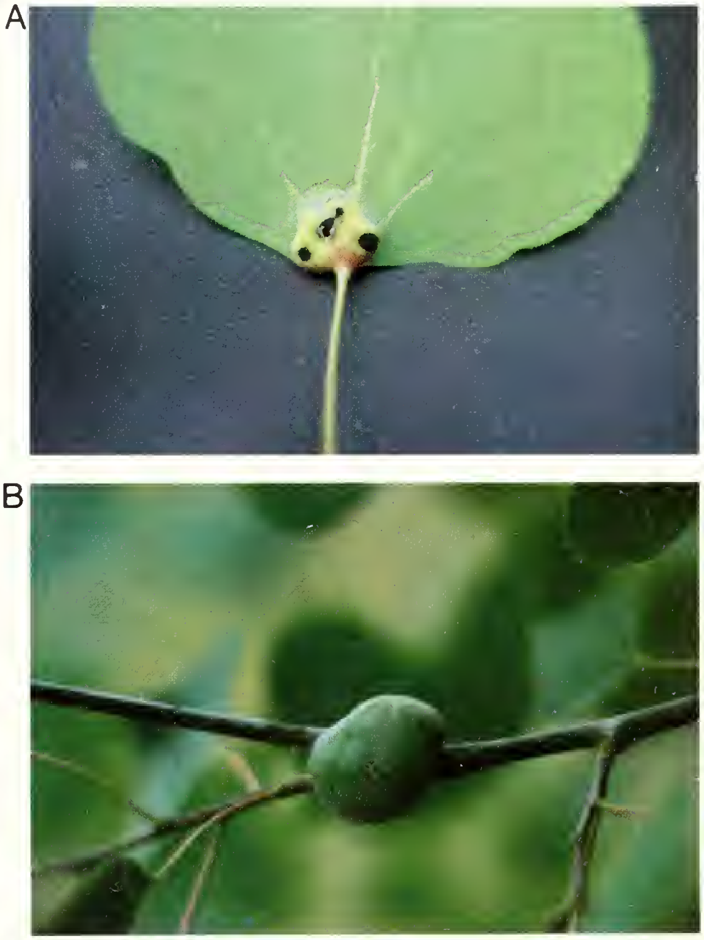

Figure 2.—Some insects leave obvious evidence of their presence. Their feeding causes some abnormal plant growth that results in galls. (A) Leaf gall. (B) Branch gall.

Defoliating Insects

Tent Caterpillars

The western tent caterpillar, *Malacosoma californicum*, the most prevalent species, has been responsible for periodic defoliation of aspen over widespread areas in the West. Its known range extends from Mexico to Washington (fig. 3). This species contains six subspecies (Furniss and Carolin 1977). One of these, *M. c. fragile* (Stretch), which formerly had species status, is commonly known as the Great Basin tent caterpillar. This subspecies is most damaging to aspen in the interior West. Another subspecies, *M. c. pluviale* (Dyar), the northern tent caterpillar, feeds on aspen through much of Canada. It also occurs in northern Idaho and western Montana (Stehr and Cook 1968), but has not been a serious aspen pest in the United States.

A similar insect, the forest tent caterpillar, *Malacosoma disstria* Hubner, is a serious defoliator of aspen in the north central United States (Batzer 1972). For example, an outbreak in 1976-1979, in the Turtle Mountains of North Dakota, defoliated 150,000 acres (61,000 ha) of aspen.[2] This species is found in the East

Figure 1.—A variety of insects inhabit aspen trees: (center) ants tending aphids; (upper left) an Agromyzid leafminer; (upper right) a leafhopper.

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[1] *Unpublished data and observations by Diane M. Bowers on file at the Biology Department, Utah State University, Logan.*

[2] *Personal communication from Scott Tunnock, Northern Region, USDA Forest Service.*

and in Canada, as well as throughout the interior western mountains as far south as southern New Mexico (Stehr and Cook 1968). The forest tent caterpillar has not been a major threat to aspen stands in the western United States, where it prefers other hosts, most notably common chokecherry (*Prunus virginiana*).[3] However, in a 1963-64 epidemic in northern Idaho, both the aspen and other deciduous trees and shrubs were defoliated (FIDC 1964).[4] Infection by hypoxylon and nectria cankers and attack by borers was shown to increase with increasing severity of defoliation by *M. disstria* of aspen in Minnesota (Churchill et al 1964).

The western tent caterpillar feeds on the leaves of many deciduous trees and shrubs; but, from New Mexico north to southern Idaho, aspen is preferred. Farther north it occasionally feeds on aspen but appears to prefer other, more prevalent species (FIDC,[4] Stehr and Cook 1968). Sustained outbreaks in aspen have been reported from the Pikes Peak area of central Colorado, the Chuska Mountains of northeastern Arizona, and the San Juan and Sangre de Cristo Mountains of northern New Mexico and bordering districts of Colorado (Boss 1972, Clark 1958, FIDC,[4] Gardner 1905, Stelzer 1968).

Four successive years of complete defoliation killed entire trees and top killed others in many aspen stands in New Mexico and southern Colorado, during the 1950s and 1960s (fig. 4). Stands lightly defoliated or defoliated only 1 or 2 years in sequence had minor damage (Boss 1972, Stelzer 1968). Typically, an outbreak persists in a locale for several years, flaring up in one stand and then another without repeated stripping of the same stand.[5]

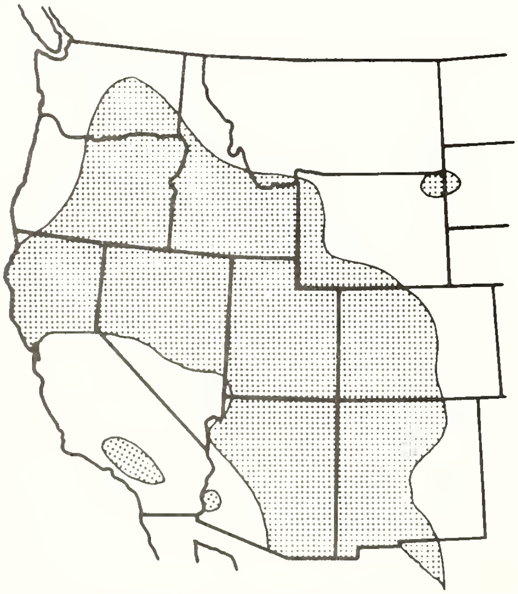

Figure 3.—Distribution of western tent caterpillar in the United States (adapted from Stehr and Cook 1968).

Diameter growth is markedly affected by tent caterpillar defoliation. Stelzer (1968) reported that during 3 years of complete defoliation, ring widths of surviving stems in New Mexico were less than the average of the six preceding years by 2.4%, 52.2%, and 74.6%, respectively. In Minnesota, aspen defoliated for as little as 1 year by *M. disstria* grew much less in diameter than normal during that year and the next year (Churchill et al. 1964, Duncan and Hodson 1958). Pollard (1972b) studied a mature Ontario stand after a 3-year outbreak of *M. disstria*, and found that growth scarcely improved at all during the first post-outbreak year, and to only about 50% of their pre-outbreak level by the third year.

Diameter growth was assessed on plots in the western tent caterpillar outbreak area of New Mexico and southern Colorado, after the population collapsed.[6] Very narrow growth rings were found in the upper boles; but none could be found at stump height or breast height. Considering that the sampled aspen stands had not been conspicuously damaged, these observations suggest surprisingly severe growth reduction from tent caterpillar defoliation. There is a possibility, however, that the small "extra" rings in the upper boles might be false rings.[7] Perhaps a small amount of growth occurred in spring from stored carbohydrates and initial photosynthates; then defoliation stopped diameter growth until the trees releafed in mid-summer; then another spurt of growth occurred in late summer. Thus, two narrow growth rings could have developed in each year of defoliation.

Defoliation by western tent caterpillar is extensive by the time cambial cells begin to divide (Stelzer 1968, 1971). Because the buds and young leaves are sources of growth-regulating compounds (Wilcox 1962), cambial growth is strongly inhibited in defoliated trees by a lack of regulatory compounds (Kozlowski 1969). Thus, this defoliation drastically reduces photosynthesis and upsets the growth regulating processes in the tree, both of which inhibit growth (see the GROWTH and the VEGETATIVE REGENERATION chapters).

The western tent caterpillar overwinters as eggs. The larvae emerge and begin to feed when aspen leaf buds begin to open. Trees may be stripped of leaves by the end of June. The larvae mature in 30 to 40 days, then pupate (Stelzer 1968, 1971). Later in the summer, the trees put out new leaves (FIDC 1974).[4] In New Mexico, the moths emerge mostly in July, mate, and lay their eggs (Stelzer 1968).

During heavy infestations, all leaves may be eaten before most larvae are mature; many larvae then starve (Stelzer 1968). Also, newly hatched larvae may starve in the spring, if cold weather delays leaf emergence or if a late freeze kills emerging leaves. However, it is doubtful if starvation collapses many tent caterpillar outbreaks

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[3] *Personal communication from Mark McGregor, Northern Region, and William Klein, formerly with the Intermountain Region, USDA Forest Service.*

[4] *"Forest Insect Conditions in the United States" was published by the USDA Forest Service from 1951 to 1970. It was expanded to "Forest Insect and Disease Conditions in the United States" in 1971. It presents the status of known significant outbreaks in all regions of the country.*

[5] *Personal communication from Robert Acciavatti, formerly with the Southwestern Region, USDA Forest Service.*

[6] *Personal observation by John R. Jones.*

[7] *Personal communication from Gene Lessard, formerly with the Southwestern Region, USDA Forest Service.*

Figure 4.—Deteriorating aspen stand 1 year after collapse of a western tent caterpillar infestation. The stand had been completely defoliated for three consecutive years (Stelzer 1968).

(Smith and Raske 1968). Also, parasitic and predatory insects kill eggs, larvae, and pupae of the western tent caterpillar; but heavy parasitism has not been reported (Stelzer 1968) and, therefore, does not appear to be an effective control either. Instead, buildup of a nuclear polyhedrosis virus, specific to tent caterpillars, appears to be the key factor responsible for collapsing outbreaks (Clark 1955, 1958; Stelzer 1965, 1968). In each reported instance, it took several years for this virus to naturally reach effective levels in the major outbreak areas.

Stelzer (1965, 1967, 1968) demonstrated that new outbreaks of western tent caterpillar could be quickly aborted on a practical field scale by aerial spraying with a water suspension of the virus mixed with *Bacillus thuringiensis*. The virus persists on the trees for at least 1 year after collapse of the caterpillar population (Clark 1958). That persistence should drive the insect population to extremely low levels and prevent quick new buildups on the site.

Large Aspen Tortrix

The larvae of the large aspen tortrix, *Choristoneura conflictana* (Walker), first mine the buds and later roll the leaves into feeding shelters. This moth is found through much of the range of aspen in the West (Beckwith 1973). Extensive outbreaks have occurred in Alaska, Manitoba, and Minnesota (Batzer 1972, FIDC[4]). Occasional local outbreaks of varying severity have been reported in the western United States.[4] Apparently, these have not caused heavy tree losses (Davidson and Prentice 1968, FIDC 1972[4]). A substantial outbreak of the large aspen tortrix persisted for 3 years on the Kaibab Plateau, in northern Arizona. Limited branch mortality but no conspicuous tree mortality was noted.[5] Beckwith (1973) reviewed the factors that tend to keep tortrix populations in check: birds, predatory and parasitic insects, a fungus which kills larvae in winter, and spring freezing. He doubted, however, that any of these mortality factors cause major declines when populations are high. Perhaps starvation is important (Furniss and Carolin 1977).

Aspen Leaftier

The larvae of the aspen leaftier, *Sciaphila duplex* (Walsingham), skeletonize, roll, and then tie the rolled leaves together as they feed (Furniss and Carolin 1977). Heavy feeding may completely defoliate a tree in one season. This moth is widespread; it occurs in the western Canadian Provinces, and in California, Idaho, Nevada, Utah, and Wyoming. In the 1960s a large outbreak occurred in Idaho, Utah, and Wyoming (McGregor 1967). This outbreak, as well as other leaftier outbreaks, sometimes are associated with aspen tortrix outbreaks.[4]

Geometrid Moths

The caterpillars of five species of geometrid moths feed upon the leaves of aspen in the West (Furniss and Carolin 1977). These larvae are commonly known as loopers, spanworms, or inchworms. The fall cankerworm, *Alsophila pometaria* (Harris), is very widespread and attacks many deciduous trees and shrubs, including aspen. The pepper-and-salt moth, *Biston cognataria* (Guenee), occurs across the northern States and Canada. This large larva (7.5 cm long) is a solitary feeder, commonly on aspen. In British Columbia and Oregon, a third species, *Erannis vancouverensis* Hulst, sometimes severely defoliates aspen. *Itame loricaria* (Eversmann) is a common species, at least in Alberta, where it causes light defoliation of aspen from mid-May through June. The Bruce spanworm, *Operophtera bruceata* (Hulst), occurs across Canada, where it prefers aspen and willow as hosts (Furniss and Carolin 1977). In the U.S., it heavily defoliated some aspen stands in northern Idaho in the late 1960s; and, in 1973 it infested thousands of acres in the Turtle Mountains of North Dakota.[2]

Leafrollers

Four species of leafrollers have been noted on western aspen (Furniss and Carolin 1977). A solitary leafroller, *Epinotia criddleana* (Kearfott), feeds primarily on aspen and occurs from Alberta eastward in Canada. Another, *Pandemis canadana* Kearfott, is transcontinental and quite prevalent from Alberta to Manitoba. It feeds largely upon aspen, willow, birch, and poplar. A third solitary leafroller, *Pseudexentera oregonana* (Walsingham), is common on aspen in Oregon and in western Canada. A fourth leafroller, *Anacampsis* [*Compsolechia*] *niveopulvella* (Chambers), is a transcontinental species that is common in the North. It was credited with causing considerable defoliation in an Arizona locale, too (FIDC 1974).[4]

Other Defoliators

Larvae of several other western moths defoliate aspen. Within Noctuidae, the cottonwood dagger moth, *Acronicta lepusculina* Guenee, larvae feed most of the summer on leaves of several genera within Salicaceae, with aspen its favorite host (Furniss and Carolin 1977). A second member, *Orthosia hibisci* (Guenee), is a common moth on aspen in the Pacific Northwest, Alberta, Manitoba, and Saskatchewan. A member of the Notodontidae family, the redhumped caterpillar, *Schizura concinna* (J.E. Smith), is a leaf skeletonizer that occurs throughout the West, and is an occasional pest of forest, fruit, and shade trees. It has severely defoliated aspen in British Columbia and Saskatchewan (Furniss and Carolin 1977).

Baker (1925) reported that the tiny larvae of unspecified Chrysomelid beetles strip aspen in some locales; but the outbreaks normally last just one season. He listed the cottonwood leaf beetle, *Chrysomela scripta* F., as an aspen defoliator in Montana; however, Furniss and Carolin (1977) specifically stated that this species does not feed on aspen. However, they listed two leaf beetles that do: the aspen leaf beetle, *C. crotchi* Brown, feeds on aspen, and occurs in the West from New Mexico to Alaska; and the American aspen beetle, *Gonioctena americana* (Schaeffer), periodically defoliates aspen in Canada. An unidentified *Chrysomela* heavily defoliated stands of aspen and paper birch for two consecutive years, in the Black Hills of South Dakota (FIDC 1963, 1964).[4] Baker (1925) also reported defoliation by a small leaf weevil, *Thricolepis inornata* Horn.

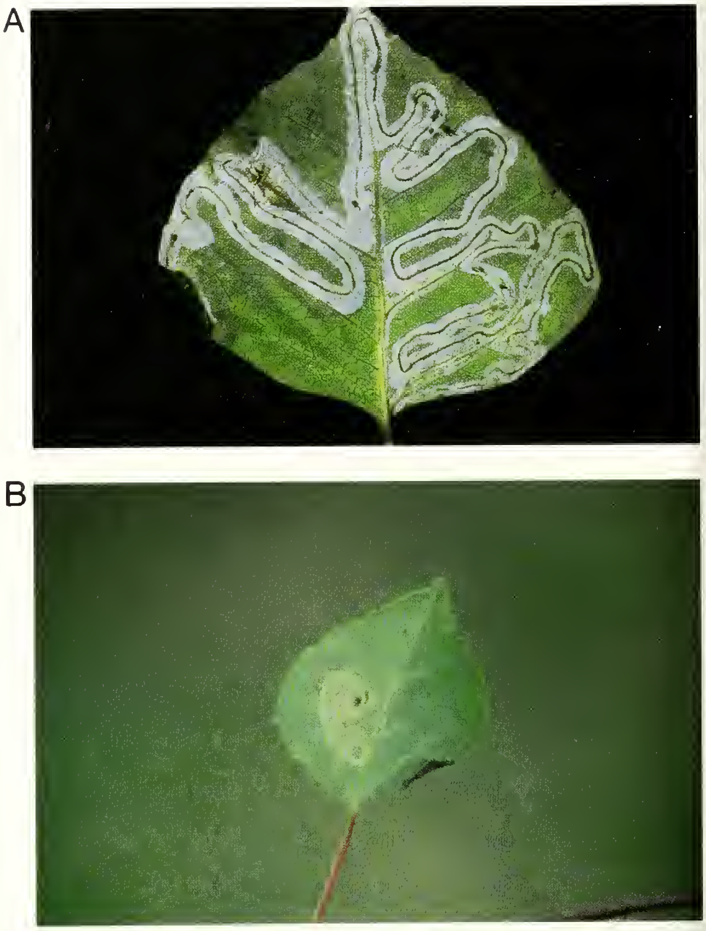

Figure 5.—(A) The aspen leafminer has a very serpentine mine. Note the folded edge of the leaf in the upper right, where the pupa is located. (B) The aspen blotchminer gets its name from the rounded mining activity.

Other Leaf and Branch Insects

Aspen Leafminer

To the casual observer, the aspen leafminer, *Phyllocnistis populiella* Chambers, is one of the most common and visually significant insects on aspen throughout much of the West (fig. 5A). During most years, however, leafminer infestations are not severe enough to significantly affect the well-being of aspen trees. There are exceptions. Considerable tree deformity and some mortality resulted from an outbreak lasting at least 15 years in western Wyoming and southeastern Idaho (FIDC 1959 et seq.).[4] Canadian infestations of this insect have caused some mortality and a considerable reduction in height growth (Conrashoff 1962, Davidson and Prentice 1968). Attempts to rear leafminers from northern Utah were unsuccessful because of parasitism, which indicated that a variety of Hymenoptera parasites attack this insect.[1]

Agromyzid flies also mine aspen leaves. This mining easily can be overlooked, especially early in the season, because of its similarity to the pattern of the aspen leafminer. Comparison of the mines makes field distinction relatively easy. The mines of Agromyzid flies are distinctly narrower, shorter, and more jagged (fig. 1) than those of the leafminer.

Aspen Blotchminer

The aspen blotchminer, *Lithocolletis* [*Phyllonorycter*] *tremuloidiella* Braun, sometimes destroys most of the leaves in the lower portion of tree canopies. Its common name is derived from the circular blotch shape of the mine (fig. 5B). This insect has been reported from California, Idaho, Utah, and western Canada (Furniss and Carolin 1977, FIDC 1961,[4] Keen 1952). In northern Utah, the aspen blotchminer was much rarer than the aspen leafminer; but sometimes both species were found in the same leaf.[1]

Sawflies

Larvae of common sawflies (Tenthredinidae) frequently were found feeding on aspen leaves in northern Utah.[1] While not always obvious, these caterpillar-like insects or evidence of their skeletonizing activity can be found in rolled and folded leaves (fig. 6). These larvae readily can be distinguished from Lepidoptera caterpillars by their more than five pairs of fleshy legs.

Figure 6.—Common sawfly larvae (A) are not always readily visible because (B) they commonly are found in folded leaf edges.

Figure 7.—*Idocerus* probably is the most common leafhopper on aspen.

Leafhoppers

The leafhoppers, all in the Cicadellidae family, are small insects that suck juices from leaves and succulent twigs (fig. 7). They lay their eggs in slits cut into new twigs. Leafhopper feeding may be severe enough to cause aspen leaves to curl, wither, or turn brown. In Michigan, they are likely to be involved in early thinning of sucker stands at about 5 years of age (Graham et al. 1963). No literature was found on the impact of leafhopper feeding on aspen in the West. However, Bowers[1] noted that leafhopper nymphs were so numerous on young aspen in northern Utah in 1978, that their feeding had bleached leaves to a pale greenish yellow (fig. 8).

Boss (1972) listed three species of leafhoppers on aspen in Colorado: *Idiocerus formosus* Ball, *I. lachrymalis* Fitch, and *I. suturalis* Fitch. He found several fungi associated with the egg slits of these leafhoppers, including *Cytospora* sp. and *Dothiorella* sp. In northern Utah, in addition to *Idiocerus*, Bowers[1] found leafhopper species in the subfamilies Deltocephalinae, Macropsinae, and Typhlocybinae on aspen. Her observations suggest that some leafhopper species restrict feeding to specific areas on aspen trees, such as twigs or petioles. These species were cryptically colored to match their location and were not apparent by casual observation.

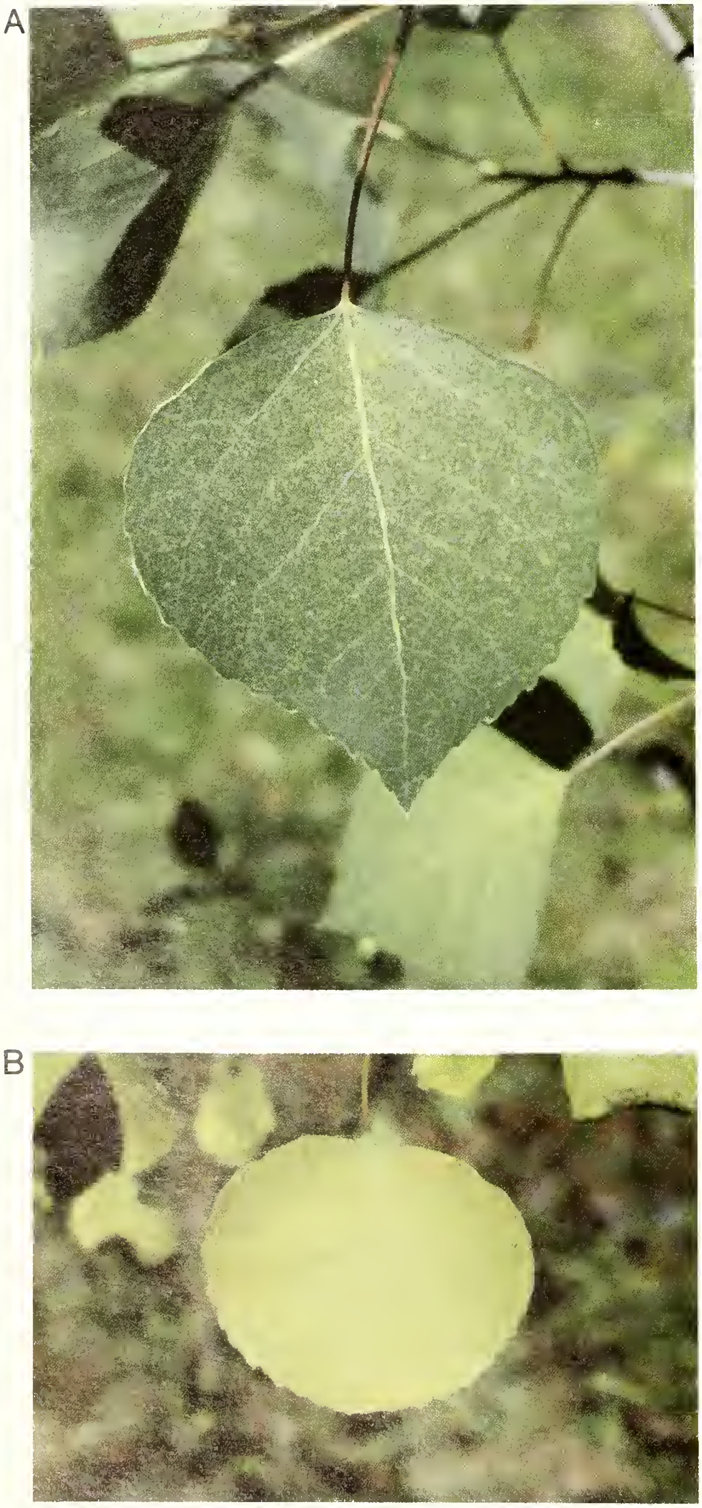

Figure 8.—Yellow spots on aspen leaves (A) are caused by sucking insects. If leafhopper nymphs extensively feed on aspen, the entire leaf may turn yellow (B).

Aphids

The poplar leaf aphid, *Chaitophorus populicola* Thomas, occurs in western Canada and at least in Colorado and Utah. It sometimes causes leaf drop in aspen by feeding on the apical twigs and developing leaves (Furniss and Carolin 1977). Aphid abundance may be positively affected by ants. Some ant species protect aphids and "milk" them for the excess sugars (honeydew) they secrete. Aphids can be most readily located by looking first for concentrations of ants on aspen trees (fig. 9).[1]

Oyster Scale

The oyster scale, *Lepidosaphes ulmi* (L.), attacks aspen in the West. These insects congregate as solid crusts on limbs and twigs. Heavy infestations often kill infested trees (Keen 1952). Survivors show areas of roughened bark (Graham et al. 1963).

Others

A variety of bugs (Hemiptera) were found on aspen in northern Utah.[1] They were in the families Anthocoridae, Lygaeidae, and Miridae. None were numerous. Their effects are unknown. Also, occasionally unidentified species of weevils (Curculionidae) and click beetles (Elateridae) were found on these northern Utah aspen.

Boring Insects

Insects that bore into the bark and wood directly injure aspen trees, and also act as vectors for diseases, such as canker and trunk rot (Bird 1930, Graham and Harrison 1954, Graham et al. 1963, Hinds 1972b, Hofer 1920, Sandberg 1951). In an extensive sample of mature and overmature aspen stands in Colorado, bark injuries by boring insects were found on more than 3% of the trunks and on 52% of the plots (Hinds 1964). In some cases, *Cytospora* also was present, indicating active infection of the recent wound by a canker fungus. Bark injuries by borers were most frequent on good sites and at upper elevations.

Poplar Borer

The adult beetles of the poplar borer, *Saperda calcarata*, are elongate, gray, and 20-30 mm long. Early surveys throughout the Rocky Mountains listed this roundheaded borer as one of the main insects attacking aspen (Baker 1925). Hofer (1920) credited the poplar borer with killing many aspen in the Pikes Peak area between 6,500 and 8,000 feet (2,000 m and 2,500 m) elevation.

The poplar borer may prefer certain aspen associations. At least, in the aspen grovelands east of the Rocky

Mountains in northern Montana, Lynch (1955) found infestations restricted to the *Populus-Symphoricarpos* association, where impacts often were severe; whereas the borer was nonexistent in the *Populus-Osmorrhiza* and *Populus-Aster* associations.

The poplar borer infests aspen from saplings to mature trees (Hofer 1920). Large trees are attacked anywhere on the stem. Many attacks are abortive. Eggs usually are laid after an egg niche is cut. After hatching, the larvae may not always successfully mine away from the vicinity of the niche. According to Graham et al. (1963), fungi and bacteria invariably invade the egg niche; and, if fungal growth is rapid, the larvae die because they are deprived of the living wood cells required for food.

The larvae feed in the sapwood and heartwood for 2 or 3 years, expelling coarse fibrous frass through slits in the bark. Borer activity is marked by accumulations of ejected frass and by streaks of varnish-like dried sap on the bark beneath the opening. Callus growth and rough bark around these openings, and secondary attacks by callus borers and fungi, give a rough appearance to heavily attacked trees (Graham et al. 1963). Successful attacks result in extensive staining of the wood. Even unsuccessful attacks cause staining. Stain from an unsuccessful attack by *Saperda calcarata* may extend as much as 10 feet (3 m) below the attack site (Graham et al. 1963).

In Canada, Michigan, and Colorado, the mines of the poplar borer have been described as important sites for infection and rapid growth of the trunk rot fungus, *Phellinus tremulae* (Bird 1930, Graham et al. 1963, Hofer 1920). In Lower Michigan, most hypoxylon cankers on the boles of aspen started in poplar borer wounds (Graham and Harrison 1954).

In Colorado, Hofer (1920) found attacks by *S. calcarata* concentrated in certain trees, which he called "brood" trees. Brood trees develop because adult beetles tend to lay eggs in the same tree from which they emerged.[8] Hofer (1920) noted that fungi often develop rapidly in brood trees, destroying many larvae. Brood trees often break in the wind because of extensive mining of the wood; and many larvae in these windbroken trees fail to mature and emerge.

Figure 9.—Ants often are found tending aphids on aspen.

Successful attacks by the poplar borer in the Lake States are concentrated in larger trees; and infestations are greater in poorly stocked stands (Ewan 1960). Graham and Harrison (1954) noted that the beetles cut many holes but did not lay eggs in the more vigorous trees. Riley and Hildahl (1963) reported that drought stricken Canadian aspen were heavily attacked by *S. calcarata*. Colorado aspen defoliated by the western tent caterpillar were selected by the borer.[8] Hinds (1976a) found that Colorado aspen exposed to the sun by construction of roads and campgrounds suffered increased attacks by unidentified borers. Attacks also increased markedly in stands that had been selectively logged.[9]

Poplar Twig Borer

The poplar twig borer, *Saperda moesta*, is related to the poplar borer but the adult beetle is somewhat smaller (about 12 mm long), and colored dark gray to black. It infests and forms galls in aspen twigs and small suckers. The infested branch or sucker is not directly killed; but it becomes weakened and breaks easily from snow or wind (Boss 1972, Graham et al. 1963). Boss (1972) considered damage caused by *S. moesta* to be significant in Colorado. The egg slit is distinctive; a U-shaped flap is formed that opens downward, and the eggs are laid beneath it.

Poplar Branch Borer

The poplar branch borer, *Oberea schaumii* LeConte, is a widespread species that mines and sometimes kills the branches of *Populus* trees; but it is not considered a serious pest (Furniss and Carolin 1977).

Poplar Butt Borer

The poplar butt borer, *Xylotrechus obliteratus* LeConte, has killed large areas of aspen above 7,000 feet (2,100 m) in Colorado and Utah (Keen 1952). This beetle, about 15 mm long, is somewhat smaller than *S. calcarata*, is dark colored, and is marked with three yellow bands across the wing covers. Unlike the adults of most other roundheaded borers (also called longhorned beetles because their antennae are at least as long as their bodies), the antennae of the poplar butt borer are only slightly longer than the head. Tree bases are most heavily attacked (Hofer 1920, Keen 1952). Attacks are repeated until the heartwood is completely honeycombed and the trees break off during wind or snow storms (Furniss and Carolin 1977, Keen 1952).

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[8] *U.S. Department of Agriculture, Forest Service. 1962. Timber management guide for aspen. 14 p. U.S. Department of Agriculture, Forest Service, Rocky Mountain Region, Denver, Colo.*

[9] *Personal communication from T. E. Hinds, Rocky Mountain Forest and Range Experiment Station, USDA Forest Service.*

Poecilonota cyanipes (Say)

A flatheaded borer, *P. cyanipes*, also has been reported in aspen in the West. In Colorado, Boss (1972) found it attacking only the bases of trees, and only trees with bark already damaged, perhaps by sunscald. On exposed aspen boles, borer attacks were found on all sides except the north. They were not found in any tree whose base was shaded. Attacks were common on poor sites and in sparsely stocked stands. *P. cyanipes* also was common along sun-facing margins of dense stands. In the Lake States, *P. cyanipes* is not restricted to the bases of trees; there Graham et al. (1963) found it most common near branch stubs.

Bronze Poplar Borer

The bronze poplar borer, *Agrilus liragus* Barter and Brown, is a flatheaded borer that attacks weakened aspen. Trees whose phloem has been partially girdled, such as by gnawing by elk, are most commonly attacked. Aspen in campgrounds, carved by tourists, often are attacked, too. Symptoms of *A. liragus* infestation include subnormal leaf size, fading leaf color, and early leaf fall (Boss 1972). A related species, the bronze birch borer (*A. anxius* Gory), also girdles and kills aspen twigs (Keen 1952).

Aspen Root Girdler

The root girdler, *Agrilus horni* Kerremans, has been collected in Arizona and South Dakota (Nord et al. 1965) and probably occurs elsewhere in the West. The larvae form spiral galleries in young suckers and often girdle the main roots and lower stems. In Wisconsin and Michigan, the girdled suckers died before normal leaf abscission. These suckers kept their dead brown leaves over winter and were readily recognized when the rest of the stand was bare. Damage has been of little consequence in heavily stocked regeneration but may be serious in lightly stocked sucker stands (Nord et al. 1965). Root damage in aspen plantations in Wisconsin also has been reported (Benson and Einspahr 1967). With increased efforts to regenerate aspen in the West, *A. horni* may significantly impact young sucker stands in the West, too.

Bark Beetles

Three species of bark beetles are listed by Furniss and Carolin (1977) as infesting aspen trees in the West: *Procryphalus mucronatus* (LeConte), *Trypophloeus populi* (Hopkins), and *T. thatcheri* Wood. These and other species of these two genera mine the bark on the bole and large branches of living hardwood trees. The adults of all species are small (1.5-2.0 mm long) and brown to black. In central Utah, Petty (1977) found that *P. mucronatus* favored dead bark of aspen and had little affect on the tree, whereas *T. populi* used the green bark of unhealthy aspen and hastened the death of trees.

Other Boring Insects

The ambrosia beetle, *Typodendron retusum* (LeConte), invades the sapwood of living but declining aspen throughout the West (Hinds and Davidson 1972). Species of *Ceratocystis* and other fungi are associated with these pinhole galleries and with young adult beetles.

Keen (1952) listed two species of flatheaded borers, *Chrysobothris femorata* (Oliver) and *C. mali* (Horn), as attacking aspen twigs. Two others, *Buprestis confluenta* Say and *Dicerca tenebrica* (Kirby) (= *D. prolongata* LeConte), mine aspen logs.

A powderpost beetle, *Ptilinus basalis* LeConte, attacks dead and cured wood of aspen and other hardwoods from California to British Columbia (Hatch 1962 cited by Furniss and Carolin 1977).

In western Canada, the ghost moth, *Sthenopis quadriguttatus* Grote, larvae bore into the roots of aspen and other members of the family Salicaceae (Furniss and Carolin 1977).

Miscellaneous Insects and Other Invertebrates

Several species of beetles have been found by Hinds (1972b) to carry the fungus *Ceratocystis fimbriata* Ell. & Halst., which causes black cankers on aspen. Two of these vectors are sap beetles (Nitidulidae)—*Epurea* sp. and *Colopterus truncatus* Randall; two are rove beetles—*Nudobius corticalis* Casey and *Quedius raevigatus* Gyllenhal; and one is the root eating *Rhizophagus brunneus* (Horn). Nitidulid beetles are attracted by fresh wounds on aspen and are believed to be the principal vector of black canker in Colorado (Davidson and Hinds 1968, Hinds 1972b).

Nematodes of several genera, all associates or parasites of nitidulid beetles, have been recovered from black and sooty-bark cankers in Colorado and New Mexico. These small worms may influence the establishment and development of cankers (Massey and Hinds 1970).

Cutworms, larvae of moths in the family Noctuidae, kill succulent new suckers by cutting them off at the ground line. At least in Michigan, this mortality source is significant (Graham et al. 1963).

The larvae of a moth in the family Olethreutidae (which includes the aspen leaftier), *Laspeyresia populana* Busck, feeds on the cambium of aspen. It has been reported from both Montana and Alberta (Furniss and Carolin 1977).

Eriophyid mites feed on a wide variety of plants, including broad-leaved trees. Some cause galls. Probably most noticeable on aspen is the one that causes pimple-like galls on leaves. Feeding by *Eriophyes parapopuli* Keifer results in woody gall formation around the buds of aspen and poplars in the West. It also stunts tree growth. Another species, *E. neoessigi* Keifer, occurs from Alberta to California, and forms galls in the catkins of *Populus* trees (Furniss and Carolin 1977).

ANIMAL IMPACTS

Norbert V. DeByle

The aspen ecosystem is rich in number and species of animals, especially in comparison to associated coniferous forest types. This natural species diversity and richness has been both increased and influenced by the introduction of domestic livestock. The high value of the aspen type as a forage resource for livestock and as forage and cover for wildlife makes the subject of animal impacts important to understanding and management of this ecosystem.

This chapter examines both individual and compound influences of mammals and birds on the aspen ecosystem. Knowledge of other forms of animal life in this ecosystem (except for insects, which are discussed in the INSECTS chapter) is too limited to warrant inclusion. Information about forage production, effects of the aspen ecosystem on animals, and consideration of values or production of wildlife, is presented in the FORAGE and the WILDLIFE chapters.

Single Impacts

Grazing

The aspen type annually produces an abundance of forage, often more than 1,800 pounds per acre (2,000 kg per ha) (Houston 1954). This is as much as many grasslands and more than 10 times that produced under associated conifers (Reynolds 1969). Especially heavy and virtually uncontrolled livestock use of many mountain ranges during the first half of the 20th century caused negative, long-term changes to this ecosystem (Croft and Bailey 1964). Although almost all of this abusive use has been halted, grazing continues. Cattle and sheep grazing the aspen understory has been the primary consumptive use of the aspen forest type in the West.

Most grazing occurs only during summer and early autumn. Although there is some additional consumption of above-ground herbaceous material during winter by pocket gophers and other rodents burrowing under the snowpack and by wild ungulates pawing away the snow, winter grazing is poorly quantified. In contrast, summer forage consumption is well documented.

Wild ungulates shift from browse to herbaceous plants during summer (Deschamp et al. 1979, McCaffery et al. 1974, Smith 1953). This shift to succulent food occurs when these animals usually are scattered over heir summer range, making their impact on the forage resource minimal to moderate, and often not even measurable. In contrast, many domestic livestock are allowed to graze on aspen-covered ranges during the peak of the growing season. They commonly use at least 50% of the annual production of palatable forage. On ranges in good condition, this is considered acceptable.[1]

Other vegetation types in the elevational zone occupied by aspen also are grazed. Movement from one type to another is free and uninhibited; the animal chooses the type that furnishes the best forage, comfort, and security. For that reason, the aspen type cannot be viewed as a discrete entity when animal impacts, especially grazing and browsing, are considered. The size of vegetation units, and the relative amount of each type in the animal's home range or in the grazing allotment or pasture controls the amount, season, and nature of use and impacts in the aspen type.

Ellison and Houston (1958) noted that livestock grazing an aspen-grassland mix apparently preferred open grasslands; but, if aspen groves are isolated and comprise only a small portion of the range, this relationship may be reversed,[1] probably because the livestock use the groves for shade. Aspen groves in the conifer forest in Arizona produced 15 times as much forage and were used much more by cattle, elk, and deer than the surrounding conifers were used (Reynolds 1969). A summary paper by Turner and Paulsen (1976) discusses in detail the mountain grasslands, their association with aspen and other vegetation types, and their management.

Direct effects of grazing include removal of plant cover (an immediate impact but usually of only seasonal duration) and alteration of the plant community by selective grazing pressure on the species mix (Ellison 1960). If excessive, the former may contribute to erosion potential. Both may alter wildlife habitat. For example, movement of grouse broods from grazed to ungrazed aspen range has been documented (Robertson 1976). Any ground-nesting bird can be adversely affected by heavy grazing during the nesting season. Small mammal habitat above ground is severely depleted by livestock grazing. Cover for all animals and forage for the grazers in the small mammal community are reduced. Predation also is made easier. These effects of grazing by livestock may alter populations and relative species abundance in the small mammal and bird communities. Pocket gophers, however, maintain abundant populations even on heavily grazed ranges (Ellison 1946); but they are essentially subterranean.

Weatherill and Keith (1969) found the aspen overstory in Alberta was little affected by grazing for 10 or fewer years; but, in the understory, taller herbaceous plants were replaced by shorter, often exotic species.

[1] *U.S. Department of Agriculture, Forest Service. 1970. Range environmental analysis handbook. U.S. Department of Agriculture, Forest Service, Intermountain Region, Ogden, Utah.*

Livestock grazing tends to shift plant species composition in the understory to those of lower palatability; and, if excessive, *Rudbeckia* spp. and many annual plants gain in importance (Ellison 1960)[2] (fig. 1). Pocket gophers graze disproportionately more on forbs (Ward and Keith 1962); this results in grasses increasing and forbs decreasing on ranges heavily populated by these rodents (Laycock and Richardson 1975). Excessive grazing pressure by cattle often will produce a range dominated by forbs, whereas excessive grazing by sheep will result in one dominated by grasses (Ellison 1954).

Sampson (1919) concluded that grazing by cattle to a level at which 50-60% of the palatable forage was cropped was acceptable in both mature stands and in young sucker stands of aspen. But similar levels of grazing by sheep damaged or killed most of the aspen suckers.

Figure 1.—Western coneflower is endemic on much of the aspen range in the West. Because it is not palatable to livestock, it is an increaser under grazing pressure. An understory dominated with this species usually indicates past or currently heavy grazing.

Figure 2.—An aspen sucker that was repeatedly browsed by livestock or wild ungulates, thus restricting its height to about 1 foot, even though it is at least 10 years old.

Browsing

Browsing has a direct impact on aspen trees in this forest community. Through the early sapling stage, browsing reduces aspen growth, vigor, and numbers (fig. 2). Heavy browsing by sheep can eliminate aspen sucker regeneration (Houston 1954, Sampson 1919, Smith et al. 1972) (fig. 3). Deer browsing, during a time of high population density, prevented aspen regeneration on small clearcuts as well as in the untreated aspen forest of southern Utah (Mueggler and Bartos 1977). Suckers can be drastically reduced or eliminated by big game browsing on their winter range (Graham et al. 1963, Krebill 1972, Packard 1942). Elk can be particularly damaging where they are concentrated on winter ranges near feed grounds[2] (Krebill 1972, Packard 1942), where they effectively can prevent successful aspen regeneration and eventually may eliminate aspen from the landscape (fig. 4).

In contrast, observations in western Wyoming and southern Idaho indicate that browsing by large populations of moose may markedly retard or even prevent subalpine fir regeneration in some areas.[3] Peek (1974b) cited selective browsing on subalpine fir trees; some seedlings or saplings were almost stripped by repeated browsing by moose, while other firs nearby were left untouched. Because subalpine fir is one of the major conifers to invade and ultimately replace seral aspen

[2] *Gruell, G. E. and L. L. Loope. 1974. Relationships among aspen, fire, and ungulate browsing in Jackson Hole, Wyoming. U.S. Department of Agriculture, Forest Service, Intermountain Region, and U.S. Department of the Interior, National Park Service, Rocky Mountain Region. 33 p.*

[3] *Personal communication from George Gruell, Intermountain Forest and Range Experiment Station, Missoula, Montana.*

stands, the presence of moose in these stands may retard conifer succession. However, moose can damage aspen stands, also. Where heavy browsing occurs on the same areas, moose have a height advantage over other herbivores. Moose also will obtain browse beyond the usual maximum height of their reach (8 feet (2.4 m)) by breaking down saplings of selected species. Telfer and Cairns (1978) documented breakage of aspen, balsam poplar, birch, and willow stems up to 4 inches (10 cm) d.b.h. by moose in Alberta. They cited similar moose behavior in Minnesota and Sweden.

Both browsing and grazing have seasonal impacts; browsing is seasonal by animal species, whereas grazing is seasonal because of forage availability. Domestic livestock browse the aspen with increasing pressure through summer and early fall. This browsing can be very severe, especially on young and succulent sprouts (fig. 5), and especially by sheep. But much of the browsing is incidental to grazing; if grazing is light to moderate, the browsing will be, also. This is particularly true for cattle, but less so for sheep and wild ungulates. Domestic sheep readily browse aspen suckers within their reach (Sampson 1919).

Deer predominantly browse during much of the year; but in summer, they primarily eat herbaceous material (Collins and Urness 1983, McCaffery et al. 1974, Smith 1952). Broad averages for the diets of mule deer in the West are 60%, 74%, and 49% composed of trees and shrubs in fall, winter, and spring, respectively (Kufeld et al. 1973).

In large numbers, elk can have a greater impact than deer on aspen because (1) elk are larger, eat more per animal, and are able to reach higher than deer; (2) elk may remain in the aspen zone throughout most winters, whereas snowpack depth in this zone usually forces deer to lower elevations for much of the winter and early spring; and (3) elk chew the bark off large aspen trees.

Figure 3.—Mature aspen stands that are heavily used by domestic sheep, such as this one in central Utah, do not regenerate successfully as the old trees mature and die.

Figure 4.—Aspen stands on heavily used elk winter range, illustrated here in western Wyoming, do not regenerate successfully when the overstory dies unless they are given protection.

The physiological effect on woody plants may be different if they are repeatedly browsed during the growing season than if browsed while dormant. Removal of a significant portion of the plant early in the growing season, just after full leaf growth, would have the greatest impact on a shrub or tree seedling. Carbohydrate reserves are lowest then (Schier and Zasada 1973). Repeated browsing of regrowth later in the same growing season would further weaken the plant. In contrast, browsing during winter may affect growth form and size but is less likely to kill. Winter browsing is a pruning process. Often, it appears that stored food reserves are used in the remaining portion of the plant for augmented growth during the next growing season.

Fortunately, browsing is least when it would have the greatest impact, because other succulent herbaceous forage is most abundant at the same time. Dormant season browsing, the pruning process, often causes shrubby growth forms to develop, a form that ultimately produces the maximum available browse annually (Willard and McKell 1978) for the animals during this season of greatest need. Repeated heavy browsing produces dense, hedged, shrubs out of most deciduous woody plants, including aspen. However, when browsed, aspen suckers will maintain better growth form than many hardwoods, because aspen usually sends up a single dominant shoot from the lateral bud immediately below the browsed terminal (Graham et al. 1963).

The impacts of browsing are greatest on shrubs and on trees less than approximately 13 feet (4 m) tall. In much of the West, most browsing pressure on aspen is from domestic livestock. Terminals of aspen sprouts are effectively out of their reach when they are only 5 feet (1.5 m) tall (Smith et al. 1972). Sheep will browse up to 45 inches (114 cm), cattle up to 5 feet (1.5 m) (Sampson 1919). When pressed for browse, white-tailed deer, at least, will break off stems that are 0.8 inch (2 cm) diameter at the height they can reach (Graham et al. 1963).

Dense even-aged stands of aspen can withstand considerable tree loss during these early years, as long as approximately 400 well-formed stems per acre (1,000 per ha) remain when they reach the 13-foot (4-m) height. Sampson (1919) recommended at least 2,500 sprouts per acre (6,200 per ha) after 3 years, or when about 3 feet (1 m) tall. In New Mexico, it took 6 to 8 years growth before aspen suckers stimulated by fire outgrew the reach of deer and elk (Patton and Avant 1970). After bigtooth aspen were clearcut in Michigan, Westell (1954) estimated young sucker stands of approximately 10,000 stems per acre (25,000 per ha) could yield 100 to 150 deer days use per acre (250 to 375 per ha) per year for the first 3 years without undue damage to the developing forest. However, sucker stands in the Lake States grow about twice as fast during early development than do aspen in much of the mountain West.

Advanced regeneration in uneven-aged aspen stands usually is sparse and comparatively slow-growing. An equal browsing pressure will impact these sucker stems more severely and for a longer time than it would a dense stand of fast-growing, even-aged suckers that resulted from fire or clearcutting (figs. 3 and 4). Yet, the uneven-aged aspen stand is dependent for its perpetuation on these low-density, slower-growing suckers in the understory. In Wyoming, for example, wild ungulate browsing in mature aspen stands effectively prevented regeneration even as the stands broke up[2] (Beetle 1974, Krebill 1972).

Animals other than ungulates browse aspen and associated woody plants. Snowshoe hares and cottontail rabbits nip off young suckers. Their effects have not been quantified in much of the aspen type in the West; but their impacts appear to be incidental in the southern Rocky Mountains. This may not be so in Canada and Alaska, where snowshoe hare abundance at cyclic peaks may exceed the winter food supply. More than 50% of available browse (less than 0.5 inch (1.5 cm) diameter) was removed in winter by hares during population highs in Alberta (Pease et al. 1979).

Beaver, pocket gophers, and perhaps porcupines also may "browse." Again, the impacts of this browsing have not been adequately measured. Pocket gophers may feed on young aspen sprouts and may be destructive locally, especially if their populations increase after clearcutting (Marston and Julander 1961).

Barking

Among the hardwoods, aspen is especially susceptible to gnawing or stripping of its bark by several species of mammals. In the West, elk are the primary barkers of mature aspen stems (fig. 6). Most of this damage is restricted to elk winter ranges. Where the animals are concentrated, such as near artificial feed grounds, bark damage or removal can be quite severe and can adversely affect the aspen stand (Krebill 1972, Packard 1942). Other members of the deer family, particularly moose, may chew bark from aspen trees. Evidence of moose barking aspen trees on their summer range has been observed in both Wyoming and Utah.[4] Such damage must be incidental, because reports in the literature are lacking.

Figure 5.—Cattle were excluded from the area to the left of the fence since herbicide spraying in 1965. Grazing continued on the right. After 18 years, within the exclosure profuse aspen suckers are likely to develop into trees despite light browsing by both deer and elk. Only aspen skeletons and severely browsed aspen suckers are found on the outside.

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[4] *Personal communications from George Gruell, Intermountain Forest and Range Experiment Station, Missoula, Montana; and Philip Urness, Utah State University, Logan, Utah, respectively.*

All native members of the deer family may use small trees, often aspen, to rub the velvet from their antlers in late summer. This strips off much of the bark. Although this can be disastrous for the individual tree, the impact to the forest as a whole is insignificant.

Rabbits and hares may remove bark for food. This may girdle small trees. A high population density and a shortage of other palatable foods can result in damage to aspen sprouts and saplings. Dickmann (1978) found marked differences in the amount of winter bark damage by rabbits among poplar clones in Michigan. Rabbits and hares feed upon buds, twigs, and bark in winter; then, like the ungulates, they switch to more succulent plant material in the growing season.

Mice and especially voles may eat large patches of the surface bark from aspen trees in winter. The damage can extend from ground level up through the entire snowpack depth (see figure 2 in the MORPHOLOGY chapter). This barking may be extensive on most stems in a stand when these rodent populations are at a peak. It can kill sprouts and small saplings (Baker 1925, Sampson 1919); but on larger trees, most of the damage is superficial, because only the periderm is removed. However, subsequent drying and cracking of this damaged bark could provide a source of entry for disease organisms (Krebill 1972).

Porcupines readily remove the bark from aspen. Where both hardwoods and softwoods are available, porcupines appear to prefer the smooth barked hardwoods and hemlock as food sources (Curtis 1941, Krefting et al. 1962). Lynch (1955) reported aspen bark removal by porcupines and snowshoe hares in the grovelands of northwestern Montana. Graham et al. (1963) stated that porcupine injury was restricted to locations where they are especially numerous. In summer, their feeding on leaves and twigs was incidental. But, in winter, porcupines fed on the smooth bark of the trunk and branches; they removed the periderm, and exposed the inner bark and cambium to desiccation and possible death, thereby girdling trees. Graham et al. (1963) reported extensive destruction of merchantable aspen by porcupines on restricted areas of Michigan.

Budding

Aspen buds are an important winter food source for wildlife. Hares, rabbits, and small rodents may feed on the buds and twigs near ground level. Birds may remove buds at any level. Ruffed grouse particularly depend on aspen buds as a winter food. In Utah, aspen buds made up 85% of the volume in the crops of winter-harvested grouse (Phillips 1967). In the Lake States, they feed almost exclusively upon male aspen floral buds during the winter (Svoboda and Gullion 1972). The total impact of budding on the aspen forest has not been assessed; but it does not appear to be a significant ecological impact on the plant community.

Figure 6.—Elk chew the bark from aspen trees on their winter range. On heavily used range, this can have a significant impact on the mature trees. Although girdling is not common, the damage provides entry for pathogens.

Cutting

Only beaver, among the animals, has the ability to cut and, in part, remove saplings to mature sized aspen trees. Throughout most of their range, beaver are virtually dependent upon the willow family, of which aspen is a part, for their sustenance. However, they will use other hardwoods and shrubs for food, notably cherry (*Prunus* spp.), alders (*Alnus* spp.), maple (*Acer* spp.), and serviceberry (*Amelanchier* spp.) (Bailey 1922).

They cut aspen of all diameters, feed on the bark and small branches of the felled trees, and utilize stems of medium diameter in their dams (fig. 7). Trees more than 3 feet (1 m) in diameter have been cut; but seldom are those greater than 4-6 inches (10-15 cm) diameter cut into bolts and moved from where they fall (Bailey 1922). This results in clearcut, and often flooded, areas in the vicinity of each beaver dam. The cutting progressively will extend away from the stream. The distance away depends upon the area flooded by the dam, the ability of beaver to extend canals beyond the stream or flooded area, and the courage or success of beaver while exposing themselves to predation while on land.

Typically, beaver activity extends about 300 feet (100 m) from the water, except where steep slopes facilitate skidding (Graham et al. 1963). Often, about 1 acre (0.4 ha) is included in the ponded and clearcut area around a colony; the area may be larger where slopes are gentle. Usually, a series of dams are built in the stream, and the aspen along the entire reach are used.

The meadows adjacent to many mountain streams in the West probably were caused by high beaver populations in the past. Graham et al. (1963) lamented that some of the finest aspen growing along streams and lakes in Michigan in 1920 was cut by beavers and later replaced by other vegetation, such as bracken fern, conifers, grass, and brush. Flooding for several years kills aspen roots in the inundated areas. When the dams fail, willows and grasses invade the floodplains. The willows alone may support later beaver colonies (Hall 1960, Packard 1942). Reinvasion of these formerly inundated areas by aspen suckers is a very slow process that is dependent upon the growth of roots from aspen adjacent to the meadow. Also, after a dam fails, it may be several years before the previously flooded soil will again support a vigorous forest stand (Wilde et al. 1950).

In summary, beaver effects can be placed into two categories: that from cutting alone, and that from dam building and flooding. Cutting alone stimulates abundant suckering. If beaver abandon that section of the stream for a sufficient time (15 or more years) and ungulate use is not excessive, a new stand of aspen will develop (fig. 8). Flooding changes the entire plant community and, to some extent, even the landscape. Siltation behind beaver dams results in a series of benches, each relatively flat and wet (often too wet for aspen to develop), along the stream course. These benches may remain dominated by other vegetation for centuries.

Trampling

Virtually all of the trampling damage in the aspen type is associated with grazing and browsing by ungulates, usually sheep and cattle. Sometimes elk do equal damage immediately after snowmelt, where they are concentrated on and near their winter ranges (Packer 1963). Humans trample much vegetation in areas of critical concern to managers, such as developed campgrounds, where soil and plant cover may be markedly altered (Wagar 1964).

Figure 7.—Beavers clearcut aspen within range of their lodges. Bark and twigs are used as food; branches and small stems are used for construction of lodges and dams.

Figure 8.—Successful aspen regeneration several years after beavers clearcut the parent stand, exhausted the food supply, and then abandoned the site.

Trampling smashes vegetation that is stepped on, crushes the litter cover on the soil surface, and compacts the mineral soil immediately underneath (Lull 1959). Although research has seldom effectively separated the effects of trampling from those of grazing or browsing (Laycock and Harniss 1974), for practical purposes, they do not need to be separated. It is impossible for grazing or browsing to occur without trampling. Their combined effects on the plant community and related soil-watershed conditions usually are reported as effects of grazing.

Marston (1952) and Meeuwig (1970) both reported that a ground cover (plants, litter, and rock) of 65% or more was necessary on most aspen covered range in the mountainous West to control overland runoff and erosion. Excessive grazing, browsing, and trampling will readily reduce cover below this threshold level. Downstream damage may be dramatic and severe, such as along the Wasatch front during the 1920s and 1930s (Bailey et al. 1934, 1947). (Watershed effects are discussed more fully in the WATER AND WATERSHED chapter).

Some plant communities can be damaged by trampling, whether or not the plants are grazed or browsed. This applies particularly to the aspen type, where an abundance of species grow in a loose, friable, soil that usually is completely covered with litter and is high in organic matter. In most aspen communities, the mix of plant species that occupies a surface after years of severe trampling likely will be much different than that on an undisturbed surface.

Unless severe enough to decrease stocking at stand maturity, trampling of aspen suckers by livestock would only reduce initial growth, perhaps setting it back 2 to 4 years in a heavily impacted stand. Sampson (1919) considered trampling effects by both sheep and cattle on aspen suckers to be light in his Utah studies. Cattle trampled fewer than 10% of the sprouts on several cut sites in Utah; snow damage probably was greater (Smith et al. 1972). However, there is serious concern that this damage provides entry for disease and stain-producing organisms. Hinds[5] found staining was especially common in the wood of aspen suckers growing on sites that had received moderate to heavy livestock grazing during the first few years after clearcutting, during the time that the suckers were young, were less than 9-10 feet (3 m) tall, and were easily damaged by cattle.

Digging

Pocket gophers cultivate aspen soils by burrowing immediately beneath the soil surface during the snow-free season, and at the surface during winter and spring. The material moved by underground burrowing is pushed to the surface as small mounds of mineral soil. After snowmelt, the soil surface activity under a snowpack leaves what appears to be the equivalent of giant-size worm castings of mineral soil lying atop the litter layer (fig. 9).

Pocket gopher activity has been studied on many western range sites. Much of this research has emphasized the gopher's effect on the plant community, especially the impact on forage production, and adverse effects on conifer regeneration (Crouch 1982). Pocket gophers may consume up to 23% of the net belowground plant productivity in the aspen type (Andersen and MacMahon 1981). Gopher activity may turn over 5 tons of soil per acre (11 metric tons per ha) per year; this soil then covers about 3.5% of the surface (Ellison 1946). Fresh mounds and castings provide new microsites for invading, seral understory plant species, especially annuals and aggressive perennials, such as western coneflower. The important invading species in northern Utah were: *Nemophila breviflora, Polygonum douglasii, Veronica biloba, Bromus carinatus, Rudbeckia occidentalis, Agropyron trachycaulum*, and *Senecio serra* (McDonough 1974). Succession occurs, and these species give way to a preponderance of perennials after 3 to 4 years. It appears that pocket gopher activity may contribute to plant species diversity within the aspen understory by providing a continuous series of microsites for plant establishment and succession (Laycock 1958, McDonough 1974). Thus, there is always a niche for plants at all stages in the aspen understory sere.

igure 9.—Pocket gophers turn over and expose a significant amount of mineral soil in many stands. Winter activity under the snow leaves soil castings on the litter surface. Summer activity leaves small conical mounds of soil.

Pocket gopher digging may be severe enough, especially if plant cover is depleted by other causes, to further destroy cover and expose soil to overland flow and erosion (Ellison 1946, Marston and Julander 1961).

Several other mammals dig in the aspen forest type. Their combined effects probably are less than that from pocket gophers alone. Individually, their effects probably are insignificant. Some of these animals are: beaver, small burrowing rodents and shrews, and the predators that pursue these burrowing creatures—skunk, badger, coyote, bear, and others. The digging by all except beaver is scattered throughout the aspen type. Canal digging and bank burrowing by beavers is concentrated, as noted earlier, to a relatively narrow zone adjacent to streams and the inundated zone behind each beaver dam.

Digging directly affects the soil itself. Organic matter is mixed into the mineral soil. If enough is turned over annually, as it is in much of the aspen forest, a mineral soil horizon rich in organic matter forms beneath a relatively thin litter layer (Tew 1968). Digging by all creatures, from earthworms to mammals, decreases soil bulk density and provides an abundance of macropores in the disturbed soil. Laycock and Richardson (1975) found pocket gopher activity to apparently increase noncapillary porosity, organic matter, nitrogen, and phosphorus in the mineral soil. This increases the amount and rate of water infiltration and percolation, and alters the rooting media for plants. Some plant species may be favorably affected, others unfavorably. Large pores in a well aerated and dry soil will kill some plant roots by desiccation. In other instances, these pores may provide root passages through dense and virtually impermeable clays.

Other Impacts

The remaining impacts on the aspen ecosystem by animals are relatively minor; but some are visually significant. These include nest construction and related activity by birds, cavity building or enlarging by birds, and feeding activities by woodpeckers and sapsuckers.

Nest building and related breeding activities of all avian species that do not nest in cavities have no apparent effect on the plant ecosystem. (However, the converse is very significant—plant community structure, for the most part, controls what bird species will be found in the aspen ecosystem.)

Cavity nesting birds include more than 40 species in the Southwest alone, most of which inhabit the aspen

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[5] *Personal communication from Thomas E. Hinds, Rocky Moun-ain Forest and Range Experiment Station, Fort Collins, Colo.*

and mixed conifer types (Scott and Patton 1975). Some, such as flickers, excavate their own nest cavities. Others, such as the small owls, use natural or abandoned nest cavities. When cavities are made in live trees, damage may occur, usually by entry of decay organisms (fig. 10). However, most cavity excavation in aspen occurs in dead portions of trees or in trees that already have heartrot. The beneficial effects of the cavity nesters in controlling forest insect pests far outweighs any possible damaging effects from occasional cavity construction in live trees.

Woodpeckers remove insects from beneath the bark of infested trees. They rid the tree of damaging larvae and, at times, adult insects; but their feeding also provides portals for disease organisms to enter the tree. Most biologists and foresters feel that the balance is positive for a healthy forest. The removal and control of insect pests more than compensates for the risk of disease or decay at a later time.

Feeding on the sap or cambial layer of aspen and other hardwoods by sapsuckers has a direct impact on the tree (fig. 11). Sapsucker holes provide many ports for microorganisms to enter the tree, thus changing what is probably an innocuous impact into a potentially important one. Packard (1942) reported sapsucker damage on trees larger than 2 inches (5 cm) diameter was common in Rocky Mountain National Park, in Colorado. Almost all trees with sapsucker holes were infected with *Cytospora* fungus. Yet, with the exception of local damage, sapsuckers apparently are not numerous enough to have a significant negative impact on aspen in the West. The negative aspects of sapsucker feeding on aspen trees is partially offset by their consumption of insects.

Figure 10.—Woodpeckers excavate nest cavities in live aspen trees.

Figure 11.—The yellow-bellied sapsucker feeds on insects in aspen, leaving horizontal lines of holes in the bark, which may become portals for pathogen entry.

Combined Influences

There are interactions and interspecific competition among the animals inhabiting the aspen ecosystem. There are also coactions by these species upon the supporting plant community. The coactions are considered here, with competition and interactions among animals discussed only as they influence the aspen plant community. Most past research deals with livestock versus big game, with different species of livestock, and with pocket gophers versus livestock.

Cattle and Sheep

Most of the western aspen type is grazed by cattle and/or sheep. Generally, the low- to mid-elevation aspen lands are predominantly grazed by cattle, and the forage on high elevations is grazed by sheep. However, because cattle prefer grass, those ranges with an abundance of grass, either in the understory or as extensive mountain grasslands and meadows, are often reserved for cattle, and the aspen lands with a predominance of forbs in the understory are used for sheep. Sometimes, especially on private lands, both graze. If grazing is heavy, the combined effect of both can be disastrous to the aspen community. The sheep remove the forbs and browse; the cattle remove the grass and some forbs and trample the remainder; and only the large trees remain undamaged.

In most instances, cattle and sheep grazing are separated by space or time. Generally, sheep pass through an area at the height of the growing season, devour half or more of what is available and palatable, and then move on. Although the grazed area appears denuded of desirable forage immediately afterwards, the rest of the summer remains for vegetation recovery. Cattle, in contrast, may have much less of an immediate impact; but they usually remain on an area for much of the growing season. Although the grasses keep regrowing and provide a continuous forage supply, the impact of cattle grazing on the rest of the plant community is cumulative. Especially near water supplies, where cattle tend to congregate, most palatable plants, other than large trees and sod-forming grasses, are virtually removed from heavily grazed ranges by the end of most growing seasons.

When grazed at similar intensities, sheep were four times more destructive to aspen suckers than cattle (Sampson 1919). They readily browsed to more than a 3- to 4-foot (1-m) height, whereas cattle selected herbaceous material, if available. Sampson (1919) felt that sheep grazing should be prevented in aspen clearcuts for 4 or 5 years after harvest to permit the sucker stand to grow out of their reach, but that light grazing by cattle was acceptable.

Cattle and Elk

Cattle and elk compete because they both graze and both prefer grasses when succulent forbs are not available. The summer ranges of cattle and elk overlap, although the elk commonly retreat to the steeper, higher, and more inaccessible areas. Where they overlap, there is some competition for choice forage. After the impact of livestock, the additional impact of elk scattered over their summer range is seldom even measurable.

There is real potential for competition and for compounded impact by cattle and elk on the elk winter range that is grazed by cattle during summer. If snow depth is not excessive, elk will paw it away and feed on the grasses and forbs that remain. If these were removed by cattle during the previous growing season, the elk will be forced to rely upon any available browse or upon supplementary feed. Available browse often includes aspen sprouts and understory shrubs in the aspen ecosystem.

Cattle, Sheep, and Deer

Deer summer range and cattle grazing areas overlap throughout the aspen type in the West. If grazing is light to moderate, there appears to be little competition. The cattle graze principally grass; the deer browse and graze principally forbs. Deer use is scattered and light. If grazing by cattle is heavy, especially on overstocked deer range, severe competition for choice browse and forbs can occur (Julander 1955). Deer winter range generally is below the aspen zone.

Sheep and deer compete, especially for forbs, on the summer range. But, again, comparatively speaking, deer use is scattered and light, and probably has little additional impact on the plant community after moderate to heavy grazing by sheep.

Sheep and Elk

Sheep grazing upon elk winter range can have greater impact upon the available forage for elk and upon the plant community than does cattle grazing. With proper management, however, that need not be true. For example, late spring and early summer grazing by sheep on a big game range in northern Utah was mostly on herbs and, therefore, had a negligible impact on browse production (Jensen et al. 1972).

Sheep use of forage under aspen on the elk summer range influences the use of that range by elk, at least temporarily. Both then prefer forbs (Jensen et al. 1972, Mackie 1970). Without available succulent forage, and without appreciable cover at ground level, the elk will literally move on to "greener pastures." On summer ranges, domestic sheep use usually predominates, and the scattered use by elk is barely discernible.

Deer and Elk or Moose

The large wild ungulates compete with each other to some degree. In large numbers, elk will adversely impact deer ranges. Elk are less selective than deer. Their ability to utilize a greater variety of forage give elk a competitive advantage (Collins and Urness 1983, Mackie 1970). However, most of the important competition is on the winter range, where both species plus moose may be concentrated during severe winters on critical but relatively small areas. Most of these areas are in the brushlands below the aspen elevational zone. If aspen is present, and two or three of these species simultaneously browse it, a severe and lasting impact on the aspen sucker and sapling stand is likely.

Gophers and Grazers

Pocket gophers and grazing ungulates directly compete for many of the same plant species. If pocket gopher populations are high and grazing pressure is heavy, the combined impact can reduce plant cover below acceptable levels, can change composition to a less productive seral stage, and can have an impact on range carrying capacity.

PART III. RESOURCES AND USES

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FORAGE

W. F. Mueggler

The extensive forests and isolated clones of quaking aspen in the western United States have been valued for many years as wildlife habitat and livestock summer range (Sampson 1919). The actual amount of forage produced beneath the aspen trees differs appreciably among sites. Houston (1954) indicated that although many sites produce 1,000 to 2,000 pounds per acre (1,120 to 2,240 kg per ha), some produce more than 4,000 pounds per acre (4,480 kg per ha), and others less than 500 pounds per acre (560 kg per ha). Such variability is caused by environmental differences, levels of livestock grazing, and the successional status of the community.

Ellison and Houston (1958) noted that although aspen communities are generally capable of supporting much forage for livestock and wildlife (fig. 1), most aspen communities in the Intermountain Region have been depleted by prolonged overgrazing. Overgrazing probably has adversely affected many aspen rangelands throughout the West (see the ANIMAL IMPACTS chapter). Excessive grazing generally alters forage composition (fig. 2) and frequently reduces production (Houston 1954). Fortunately, unless grazing abuse is extreme, the potential productivity of most sites is not reduced appreciably by soil erosion. However, livestock grazing (Sampson 1919) and also local concentration of big game animals can jeopardize the perpetuation of aspen dominated communities (see the ANIMAL IMPACTS chapter).

Forage Composition and Use

As discussed in detail in the VEGETATION ASSOCIATIONS chapter, the undergrowth of aspen communities in the West is generally composed of a multilayered, complex mixture of shrubs, forbs, and graminoids. In the Intermountain Region, this mixture consists of an almost unlimited combination of some 300 species (Houston 1954). Costello (1944) reported that 10 to 15 species of graminoids, 20 to 40 species of forbs, and several shrubs are commonly encountered on a single, 100-foot-square (9-m^2) area, on aspen rangelands in Colorado and Wyoming. Such species diversity is typical of aspen communities throughout the West. However, exceptions exist where only a few species of graminoids and forbs are prominent. Such floristic simplicity may be attributed to a long period of grazing abuse (Costello 1944, Beetle 1974), to the effects of a coniferous understory, or also may reflect the natural undergrowth characteristics of adjacent vegetation types (Houston 1954) (fig. 3).

Not all plants within a community produce forage. Plant species differ greatly in relative palatability to grazing animals, and different kinds of animals prefer different plants. A common perception is that sheep and deer prefer forbs and browse, and cattle prefer grass. Although these ungulates can be highly selective in forage preferences, they are also very adaptive. Even plants somewhat distasteful to the animals will be readily eaten if little else is available. In complex vegetation, such as the aspen type, many species are eaten by all kinds of grazing animals. The most palatable are often specifically sought out and usually the first to decrease under continued grazing pressure; species not readily eaten frequently increase in abundance because of reduced competition. As the more palatable species decrease, the less palatable are more readily eaten. Under prolonged grazing, then, community composition changes gradually to a mix of fewer species and greater abundance of plants low in palatability.

Figure 1.—Many aspen communities in the West can support a wide variety of undergrowth species that produce more than 2,000 pounds per acre (2,240 kg/ha) of forage for livestock and wildlife.

Figure 2.—Prolonged sheep grazing gradually can alter a rich mixture of forbs and graminoids in aspen undergrowth into grass-dominated cover with little species diversity (Dixie National Forest, Utah).

These changes in species composition under grazing can be used as indicators of general forage preferences. Forage desirability ratings of species commonly are based upon this concept. Table 1 lists desirable, intermediate, and least desirable livestock forage species frequently found in aspen communities in the West.

Table 1 does not distinguish differences in palatability between kinds of animals nor differences attributable to the amount of each species that is present. For example, many of the forbs and shrubs listed as intermediate may be avidly eaten by sheep, but only moderately by cattle; the reverse would be true for grasses and sedges. Usually the more abundant a moderately palatable species is in the community, the less will be eaten of each individual of that species. However, intense grazing pressure may force animals to eat even the least desirable species.

In some instances, a species which is quite palatable to one kind of animal may be toxic to another. *Delphinium barbeyi* and *D. occidentale* (tall larkspurs), common members of aspen communities in the West, are readily eaten by sheep but are highly poisonous to cattle.

In one of the few studies of actual forage consumption by livestock in the aspen type, Paulsen (1969) found that a sedge, *Carex geyeri*, and a forb, *Thalictrum dasycarpum*, provided most of the forage consumed by cattle on Black Mesa, in Colorado. Other major forage producing forbs on this cattle range were *Helianthella quinquinerius*, *Erigeron macranthus*, *Lathyrus leucanthus*, and *Agoseris* spp. Paulsen found that the forbs, as a group, decreased in the cattle diet as they became dry toward the end of August, even though their content of crude protein, phosphorus, and calcium remained adequate for animal nutrition. Costello (1944) found that *Symphoricarpos oreophilus* (a shrub) and *Carex* spp. were valued sheep forage in the aspen type of Colorado and Wyoming. He also observed that the continued presence of *Thalictrum fendleri*, *Vicia americana*, *Lathyrus leucanthus*, and *Galium boreale* were indicators of moderate but not excessive sheep use; these species became scarce with prolonged, heavy sheep grazing.

Figure 3.—The unusually species poor undergrowth dominated by pine grass in this aspen community within the Cliff Lake Bench Natural Area, in southwestern Montana, reflects the natural undergrowth characteristics of nearby lodgepole pine stands.

Wild ungulates have somewhat different forage preferences than livestock. Smith (1952) found the following species to comprise the bulk of the summer diet of deer in the aspen forests of central Utah: *Populus tremuloides*, 27%; *Lupinus alpestris*, 27%; *Stipa columbiana*, 4%; *Carex* spp., 3%. Collins (1979) and Collins and Urness (1983) determined summer diet composition of both deer and elk in an aspen forest in north central Utah. Using a bite-count technique with tame animals enabled them to determine species preferences on a dry-weight intake basis (table 2). The most abundant undergrowth species were *Symphoricarpos oreophilus*, *Agastache urticifolia*, *Rudbeckia occidentalis*, *Prunus virginiana*, *Valeriana occidentalis*, *Mertensia arizonica*, and *Senecio serra*. The diet of the deer consisted of 38% shrubs, 61% forbs, and less than 1% graminoids; the elk diet consisted of 24% shrubs, 51% forbs, and 25% graminoids.

Aspen reproduction is a nutritious forage that, when abundant, can form a substantial portion of the diet of both livestock and wild ungulates. Tew (1970b) found that aspen leaves averaged 17% protein in June, 13% in July, and 12% in September; fat content averaged 7% in June, 8% in July, and 10% in September. The variation in nutrient content between clones, however, can be substantial.

The bark and wood of mature aspen trees also has a potential value as livestock feed. Baker, et al. (1975) determined aspen bark to be about 50% digestible and aspen wood about 35% digestible by both in vitro and in vivo tests. Singh and Kamstra (1981) found that ground and pelleted aspen wood, supplemented with soybean meal, could comprise as much as 48% of the diet of growing cattle without adversely affecting weight gains and meat quality. Aspen pellets made from whole trees also can substitute for half of the corn silage roughage ordinarily fed lactating dairy cows when they are past peak production (Schingoethe et al. 1981). Steam-cooked aspen wood is very similar to alfalfa in energy digestibility, and presumedly can satisfactorily replace much of the hay ordinarily used in ruminant feed (Al-Rabbat and Heaney 1978). Feeding trials indicate that steamed aspen can make up 30% of the dry matter diet of beef steers without adversely affecting gains or meat quality (Sharma et al. 1980), and that up to 30% steam-processed aspen chips can be used as a roughage substitute in maintenance rations for mature sheep (Sharma et al. 1979).

Forage Productivity

Productivity within a vegetation type is usually expressed as total annual production of above-ground herbage. This often is separated into vegetation classes, and sometimes it is categorized by species. Such total productivity figures, however, are only an index of usable forage production. The term "usable forage" ap-

Table 1.—Common undergrowth plants in western aspen forests, categorized according to desirability as livestock forage (Houston 1954).[1,2]

Desirable	Intermediate	Least desirable
Angelica spp.	*Amelanchier alnifolia*	*Achillea millefolium*
Aster engelmannii	*Agropyron subsecundum*	*Arnica* spp.
Deschampsia caespitosa	*Agastache urticifolia*	*Artemisia* spp.
Glyceria spp.	*Bromus marginatus*	*Aster* spp. (low)
Heracleum lanatum	*Calamagrostis rubescens*	*Berberis repens*
Ligusticum spp.	*Carex* spp.	*Circium* spp.
Mertensia spp.	*Erigeron* spp.	*Cerastium* spp.
Osmorhiza spp.	*Elymus glaucus*	*Epilobium* spp.
Phleum spp.	*Festuca* spp.	*Eriogonum* spp.
Polemonium spp.	*Galium boreale*	*Fragaria* spp.
Trifolium spp.	*Hackelia floribunda*	*Geranium* spp.
	Lupinus spp.	*Geum* spp.
	Melica spp.	*Helenium hoopesii*
	Pachistima myrsinites	*Iris* spp.
	Poa spp.	*Lathyrus* spp.
	Prunus virginiana	*Lonicera* spp.
	Rosa spp.	*Madia* spp.
	Sambucus spp.	*Nemophila breviflora*
	Senecio serra	*Pedicularis* spp.
	Symphoricarpos spp.	*Penstemon* spp.
	Thalictrum spp.	*Phlox* spp.
	Valeriana spp.	*Potentilla* spp.
	Vicia americana	*Pteridium aquilinum*
		Rudbeckia occidentalis

[1] *U.S. Department of Agriculture, Forest Service. 1968. Range environmental analysis handbook. U.S. Department of Agriculture, Forest Service, Rocky Mountain Region, Denver, Colo.*

[2] *U.S. Department of Agriculture, Forest Service. 1970. Range environmental analysis handbook. U.S. Department of Agriculture, Forest Service, Intermountain Region, Ogden, Utah.*

Table 2.—Composition of deer and elk summer diets (percentage of total weight consumed) in an aspen forest in north central Utah (Collins 1979).

Deer		Elk	
24%	*Symphoricarpos oreophilus*	20%	*Symphoricarpos oreophilus*
14%	*Valeriana edulis*	15%	*Aster foliaceus*
13%	*Aster foliaceus*	14%	*Agropyron subsecundum*
10%	*Vicia americana*	6%	*Thalictrum fendleri*
10%	*Lathyrus lanzwertii*	5%	*Heracleum lanatum*
6%	*Populus tremuloides*	5%	*Bromus carinatus*
3%	*Aster engelmannii*	5%	*Aster engelmannii*
3%	*Amelanchier alnifolia*	5%	*Lathyrus lanzwertii*
3%	*Agastache urticifolia*	4%	*Vicia americana*
		4%	*Populus tremuloides*
		3%	*Mertensia arizonica*
		3%	*Erigeron peregrinus*

lies to that portion of the total palatable vegetation that an be eaten by grazing animals without adversely afecting long-term plant vitality. Usable forage can be onverted to grazing capacity in animal unit months AUM); an AUM is one cow or five sheep for a 1-month eriod. Capacities are expressed either as the number f acres required to sustain one AUM (acres per AUM) r, conversely, the number of AUMs that can be carried n 1 acre (AUMs per acre). Recommended grazing apacities developed by the Routt National Forest in Colrado[1] for the aspen-weed type in various condition lasses are:

Range condition	Acres per AUM	Hectares per AUM
Excellent	4–5	1.6–2.0
Good	5–6	2.0–2.4
Fair	7–10	2.8–4.0
Poor	13–20	5.3–8.1

Usually, however, the amount of usable forage produced in aspen communities must be inferred from published figures on total above-ground biomass of undergrowth vegetation. These are most often expressed in the literature as air-dry production of annual herbage growth.

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[1] *U.S. Department of Agriculture, Forest Service. 1968. Range en-ironmental analysis handbook. U.S. Department of Agriculture, orest Service, Rocky Mountain Region, Denver, Colo.*

Geographical Variation

Forage production is considerably less in both the northern and southern portions of aspen's geographical distribution than in the central portion. Pringle et al. (1973) reported herbage yields from aspen communities in northern British Columbia and Alberta as low as 103 pounds per acre (115 kg per ha). Bailey and Wroe (1974) reported average annual yields of 462 ± 68 pounds per acre (518 ± 76 kg per ha) in the aspen groves of Alberta parklands. In Arizona, near the southern distribution of aspen forests, Reynolds (1969) found aspen groves producing 245 pounds per acre (275 kg per ha) of dry herbage, about an equal mix of forbs and grasses. Patton (1976) reported even lower figures—100 pounds per acre (112 kg per ha)—for an aspen-conifer forest in Arizona.

Farther north, on the Dixie National Forest, in southern Utah, Smith et al. (1972) found undergrowth production of an aspen community was 802 pounds per acre (898 kg per ha), 50% of which was forbs, 49% grass, and 1% shrubs. On the Fishlake National Forest, in southern Utah, air-dry undergrowth production in two ungrazed aspen communities was between 625 and 758 pounds per acre (700 and 850 kg per ha), more than 50% of which was forbs (Mueggler and Bartos 1977). Harper found understory production of aspen communities on the Manti-LaSal National Forest, in central Utah ranged from 700 to 1,700 pounds per acre (785 to 1,905 kg per ha).[2] On the Wasatch National Forest, in northern Utah, air-dry production of undergrowth vegetation ranged from 401 to 2,052 pounds per acre (449 to 2,300 kg per ha); the average was 1,088 ± 78 pounds per acre (1,219 ± 87 kg per ha).[3]

Still farther north, on the Bridger-Teton National Forest in western Wyoming, Youngblood and Mueggler (1981) found undergrowth production in different community types ranged from an average of 330 pounds per acre (370 kg per ha) in the least productive types to 2,095 pounds per acre (2,348 kg per ha) in the most productive type. In this same area, Bartos and Mueggler (1979) found production from three clones growing on a fairly dry hillside averaged 1,472 pounds per acre (1,650 kg per ha); between 55% and 75% of this was forbs, 12% to 35% was grass, and 10% to 27% was shrubs. Undergrowth herbage production from a sample of 144 aspen stands on adjacent National Forests in eastern Idaho ranged from 244 to 2,047 pounds per acre (273 to 2,294 kg per ha), and averaged 937 ± 34 pounds per acre (1,050 ± 38 kg per ha) (Mueggler and Campbell 1982). Composition of this herbage averaged 13 ± 2% shrubs, 45 ± 2% forbs, and 42 ± 2% graminoids. Overall suitability of the herbage as livestock forage averaged 55% desirable, 40% intermediate, and 5% undesirable. Both production and composition of the undergrowth varied appreciably among the 23 community types described.

Production of aspen undergrowth in northern Nevada ranged between 800 and 1,700 pounds per acre (897 and 1,905 kg per ha);[4] and in western Oregon (Hall 1973), production was about 1,400 pounds per acre (1,569 kg per ha). Woods et al. (1982) found the range in undergrowth production of 20 stands in northern Colorado was 498 to 2,028 pounds per acre (558 to 2,273 kg per ha), with an average of 1,482 pounds per acre (1,661 kg per ha). A sampling of 12 stands in the Black Hills of South Dakota yielded 479 to 1,186 pounds per acre (537 to 1,329 kg per ha), about equally divided among forbs, grasses, and shrubs (Severson and Kranz 1976).

Forest Versus Openings

Despite considerable forage production in most aspen communities, the overstory trees compete with the undergrowth plants for moisture, light, nutrients, and space. Consequently, adjacent vegetation types lacking such overstory competition potentially may produce more forage than the aspen forest. Bailey and Wroe (1974) found this true in Alberta, where aspen groves produced an average 462 pounds per acre (518 kg per ha) of undergrowth, whereas adjacent *Festuca scabrella* grasslands produced 1,795 pounds per acre (2,012 kg per ha). Paulsen (1969) reported similar findings for western Colorado; only half as much herbage was produced by aspen undergrowth as in adjacent *Festuca thurberi* grasslands. Ellison and Houston (1958) noted that undergrowth vegetation in aspen communities in Utah was typically taller and more productive than in openings within or adjacent to the aspen. They attributed this to a combination of heavier grazing and a harsher microenvironment in the openings. They found that where the vegetation had not been subjected to a history of livestock grazing, production in the openings exceeded that under the aspen.

Stand Density and Conifer Succession

In most forest types, the more tree overstory there is, the fewer herbs and shrubs there are. This generalization applies to aspen forests that are rapidly seral to conifers, but usually not to mature aspen communities that are stable. Warner (1971) examined 42 pure aspen stands in Utah and found no significant relationship between numbers of stems greater than 4 inches (10 cm) d.b.h. and undergrowth production. Harper[2] found no correlation between the basal area of aspen trees and annual production of undergrowth vegetation in central Utah. He determined, however, that undergrowth production decreased progressively as the proportion of conifers in the stands increased.

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[2] *Data provided by K. T. Harper, Department of Botany and Range Science, Brigham Young University, Provo, Utah.*

[3] *Data on file at the Intermountain Forest and Range Experiment Station's Forestry Sciences Laboratory at Utah State University, Logan, Utah.*

[4] *Information obtained from two typescript documents. Lewis Mont E. 1971. Flora and major plant communities of the Ruby-Eas Humboldt Mountains. U.S. Department of Agriculture, Forest Service, Intermountain Region, Humboldt National Forest, 62 p. Elko Nev.; and Lewis, Mont E. 1975. Plant communities of the Jarbridg Mountain Complex. U.S. Department of Agriculture, Forest Service Humboldt National Forest, 22 p. Elko, Nev.*

Seral aspen communities averaging 162 square feet per acre (37.2 m² per ha) total tree basal area, 15% of which was conifers, produced 743 pounds per acre (833 kg per ha) of undergrowth; those with 183 square feet per acre (42 m² per ha) basal area, 34% conifers, produced 422 pounds per acre (473 kg per ha); and those 234 square feet per acre (53.7 m² per ha) basal area, 68% conifers, produced only 213 pounds per acre (239 kg per ha) of undergrowth. Stable aspen communities in the same locality with an average basal area of 187 square feet per acre (42.9 m² per ha), all of which was aspen, produced 1,471 pounds per acre (1 649 kg per ha) of undergrowth.

Composition of the undergrowth vegetation in the seral aspen communities with 68% conifers was 44% forbs, 5% graminoids, and 51% shrubs; in the stable aspen communities, the undergrowth averaged 60% forbs, 20% graminoids, and 20% shrubs. Thus, not only was the undergrowth less productive in the strongly seral stands, but it consisted of a smaller proportion of herbs and greater proportion of shrubs as well.

Severson and Kranz (1976) also concluded that undergrowth production is not related to the basal area or stand density of the aspen trees. Kranz and Linder (1973) found that the amount of undergrowth in the Black Hills aspen communities decreased as the amount of conifers mixed with the aspen increased. A predominantly aspen type produced 590 pounds per acre (661 kg per ha) of undergrowth; a mixed aspen/ponderosa pine type produced 415 pounds per acre (465 kg per ha); and a predominantly pine type produced only 215 pounds per acre (241 kg per ha) of undergrowth. Similar relationships exist in Arizona between predominantly aspen and mixed conifer forests. Reynolds (1969) found that aspen groves produced 245 pounds per acre (275 kg per ha) of undergrowth, whereas adjacent mixed conifer forests produced only 60 pounds per acre (67 kg per ha).

Only one report on overstory-undergrowth relations in aspen forests supports the generalization that undergrowth production is negatively related to the amount of tree cover. Woods et al. (1982), comparing 20 pure aspen stands growing under similar environments in Colorado, but with widely different amounts of aspen basal area, obtained a significant coefficient of determination (R^2) of 0.61 between aspen overstory and undergrowth. They concluded that thinning aspen stands to basal areas less than 44 square feet per acre (10 m² per ha) would significantly increase undergrowth production.

Yearly Variability

Forage production varies from year to year in response to weather. Paulsen (1969) found almost a twofold yearly difference in both total undergrowth production and composition in an aspen community in western Colorado. Production over a 10-year period ranged from 582 to 1,066 pounds per acre (652 to 1,195 kg per ha) and averaged 740 pounds per acre (829 kg per ha). During this period, forbs comprised from 41% to 70% and graminoids from 28% to 59% of the undergrowth production. Bartos[5] found similar variability in undergrowth production in three aspen stands in northern Utah, over a 4-year period. Production during the high year in each of the three stands was 121%, 145%, and 168% that of the low year; means and standard errors over the four years were 1,253 ± 57 pounds per acre (1,404 ± 64 kg per ha), 1,093 ± 87 pounds per acre (1,225 ± 98 kg per ha), and 1,433 ± 168 pounds per acre (1,606 ± 188 kg per ha). In the stand that fluctuated the most, the proportion of forbs varied from 41% to 88%, and the proportion of grass varied from 10% to 56%, figures surprisingly similar to Paulsen's.

During approximately the same 4-year period in western Wyoming, undergrowth production in an aspen stand during the high year was 127% of that in the low year (Bartos and Mueggler 1979). Average production for the period was 1,780 ± 109 pounds per acre (1,995 ± 122 kg per ha). There, the proportion of forbs ranged from 64% to 71%, graminoids ranged from 11% to 25%, and shrubs ranged from 11% to 20% of the total undergrowth production.

Clearcutting

Smith et al. (1972) compared the effects of partial cutting (50% of the larger trees removed) and clearcutting on herbage production in an aspen stand in northern Utah. Average production during the first 3 years after cutting increased 36% on the partial cut and 87% on the clearcut. The proportion of forbs, grasses, and shrubs was not altered appreciably.

Bartos and Mueggler (1982) also found substantial increases in herbage production after clearcutting aspen in northern Utah. After adjusting for production variability attributable to yearly weather differences, they found that herbage production progressively increased during at least the first 3 years after cutting. By the third year, the aspen community with a predominantly forb/grass undergrowth (70% forbs, 26% grass, 3% shrubs) had a 76% increase in production. The community with a pronounced shrub stratum (59% forbs, 15% grass, and 27% shrubs) increased 137%.

The maximum increase in forage production that might be expected by clearcutting aspen as well as the time after cutting when competition and shading by aspen regeneration would begin to reduce production are not known. However, increased production might be sustained if aspen regeneration is prevented. Mueggler and Bartos (1977) found that a clearcut aspen community maintained free of aspen reproduction by deer browsing was still producing 60% more herbage than an adjacent uncut stand after 41 years. In a similar comparison at a higher elevation, however, the reproduction-free area was producing only 75% as

[5] *Data provided by D. L. Bartos and on file at the Intermountain Forest and Range Experiment Station's Forestry Sciences Laboratory at Utah State University, Logan, Utah.*

much herbaceous growth as its uncut companion after 41 years. During this period, composition of the vegetation on both of the reproduction-free areas shifted from a preponderance of forbs to more than 50% graminoids.

Burning

Information on the effects of fire on the undergrowth vegetation is meager. (See the FIRE chapter for a discussion of the effects and behavior of fire in aspen forests.) In western Wyoming, Bartos and Mueggler (1979) found a sharp decrease in herbage production in the first year after fire, followed by a dramatic increase the second and third years. After adjusting for yearly fluctuations attributable to weather, production on a moderate intensity burn decreased by 50% the first year, but increased to 175% the second year, and 200% by the third year. On a high intensity burn, production the first year was less than 25% of that before burning; but, by the third year, production was 80% greater than before burning. Herbage composition changed from less than 10% annuals before burning to 60% annuals on the moderate intensity and 70% on the high intensity burns by the third year after burning. Almost two-thirds of this "annual" category was composed of *Epilobium angustifolium*, which is actually a perennial forb that behaves as an aggressive pioneer species after fires. *Lupinus parviflorus* also was conspicuously favored by burning. Although production and composition can be expected to gradually revert to pre-burn norms, such trends had not begun by the third post-burn year.

Kleinman (1973) found that conifer reproduction generally entered seral aspen communities about 15 to 20 years after a fire. Forage production appeared to peak about this time and then rapidly decline in both quantity and quality when conifer basal area approached 50 square feet per acre (11.5 m² per ha). He concluded that if fire set back succession every 20 to 30 years in seral aspen communities, forage production would continue.

WILDLIFE

Norbert V. DeByle

Aspen forests provide important habitat for many species of wildlife (Gullion 1977b), especially in the West (see the appendix to this chapter). In the coniferous forests of the interior West, aspen groves may be the only source of abundant forage; in the grasslands they may be the sole source of cover. A primary value of the aspen ecosystem in the West during the past century has been production of forage for both wildlife and domestic livestock (see the FORAGE chapter).

This chapter examines the values of the aspen ecosystem to wildlife, specifically birds and mammals. The ANIMAL IMPACTS chapter discusses the interaction of the aspen plant community and animals from the opposite point of view—the effects of animals on the plant community.

Most of the aspen in the Rocky Mountain states is in national forests. Table 1 provides population estimates for selected wildlife species that use aspen as habitat on these forests.[1] Although aspen is not essential to all these animals, it may be quite important to some populations.

Together, Colorado and Utah have nearly 4 million acres (1,575,000 ha) of aspen forest. These stands are extensive and form a major habitat component for many species. In Montana, Idaho, and Wyoming, there are about 1 million acres (470,000 ha) of aspen. The aspen communities in these states often are interspersed with much more extensive coniferous forest lands or, in some cases, with grasslands. This distribution pattern makes these aspen very valuable for some wildlife species. The three drier states of New Mexico, Arizona, and Nevada have less than 500,000 acres (200,000 ha) of aspen. However, they also have sizable wildlife populations on their national forests.

BIRDS

The diversity and species richness of birds in the aspen ecosystem in western North America (see the chapter appendix) reflects the variation in this ecosystem over a wide geographic area, as well as the variety of understory types, elevational zones, and associated tree species within the aspen type locally. Some of the birds listed, such as the sandhill crane, are a part of the ecosystem locally; others, such as the western wood pewee, are a part of almost the entire aspen ecosystem throughout the West. Among the game species, there are six species of ducks, two species of forest grouse (blue and ruffed), two species of pigeons (band-tailed and mourning dove), the sharp-tailed grouse, and the wild turkey that utilize aspen habitats.

Both pure and mixed aspen stands are included in the aspen ecosystem; if aspen comprises more than 50% of the overstory, a stand is considered to be part of the aspen forest type. Pure aspen forests, some with and some without shrub understories, and aspen-conifer mixed forests, some with an understory of young conifers, and others with conifers in the overstory, provide markedly different habitats for wildlife, especially

Table 1.—Estimated wildlife populations on national forests in eight western states.[1]

Species	Colorado	Utah	Idaho	Wyoming	Montana	New Mexico	Arizona	Nevada
Mule deer	208,500	170,900	146,000	81,000	106,200	78,600	56,800	61,500
Whitetail deer	200	0	28,100	9,700	47,400	3,100	21,200	0
Elk	104,700	15,100	55,800	53,600	55,200	10,000	11,000	500
Moose	50	950	3,800	7,150	4,650	0	0	0
Bighorn sheep	3,700	50	2,800	4,450	2,950	650	200	300
Bison	0	0	0	240	30	0	120	0
Black bear	5,900	500	16,450	2,500	12,250	2,450	1,850	50
Mountain lion	700	650	1,600	150	900	800	1,300	300
Turkey	3,500	300	800	2,800	2,400	24,900	11,500	200
Total area in aspen type in entire state:								
× 1,000 acres	2,629	1,250	544	427	190	378	89	20
(× 1,000 ha)	(1,064)	(506)	(220)	(173)	(77)	(153)	(36)	(8)

[1] *U.S. Department of Agriculture, Forest Service. 1980. Wildlife and fisheries report 1980: Population estimates, hunter harvest, habitat accomplishments, and sportsman use. USDA Forest Service, Wildlife and Fisheries Staff, Washington, D.C.*

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[1] *U.S. Department of Agriculture, Forest Service. 1980. Wildlife and fisheries report 1980: Population estimates, hunter harvest, habitat accomplishments, and sportsman use. USDA Forest Service, Wildlife and Fisheries Staff, Washington, D.C.*

birds. Species diversity probably is greatest in the aspen-conifer mixes, because of the diversity of niches there.

Species such as evening grosbeak, long-eared owl, Clark's nutcracker, western tanager, goshawk, pileated woodpecker, gray jay, Wilson's warbler, kinglets, and the red crossbill are more a part of the conifers than of the aspen. Behle and Perry (1975) listed about 60 species of birds found in the "aspen woodland" type (the pure aspen forest type) in Utah. They also listed species found in the spruce-fir type. Eight species in their spruce-fir list were not found in the "aspen woodland;" 12 species in the "aspen woodland" list were not found in the spruce-fir.

Many bird species in the aspen ecosystem do not breed there. This is especially true during spring and fall migration. For example, of the 21 to 26 species found in a 10-acre (4-ha) Utah aspen stand during each of four summers, only 12 to 19 of them nested in the area (DeByle 1981). Similarly, Smith and MacMahon (1981) listed 71 total species, with 43 of them breeding in a northern Utah meadow-aspen-fir-spruce sere. Winternitz (1976) found similar ratios in Colorado's Front Range. Of the 24 species Smith and MacMahon (1981) found breeding in the aspen type, only 5 of them were year-round residents—the ruffed grouse, hairy woodpecker, mountain chickadee, red-breasted nuthatch, and pine siskin.

Small Birds

Most of the bird species listed in the appendix are classified commonly as songbirds. This category includes all passerine bird species plus other insectivores, granivores, and nectivores that do not fit elsewhere. As individual species, they are too numerous to discuss. Instead, they are grouped, depending on where they nest or upon where and on what they feed. Flack (1976) categorized these birds into nesting guilds: canopy, shrubs, holes, and ground. Canopy nesters, shrub or understory nesters, and ground nesters are discussed in this section. The hole or cavity nesters are discussed separately because of their importance in the forested situation and because of the profound and lasting effect forest cutting or management has on their habitat.

Canopy nesters include the pewee, robin, vireos, yellow-rumped warbler, western tanager, Cassin's finch, and least flycatcher (Flack 1976). Trees are essential for their nesting habitat. Many canopy nesters prefer to feed in the open; these species commonly concentrate on forest edges. Those species that both feed and nest in the forest are distributed throughout the stands.

Shrub nesting bird species include the *Empidonax* flycatchers; rose-breasted and black-headed grosbeaks; chipping, clay-colored, and song sparrows; yellow and MacGillivray's warblers; lazuli bunting; rufous-sided and green-tailed towhees, black-billed cuckoo; and others. Some birds, such as hummingbirds, nest in canopies of both trees and shrubs.


Figure 1.—Several bird species nest on the ground beneath the aspen canopy. An example is this dark-eyed junco nest beneath the herbaceous understory of a pure aspen stand in Wyoming.

A mature aspen forest with an herbaceous understory probably has few or no shrub nesting bird species, whereas one with an abundant tall shrub understory may have many shrub nesters (Flack 1976). When the mature aspen forest is clearcut, understory plant production increases and thousands of aspen suckers develop (Bartos and Mueggler 1982). This temporarily destroys the nesting habitat for the canopy nesters but improves it immensely for the shrub nesters. A mixed aspen-conifer forest will lose understory as the conifers mature and dominate the site; this reduction in understory as succession proceeds will reduce habitat for shrub nesting birds.

The ground nesting species include the hermit thrush, Townsend's solitaire, junco (fig. 1), white-crowned and Lincoln's sparrows, veery, ovenbird, nighthawk, and the Connecticut and mourning warblers. This group of species often depends on the aspen forest for feeding habitat and on the understory plants for protective cover around their nests. The ground nesters are very susceptible to habitat alteration and trampling by grazing animals. Flack (1976) found that the number of birds nesting or feeding on the ground decreased as litter cover on the forest floor increased.

Birds also can be grouped into feeding guilds—ground-insect, ground-seed, foliage-insect, air-perching, and air-soaring guilds. Each species can be placed in a combined nesting and feeding guild. As examples, the tree swallow is a cavity nester—air-soaring insectivorous species, the warbling vireo is a canopy nester—foliage-insect feeder, the junco is a ground nester—ground-seed eater, and the yellow-rumped warbler is a canopy nester—foliage-insect feeder.

Salt (1957) found the aspen type on a moist site, near Jackson, Wyo., had at least three times the bird biomass of any of the six vegetation types he inventoried. Although this may be a bit extreme, it illustrates the value of aspen for bird habitat. In his sample, more than 85% of this biomass was made up of secondary con sumers, mostly insectivorous birds. In the coniferous forest types sampled, there were more primary consumers and fewer bird species.

Aspen growing on dry sites have fewer species and numbers of birds than aspen on wet sites (Salt 1957, Winternitz 1980). Winternitz (1980) found 1–1.5 breeding pairs per acre (3–4 per ha) on a dry site, 2.5–3 per acre (6-8 per ha) on a moist site, and 4 pairs per acre (10 per ha) where there was standing water. Species richness increased proportionately. Not only the wetness of an aspen site, but the stability of that moisture supply also is important to the avian community. During a drought year, Smith (1982) recorded the greatest bird population decline in the aspen community of the meadow-aspen-fir-spruce sere in northern Utah. Nectivorous hummingbirds disappeared, and insectivores declined markedly. He and Winternitz (1980) both emphasized the importance of insect populations as a food resource for birds in the aspen type. Drought reduced this food base.

In an extensive survey of birds inhabiting aspen forests in the West, Flack (1976) found that species richness and bird populations both declined as tree densities increased or average tree diameters decreased. Similarly, in Utah, Young (1973) censused 20 breeding species with a density of 6 pairs per acre (15 per ha) in an open, mature aspen stand, but only 14 species with 3 pairs per acre (7 per ha) in a dense, brushy stand of small trees.

The parkland aspen habitat of north-central Montana and Canada has a different bird community than the montane aspen type of the Rocky Mountains (Flack 1976). Many of the parkland species are typically eastern, such as the eastern kingbird, gray catbird, and black-billed cuckoo. The mix of bird species was greater in the parklands than in the mountane environments to the south or in the aspen stands of the boreal forest farther north.

Cavity Nesters

Cavity nesting bird species are an important part of he aspen forests. Winternitz (1980) found 38% of the breeding species in Colorado aspen forests were cavity nesters; Scott et al. (1980) stated that a range of 17% to 50% of the birds were cavity nesters in aspen stands over a variety of sites.

Some 85 species of birds in North America use tree cavities for nesting; most of these are insectivorous Scott et al. 1977). About 34 of these species nest in the cavities of aspen in the West. They include the waterowl listed in the chapter appendix; the American kestrel and merlin; the flammulated, western screech, northern pygmy, and northern saw-whet owls; all of the apsuckers and woodpeckers in the chapter appendix; he western and great crested flycatchers; the purple martin; the tree and violet-green swallows; all of the hickadees and nuthatches listed in the chapter appendix; the brown creeper; the house wren; the western and mountain bluebirds; and the starling (Harrison 1979, Scott et al. 1977).

Figure 2.—The northern flicker is an important cavity builder in the aspen forest. It provides nest sites for itself and for the many secondary cavity nesting species that may follow. (Photo by Virgil Scott)

There is an abundance of cavity-bearing trees in most aspen forests in the West. Natural thinning proceeds as the typical aspen stand grows and matures. Trees of all sizes may be killed by competition and decay. Death and decay of trees or parts of trees permit excavation of many cavities. As trees grow and mature in a stand, opportunity for cavity nesters improves. Decay at points of injury on large trees make good cavity sites. Commonly, 6% to 20% of the standing trees in mature and overmature aspen stands are dead.[2] However, once dead, an aspen snag is unlikely to stand for more than a few years.

Aspen is very susceptible to heart rot (see the DISEASES chapter). In mature aspen stands, many of the trees that otherwise appear healthy are infested with decay fungi, especially *Fomes igniarius*. The punky interiors of these trees are readily excavated by woodpeckers and are used for nesting by them and other cavity nesting species that may follow. These live trees may stand for many years after initial decay permits cavity excavation. The number of holes drilled in the large infected trees indicates that birds prefer them for nesting (Scott et al. 1980, Winternitz 1980). Crockett and Hadow (1975) and Kilham (1971) stated that sapsuckers were attracted to trees infected by *Fomes*.

By definition, the primary cavity nesters excavate their own cavities. Only the woodpeckers and sapsuckers consistently excavate cavities, usually new ones each year, and often more than they need. Thus, they provide cavities for the secondary cavity nesting birds. Chickadees and nuthatches can excavate their own cavities in soft wood (Scott et al. 1980); other species

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[2] *Unpublished data on file at the USDA Forest Service, Intermountain Forest and Range Experiment Station's Forestry Sciences Laboratory, Logan, Utah.*

(owls, swallows, etc.) require available cavities for their nesting sites. Among the primary cavity nesters, the sapsuckers and the hairy and downy woodpeckers prefer aspen trees. Others, such as the flicker, are not as discriminating.

Scott et al. (1980) indicated the importance of the flicker as a cavity nester (fig. 2). Because it is the largest woodpecker in much of the Rocky Mountains, it provides nesting sites in a variety of tree species for many of the larger secondary cavity users. In the mixed aspen-conifer forest, the aspen component probably is essential habitat for some of the cavity nesting birds. As the forest succeeds to spruce and fir, or to pure spruce, which is too hard for most primary cavity nesters, the number of cavity dwellers could be expected to decline (Smith 1980).

Most cavity nesters are insectivorous and are considered to be mostly beneficial to human interests (Thomas 1979). (See the ANIMAL IMPACTS chapter for discussion of negative impacts of cavity construction and sapsucker feeding.) Therefore, guidelines have been developed for snag management in some of the conifer types to retain cavity nesting habitat. Although similar formal guidelines have not been written for aspen, very little modification of current management practices is needed to maximize this habitat. Little, if any, of the aspen forest is harvested until it is mature to overmature; and then, most harvesting is in the form of small (2.5- to 12-acre (1- to 5-ha)) clearcuts. This preserves natural cavity nesting habitat until the stand is overmature. Clearcutting small patches of aspen does more to enhance edge for the birds than it does to destroy some cavity nesting habitat. (Alternatives for managing aspen forests are discussed in PART IV. MANAGEMENT.)

Birds of Prey

Three species of accipiters, three of buteos, four falcons, the golden eagle, and the turkey vulture are found in aspen forests in the West. Also, there are six species of owls, varying in size from the northern pygmy to the great horned (see the chapter appendix). This variety illustrates the biological richness of this forest type. Prey, in the form of small mammals and other birds, is abundant in the aspen forest. This abundant food source attracts these species at the top of the food pyramid.

Perhaps the greatest variety of predaceous birds inhabit the mixed aspen-conifer forest. Many hawks nest in this habitat. Also, unless they can hide in burrows, owls are more likely to be encountered in the mixed forest, roosting in dense conifers in the daytime. In contrast, feeding areas for many predaceous birds are predominately in the pure aspen forest or in nearby open brush, meadows, and grasslands.

Most raptors and owls will nest in the aspen type. The golden eagle, and the peregrine and prairie falcons are least likely to be found nesting in the forest, but are most apt to be nesting on some open, precipitous rocky area in the vicinity (Harrison 1979). Others, such as the cavity nesting species, seem to prefer aspen for nest sites, although the merlin, listed as a cavity nester, probably will nest in the rocky bluffs with the other large falcons. The buteos will nest in the aspen or mixed forest, but will do much of their hunting in more open terrain. The accipiters will nest and hunt in the forest. The largest of these, the goshawk (fig. 3), and the largest owl, the great horned, are very effective predators of small game (grouse and hares) in the aspen forest.

Figure 3.—An active northern goshawk nest in a mixed aspen-conifer stand in western Wyoming.

Game Birds

Mourning Dove

Most mourning doves nest at lower elevations, beneath the zone of montane aspen. Where doves are found with aspen, however, they nest in tall shrubs and aspen trees. Because doves are ground-feeding granivores that prefer open areas for feeding, they commonly are encountered along the forest edge and in small groves of trees bordering agricultural lands and rangelands. This species is an early migrant, departing from most aspen habitats in late August or early September. Aspen appears to be incidental to habitat requirements of mourning doves throughout most of their range.

Band-tailed Pigeon

Band-tailed pigeons nest in the mountains within the southern range of montane aspen, from central Utah and Colorado southward. According to Harrison (1979) they prefer to nest in broadleafed trees; therefore aspen may be chosen for nesting. However, they feed on acorns and berries, and are generally found in the Gambel oak and ponderosa pine zone, at an elevation below that where aspen commonly grows (Jeffrey 1977).

Wild Turkey

The range of the wild turkey and that of aspen overlap in the southern Rocky Mountains, especially in Arizona and New Mexico. This ground-nesting bird prefers the coniferous and pine-oak forests of the mountains (Harrison 1979).

Turkeys will use the mixed aspen-conifer type;[3] but, they basically inhabit the ponderosa pine and bordering types (Hoffman 1968). The turkey is a seed-eater that does well where a reliable supply of mast and grass seeds are available. They also forage on insects, which are abundant in the aspen type (Winternitz 1980), and on many of the forbs and grasses available in the typical aspen understory (Korschgen 1967).

Sharp-tailed Grouse

The sharp-tailed grouse in the parklands aspen habitat will use aspen trees in the winter and spring; but they prefer and select grassland and grassland-low shrub cover throughout most of the year. During the winter, small aspen and shrubs offer this grouse protective cover and food. They feed on aspen buds in winter and spring (Hamerstrom 1963, Moyles 1981). Aspen is useful as small thickets of young growth (3–6 feet (1–2 m) tall) and as larger patches of taller trees for winter use (Evans 1968, Hamerstrom 1963). During much of the year, aspen, except as a shrub, seems to be of little or no importance, perhaps even a detriment, to the sharp-tailed grouse. The presence of aspen near breeding arenas discourages their use (Moyles 1981). Moyles (1981) cited evidence that invasion of grassland by aspen reduced sharp-tailed grouse habitat.

The sharp-tailed grouse is characteristic of early successional stages in the aspen ecosystem. They frequently utilize burned areas in which aspen regeneration is mostly shrub-sized, with some very scattered stands of mature trees that have escaped the fires. As extensive stands of trees return, the sharp-tailed grouse gives way to the ruffed grouse.

Blue Grouse

In contrast to the sharp-tailed grouse, the blue grouse is prevalent in areas that are successionally beyond the aspen stage, where much of the landscape is occupied with conifers. However, the conifer forest is particularly mportant only in winter, when blue grouse roost in the dense conifers and feed primarily upon conifer needles Beer 1943, Hoffman 1961, Stewart 1944). During summer, blue grouse prefer openings, usually at lower elevations, that are vegetated with grasses, forbs, shrubs, and aspen patches. Relatively dense grass-forb mixes are chosen first, and shrubs second (Mussehl 1960, 1963). There they nest, raise their broods, and eed upon insects, fruits, and leaves.

Aspen is not an essential part of blue grouse habitat; healthy populations are found where no aspen exists. However, wherever aspen is an extensive component of the summer and early fall home range of blue grouse, it provides significant food and cover for developing grouse broods, if it is not too heavily grazed.

Ruffed Grouse

The ruffed grouse has a wide range across North America (Aldrich 1963), is associated with hardwood and hardwood-conifer mixed forests, and is primarily a bird of the aspen and associated forest types (fig. 4).

Gullion (1977a) suggested an obligatory relationship between ruffed grouse and the aspen type wherever snow covers the ground between November and April. Aspen is heavily utilized as food and as cover throughout most of the year (Doerr et al. 1974, Phillips 1965, Schladweiler 1968) (fig. 5), providing a highly nutritious food source (Gullion and Svoboda 1972), protection from the weather (Bump et al. 1947), and escape from predators (Gullion et al. 1962). About 75% of the annual grouse harvest is taken in the six states and provinces where aspen is most abundant (Gullion 1977a). Ruffed grouse, however, are found in huntable populations in hardwood forest habitats south and west of the range of aspen (fig. 4).

Wherever aspen and grouse ranges overlap in the West, this grouse selects aspen habitat during part or all of the year[4] (Doerr et al. 1974; Landry 1982; Phillips 1965, 1967; Rusch and Keith 1971). However, this aspen community must possess suitable density and structure to make it good grouse habitat.

Aspen and associated hardwoods are important components of the habitat during the breeding and nesting season. Males select drumming logs that are under a dense overstory and are surrounded by a relatively dense shrub understory but with good horizontal visibility (Berner and Gysel 1969, Gullion et al. 1962, Landry 1982, Robertson 1976), giving them maximum protection from predators as well as visibility to receptive females. The hens choose similar cover for nesting; but, after hatching, they move their broods to areas with relatively open canopies and well-developed and dense herbaceous understories[4] (Landry 1982). In the mountain West, the broods move downslope as the season progresses, and are often found during late summer in the relatively moist and dense cover along stream bottoms (Hungerford 1951, Marshall 1946, Robertson 1976).

The foods used by ruffed grouse vary with season, age of bird, and availability of plant species; but usually include aspen, if it is a component of the habitat. The chicks feed exclusively upon insects for their first 5 weeks, which partially explains why broods select the insect-rich, dense, herbaceous understory. About 7 weeks after hatching, they assume an adult diet and

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[3] *Personal communication with David R. Patton, USDA Forest Service, Rocky Mountain Forest and Range Experiment Station's Forestry Sciences Laboratory in Tempe, Ariz.*

[4] *Stauffer, Dean F. and Steven R. Peterson. 1982. Seasonal habitat relationships of ruffed and blue grouse in southeastern Idaho. 138 p. Final report (unpublished). Forest, Wildlife, and Range Experiment Station, University of Idaho, Moscow.*

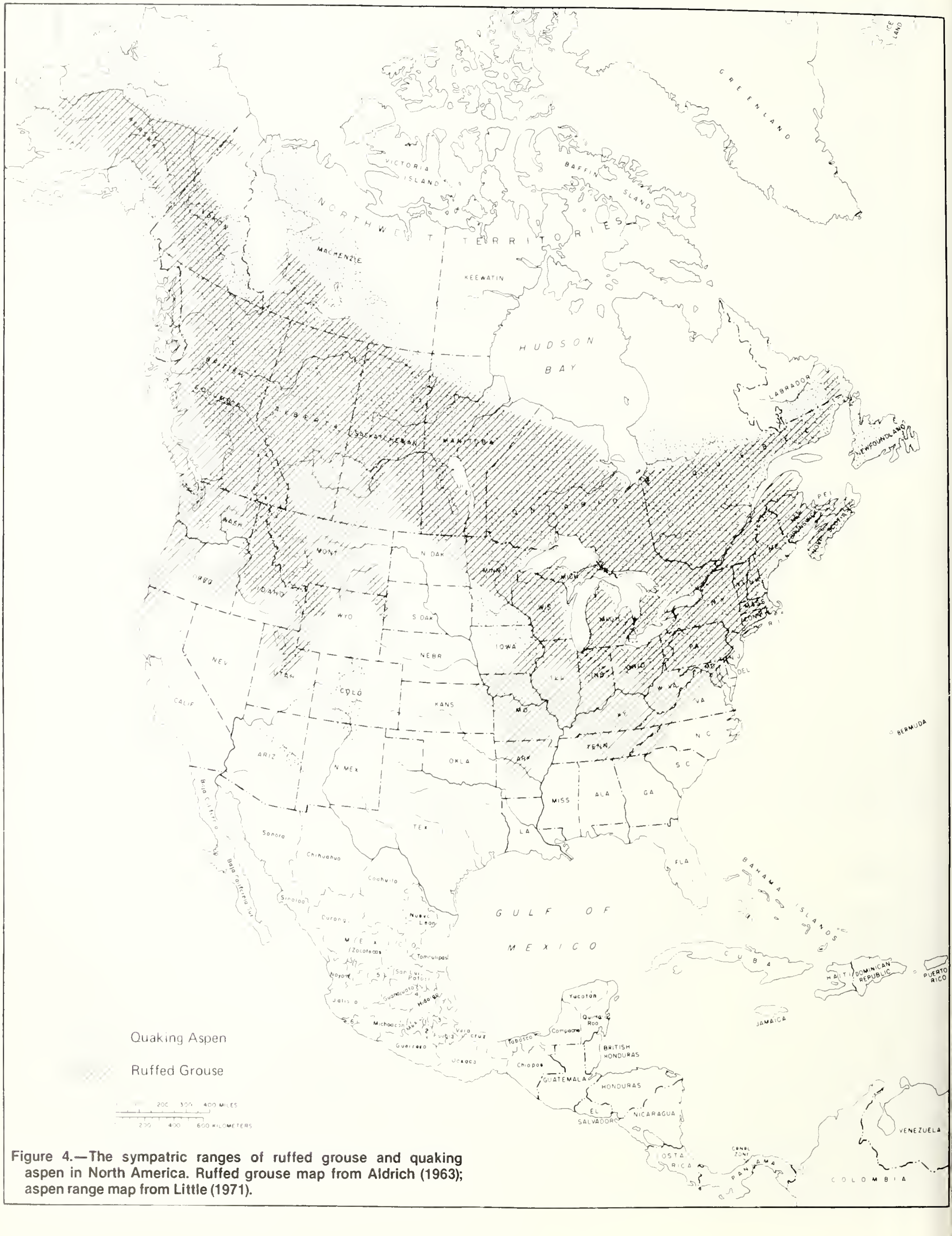

Figure 4.—The sympatric ranges of ruffed grouse and quaking aspen in North America. Ruffed grouse map from Aldrich (1963); aspen range map from Little (1971).

feed primarily on plant parts. Incubating hens eat aspen leaves and catkins (Maxson 1978, Schladweiler 1968). Gullion and Svoboda (1972) found that drumming males chose logs within sight of male aspen, which probably were used as a food source. Svoboda and Gullion (1972) stated that, in Minnesota, spring foods consisted mainly of staminate aspen buds and catkins. Adult grouse in summer feed on a variety of abundant plant materials—seeds, fruits, and leaves. In northern Utah, Phillips (1967) found that rose hips and aspen leaves made up 50% of the autumn diet. After leaf fall, and certainly after snow covers the understory, aspen twigs and buds, especially the male floral buds (Svoboda and Gullion 1972), become a dominant part of the grouse diet (Doerr et al. 1974, Phillips 1967). Willow buds, chokecherry buds, rose hips, and other available foods also are used in varying amounts (Doerr et al. 1974, Marshall 1946, McGowan 1973, Phillips 1967).

Aspen buds alone are nutritious enough to support grouse during the winter (Svoboda and Gullion 1972), especially the staminate floral buds in the upper part of the canopy (Gullion and Svoboda 1972). However, willow buds contain a greater concentration of protein and carbohydrates but less fats than aspen in winter (Doerr et al. 1974), and rose hips are especially high in protein (Welch and Andrus 1977), making them good supplements to a steady diet of aspen buds in winter and spring.

Figure 5.—Aspen floral buds are an important food for ruffed grouse. (Photo by Tom Martinson)

Breeding and nesting habitat of ruffed grouse is generally dense, pole-sized stands of aspen or mixed hardwood cover of similar structure. The dense herbaceous understory chosen by broods in summer perhaps develops best under open canopies. Solitary grouse use thickets of shrubs in spring and summer, which provide protection from precipitation, extreme temperatures, and predators (Landry 1982, Robertson 1976). In autumn, birds use diverse cover, but still prefer aspen.[4] Mixed hardwoods with brushy overgrown edges often are chosen (Berner and Gysel 1969, Robertson 1976). In winter, when there are deep snowpacks throughout most of the mountain West, ruffed grouse are found in the aspen and aspen-conifer types. During this season, the grouse use stands of trees larger than those used in spring and summer, perhaps to feed upon the abundant floral buds on mature aspen. At times, grouse are found in dense stands of conifers, where they sometimes roost.[4]

MAMMALS

The aspen ecosystem in western North America provides habitat for at least 55 species of wild mammals (see this chapter's appendix). In size, these range from the dwarf shrew to the bison. Some species occur in the aspen type as well as in many other vegetation types; others prefer the aspen forest. Those species that appear to select the aspen type, and those that are currently important as game, or for esthetics, or that have obvious or economic impact on the plant community are discussed in this chapter. These include moose, elk, deer, snowshoe hare, cottontail rabbit, beaver, porcupine, and pocket gophers.

Moose

The largest member of the deer family, the moose, makes extensive use of the aspen ecosystem (fig. 6). The range of moose and the more northerly range of aspen in North America coincide. The use of aspen and associated vegetation by moose is much more than random. Usually, moose first select willow and then aspen as browse.

Moose are primarily browsers, especially in winter. On most western ranges, they seem to concentrate on willows; in the East they often select aspen, birch, and balsam fir for browse (Peek 1974b). Forbs may be heavily used during summer and fall; but grasses seldom are a primary food source. Peek (1974b) cited studies that listed aspen among the most important species of browse in southcentral Alaska, Alberta, British Columbia, Manitoba, Minnesota, Montana, and on Isle Royale National Park in Lake Superior.

The Shiras moose, the subspecies which occupies the montane woodland of the western U.S. and adjacent Canada, has a variety of winter ranges: (1) floodplain willow bottoms, (2) willows and conifers along mountain streams, (3) aspen and conifer stands in the absence of willows, (4) pure conifer stands, especially with subalpine fir, and (5) sometimes the northern desert scrub (Peek 1974a). Where willows are its primary source of food, as on floodplains, there may be little need to consider the aspen type as essential moose habitat. But where moose use the upland types, the aspen ecosystem becomes important habitat.

Many of the understory shrubs in the aspen type are palatable and sometimes important moose browse (Peek 1974b). Browsing varies widely among the conifers associated with the aspen ecosystem. Spruces are virtually untouched by moose, lodgepole pine sometimes is used, Douglas-fir often is consumed, and subalpine fir is a preferred browse (Gruell 1980, Gruell et al. 1982, Stevens 1970).

Because the niches for moose and other cervids (elk and deer) differ, they compete very little in forested habitats of the West. Moose winter in bottoms and upland forested areas, and they eat mostly browse; elk winter in open areas with less snow and eat herbaceous material, if available (Stevens 1974). Both will use aspen browse; but elk seldom use much willow—the moose's favorite. Although both moose and deer are browsers, in typical mountainous habitats, any competition would occur mostly on the summer range. Usually food is abundant then, and both animals may browse on the same upland plant species without much interspecific competition. In winter, when snow crowds deer onto low-elevation ranges, moose often remain in willow bottoms, aspen patches, and conifer stands at higher elevations where snowpacks may be as much as 30–40 inches (75–100 cm) deep (Kelsall and Telfer 1974).

Probably because of their tolerance for cold, moose will occupy willow bottoms without much thermal cover early in winter. But, as winter progresses and snowpacks deepen, they move into densely forested uplands with less snow (Rolley and Keith 1980). Moose in Alberta selected upland aspen less than 33 feet (10 m) tall as preferred habitat, but used tall aspen and aspen-conifer mixes at about their level of availability (Rolley and Keith 1980).

Figure 6.—The Shiras moose uses aspen and aspen-conifer forest cover extensively during all seasons of the year, in several western states. (Photo by Clay Perschon)

Gordon (1976), in Montana, described ideal upland moose habitat as having a good distribution of aspen and associated trees and shrubs in a mosaic of age classes. Conifer patches for hiding cover also are desirable.

Regeneration of young vigorous stands of aspen, willow, and associated shrubs, usually after fires, improves moose habitat and results in a moose population increase (Gruell 1980, Gullion 1977b, Irwin 1975, LeResche et al. 1974). After this browse grows out of reach, the moose population decreases. LeResche et al. (1974) noted that fire-induced seral communities in Alaska had the greatest moose population densities, but that these were unstable and ephemeral.

Moose are well adapted to the aspen ecosystem. Where moose and aspen coexist in the West, it appears that young stands of aspen suckers provide the most browse, pure aspen stands of large trees provide some understory forage, and older seral stands with conifers offer cover and some browse, sometimes of choice subalpine fir. Community types with an abundance of shrubs and forbs in the understory perhaps are most valuable as moose habitat. Because conifers also provide some browse as well as escape or hiding cover, perhaps seral aspen stands are best. However, where willows are abundant in areas that can be used by moose throughout the year, the aspen is supplemental, not an essential part of moose habitat on this western range.

Elk

Elk is the second largest herbivore found in the aspen type. Thomas and Toweill (1982) provided a comprehensive review of the ecology and management of this animal in North America. Where concentrated, elk have considerable impact on the aspen ecosystem (see the ANIMAL IMPACTS chapter). The range of the Rocky Mountain subspecies of elk and the range of aspen in the West are similar. Rocky Mountain elk, however, do not depend on aspen as critical habitat throughout their range. Large and healthy herds of elk exist where aspen is only a minor component in the vegetation complex, such as in northern Idaho. Nevertheless, where aspen and elk occur together, the elk appear to select the aspen type over several other available habitats (fig. 7). At least in southern Idaho, elk were found in the aspen in much greater frequency than would be expected from random use.[5]

In the central Rocky Mountains, where aspen is most extensive, most of the aspen zone is at an intermediate elevation between elk winter and summer ranges.

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[5] *Personal communication with Lonn Kuck, and data on file at Idaho Game and Fish Department, Soda Springs, Idaho.*

Where aspen occurs on elk winter range, it is very heavily utilized by concentrations of these large cervids. Excellent examples of this can be seen in Rocky Mountain National Park in Colorado and at the National Elk Refuge near Jackson, Wyo. Aspen stands that exist on spring migration routes also are heavily browsed. Autumn migration has a lesser impact on the trees, because palatable herbaceous vegetation is more abundant. Consumption of aspen and associated understory species by elk on summer range is usually well distributed and quite light. Often, elk spend their summers at higher elevations, above the aspen zone, where they graze in meadows and use coniferous forest stands for cover.

Elk, particularly the Rocky Mountain subspecies, primarily graze. They consume essentially the same grass and forb species as do cattle. Where production of palatable herbaceous species is low, or when snowpack depths exceed 20 inches (50 cm), the elk will feed extensively on browse. According to Nelson and Leege (1982), elk prefer grasses, then forbs; and, as curing or loss of herbaceous material occurs, they will use deciduous browse species first and coniferous browse last.

Aspen is avidly sought from among the browse species. It is consumed in excess of its proportion in the vegetation and is often a major part of the elk diet. It is considered a highly valuable browse species in winter, spring, and autumn; and, if browse is used much, it is a valuable species in summer as well (Kufeld 1973, Nelson and Leege 1982). The qualitative value of aspen and associated plants as ungulate food is discussed in the section on deer. However, among the browse species selected by elk in winter, aspen had the highest percentage (39–47%) of digestible dry matter (Hobbs et al. 1981).

An aspen understory rich in forbs and grasses provides excellent quality elk feed in large quantities during the summer and early fall seasons (see the FORAGE chapter). During those seasons the aspen provides cover as well. In fall and winter, if the elk remain in the aspen zone, they will browse aspen to a height of approximately 6 feet (2 m) and will chew the bark from mature aspen trees (see the ANIMAL IMPACTS chapter). Dense stands of young aspen are valuable browse; but, this resource is ephemeral. Aspen suckers, if growing in the open and not browsed, will extend their crowns above the reach of elk in 6 to 8 years (Patton and Jones 1977).


Figure 7.—Elk are an important resource in the aspen forest type in the Rocky Mountain West. (Photo by Kem Canon)

Elk often need hiding or security cover (Thomas 1979). Although their need for thermal cover is not clear (Peek et al. 1982), they utilize it where available. Aspen-conifer mixed stands provide both cover and forage all year. Aspen stands with a dense shrub understory provide hiding cover, whereas pole-sized or larger dense conifer stands provide the best thermal cover (Thomas 1979). In contrast, pure aspen forests provide substantial cover only during summer. When dormant, mature aspen provides poor hiding cover and almost no thermal cover. In summer, the combined values of good forage and cover in the aspen forest make it especially valuable to elk. Elk then prefer the aspen stands to adjacent clearcuts that have even more palatable forage (Collins and Urness 1983).

Aspen habitat can be important during the calving season. In the spring, during the up-slope migration of elk, the pregnant cows break off from the herd several days before parturition. They usually calve and then remain in the mid-elevation forest zone for several weeks before rejoining the herd. Aspen often is a predominant forest type in this mid-elevation zone. Thus, aspen and associated vegetation provides critical cover and forage for these cow elk and young calves.

Deer

Either mule deer (Wallmo 1981) or white-tailed deer are common throughout the range of aspen in the western United States. They are less common farther north, but still prevalent in many aspen areas. The mule deer predominates in the states with the most aspen (table 1). Mule deer herds in these states are migratory—they spend summers at high elevations within the aspen zone and winters on steppe and brushlands at lower elevations, usually below the aspen zone. For the most part, aspen is summer and fall range for deer in the mountainous, semiarid West. Exceptions are where aspen grows on lands without deep winter snowpacks.

Deer utilize aspen both as cover and as browse. Many herds, especially in Colorado and Utah, are found in the aspen forest type throughout much of the summer (fig. 8). Whether or not aspen is a critical habitat component depends upon the other facets of their habitat. If adequate forage and cover exist in tall shrub types, or in a mosaic of conifer patches and openings, then the aspen type may not be critical to their welfare. Pure conifers provide cover, but little forage; openings provide forage but no cover. Aspen, in summer, provides both.

Much emphasis in both research and management has been placed upon the availability of quality forage on the winter ranges of wild ungulates. The well-being of these animals often is at least equally dependent upon their summer and fall ranges. Deer herds on good summer range, in the aspen and associated vegetation types, are more productive and healthier than those herds forced to use overgrazed and deficient summer ranges (Hungerford 1970, Julander 1962, Julander et al. 1961). Their survival through winter, when their metabolism and level of activity is lowest (Moen 1978), depends largely upon fat stores built up in late summer and autumn.

In contrast to elk, deer primarily browse throughout much of the year. Only in spring and summer, when succulent herbaceous forage is abundant, do deer consume more herbaceous plants than they browse. Like the elk, they migrate up the mountains while following the wave of new spring and summer herbaceous growth. Forbs are very much preferred. As summer progresses and the herbaceous material cures, the deer shift progressively to browse.

Aspen was among the top eight species of preferred browse for Rocky Mountain mule deer and, if available, was moderately used in winter, spring, and summer, and heavily used in autumn (Kufeld et al. 1973). Hungerford (1970) noted that aspen sprouts became a key food only after new growth matured, usually in July. Whenever available, leaves were selected from mature aspen trees. Upon leaf fall in autumn, deer consumed large quantities of aspen leaves (Julander 1952). In addition to the aspen itself, deer commonly ate several associated understory shrubs: serviceberry, barberry, pachistima, common chokecherry, rose, willow, and especially snowberry. The most used forbs in the aspen forest understory were western yarrow, aster, milkvetch, fleabane or daisy, geranium, peavine, lupine, knotweed, cinquefoil, common dandelion, valerian, and American vetch (Collins 1979, Kufeld et al. 1973).

The quality of forage taken from the aspen type by deer and elk is quite high, especially in summer. The mix taken by deer and elk in Utah during the growing season was about 65% digestible and contained 13% protein (Pallesen 1979). Protein contents of 21% for deer diets and 18% for elk diets on an aspen dominated site were measured in a later study (Collins and Urness 1983). Some shrubs in the aspen type are very nutritious. For example, rosehips have a high nitrogen free extract (60%) and are readily browsed by mule deer (Welch and Andrus 1977).


Figure 8.—In the West, mule deer are the most common big game inhabiting the aspen forest type.

The nutritive value of aspen alone compares very favorably with several other plant species important to mule deer (Short et al. 1966). They found the protein contents of aspen varied from a high of 17% in spring to 6–10% by leaf-fall in autumn; in winter, crude fat was 15–19%, caloric values were 5 calories per gram, and carotene contents were 14–18 μg per gram.

Aspen leaves are used by browsing animals during summer. Their nutrient content is high, changes during the growing season, and varies from clone to clone (Tew 1970b). Tew (1970b) found green aspen leaves to contain 12% protein, 10% fat, 2.3% Ca, 1% K, and 7.5% ash in late summer, during what is usually the peak of the summer browsing-grazing season. Upon leaf drop in the autumn, they have approximately the following nutrient contents; 1.9% Ca, 0.4% N (only 3% protein), 0.4% K, 0.1% Mg, 0.05% P, and 5.3% ash (Bartos and DeByle 1981).

Aspen bark is 50% digestible by ruminants (Baker et al. 1975), apparently palatable, somewhat nutritious, comparatively soft, and readily chewed from the tree. The nutrient content of aspen bark is: 0.5% N, 0.06% P, 0.3% K, 1.6% Ca, 0.1% Mg, and 5.0% ash (Bartos and Johnston 1978).

The production of forage in large quantities in the aspen understory usually is more important to deer on their summer range than is the production of aspen browse itself. The quantity and quality of this food production is examined in the FORAGE chapter, and can be inferred from the cited digestibility and protein values (Collins and Urness 1983, Pallesen 1979).

In comparison to larger ungulates, deer carefully select leaves and succulent portions of forbs, browse, and some grasses. Coarse material is left. The aspen understory commonly has a broad selection of palatable deer forage. Deer gravitate to it and to the cover provided by the aspen overstory (Collins and Urness 1983).

Deer make greatest use of the aspen type during summer and autumn, when aspen and associated deciduous shrubs are in full leaf, and both thermal and hiding cover are abundant. Aspen communities on the shrub-steppe western range are second only to the riparian zones in value to mule deer (Leckenby et al. 1982). Forage provided by the understory plus thermal cover provided by the overstory make this type especially attractive to deer in summer. They prefer to feed in the aspen forest rather than in clearcut openings that have twice as much forage. They commonly bed down in the aspen forest also (Collins and Urness 1983).

In terrain typical of the mountain West, deer appear to prefer habitats that are close to a water supply, especially in late summer, when forage elsewhere is cured. The aspen forest with a good understory of palatable shrubs and forbs, if near a stream or spring, is ideal summer deer habitat. McCulloch compared deer population densities in aspen, ponderosa pine, mixed conifer, spruce-fir, and meadow habitats in Arizona.[6] Greatest densities were found in aspen, especially where there was abundant forage.

The cover value of aspen and other deciduous species decreases markedly as they lose their leaves in autumn. Thermal cover probably is not needed then because of moderate temperatures; but hiding cover may be essential, especially during the hunting season. Mixed aspen-conifer stands, aspen with a dense understory of tall shrubs, and pure conifer patches then become important deer cover. Dense stands of aspen regeneration also provide good escape cover as well as forage in this season.

With the onset of winter and the accumulation of a snowpack in the mountain West, the cover value of aspen for large ungulates becomes negligible. Dense stands of small trees offer cover and browse; but only conifers provide good thermal cover in winter. Snowpacks deeper than 12–16 inches (30–40 cm) force deer to migrate to lower elevations and generally out of the aspen forest zone. Therefore, except for a brief period in late autumn, dormant aspen stands provide little cover where deep snowpacks accumulate.

Snowshoe Hares

Snowshoe hares may be present throughout most of the aspen range in the West (fig. 9). This animal, however, is more common in the associated coniferous forests. In the Rocky Mountains, winter hare habitat is lacking in most pure aspen stands because of deep snowpacks. In northern Utah, Wolfe et al. (1982) found 85% of winter use by hares was in vegetation types that had cover densities immediately above the snowpack of at least 40%. Sometimes aspen with a very dense understory of tall shrubs fits this criterion; but usually only conifers have this much cover in winter.

During summer, snowshoe hares disperse somewhat from coniferous winter cover (Wolff 1980). During the growing season, the aspen type provides adequate cover and excellent forage. Aspen is nutritious and choice food for hares (Walski and Mautz 1977), although new suckers, with high terpene and resin contents, may not be as palatable as twigs on the mature growth (Bryant 1981). During summer, snowshoe hares shift largely to a diet of succulent plant material (Wolff 1980). Because the aspen type has much more herbaceous and shrub cover than most coniferous types, in summer it probably is a more desirable habitat.

Snowshoe hare populations are cyclic in the northern part of their range. During population peaks in Alberta, Pease et al. (1979) found that browsing by hares was so great that food supplies became limiting. About 50% of the woody stems were severely browsed during the peak; but only 2% were being browsed 2 years later, after the population declined drastically. Aspen was among the six most common browse species.

Figure 9.—Aspen stands with an appreciable conifer component provide snowshoe hares with satisfactory habitat, even in winter, when deep snow buries much of the understory cover and food.

The aspen type, if well interspersed with dense conifer patches, provides adequate snowshoe hare habitat in the West. Marginal habitat is provided with aspen and a dense understory of tall shrubs, if this understory is not covered with deep winter snowpacks. It is doubtful if even the peak density of aspen suckers and shrubs on most aspen clearcuts in the West provide adequate snowshoe hare habitat in winter (Wolfe et al. 1982).

Cottontail Rabbits

Most aspen in the western United States is at elevations above the zone where cottontail rabbits are commonly found. Snowpacks may be too deep and the winters too severe for cottontails in these environments. Cottontails are found in aspen groves at lower elevations and where aspen is associated with sagebrush and similar shrublands. On these sites, dense aspen patches in mesic pockets or seepage areas within an otherwise rather exposed environment provide thermal and hiding cover for cottontails and other wildlife, especially in winter. In contrast, the cottontail in the East and Midwest finds the aspen habitat quite suitable, and is often abundantly found in recent cutovers that are well-stocked with aspen suckers (a good food source in winter) and logging slash used for hiding cover.

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[6] *McCulloch, Clay Y. 1982. Evaluation of summer deer habitat on the Kaibab Plateau. Final Report, Arizona Game and Fish Department, Project W-78-R, 20 p. [Typescript]*

Beavers

Of the larger mammals considered here, beavers are he only ones restricted for almost their entire winter ood supply to aspen and to other species in the family Salicaceae. Although beavers use other hardwoods, such as alders and maples, most beaver colonies in the nountainous West are found on streams that flow hrough or adjacent to aspen or willow (fig. 10). Both species are commonly used (although aspen is pre-erred) for food and for dam construction (Hall 1960). See the ANIMAL IMPACTS chapter for a more com-olete discussion of the aspen-beaver relationship.)

Aspen, because it is an upland hardwood type, pro-vides essential habitat for beavers along streams that do not have sufficiently wide riparian zones to support an adequate supply of willow or cottonwood. Many of the streams in the West, especially in their upper reaches, fit this description. There, beaver are found only where here is aspen.

Beaver populations along any given reach of stream are not stable. They move in, establish a series of dams and lodges, harvest the aspen and willow within reach of these inundated areas, and then depart after the sup-ply is exhausted. This is especially true in the aspen nabitat, where sucker regrowth is not fast enough to sustain the beaver population (Hall 1960). Willow is bet-er for sustaining relatively stable beaver populations along low-gradient streams, because it sprouts pro-ifically after cutting and grows rapidly in the sometimes nundated riparian zone. However, on high-gradient treams, aspen may be superior to willow for dam con-truction (Gruell 1980).

Beaver will cut any diameter aspen available (fig. 11), although they seem to have a slight preference for the 2-inch (5-cm) size class (Hall 1960). About 2–4 pounds (1-2 kg) of bark is eaten each day by a mature beaver, nost of which comes from branches and boles less than 3-4 inches (8-10 cm) diameter (Hall 1960, Stegeman 1954). Stegeman (1954) found that the degree of utilization varied from 98% on 3/4- to 1-inch (2- to 3-cm) trees to 64% on trees larger than 8 inches (20 cm) diameter. The small trees produced only about 2 pounds (1 kg) of food, whereas 10-inch (25-cm) diameter trees produced 220 pounds (100 kg) of beaver food. He estimated that 1,500 pounds (700 kg) of aspen food is required per beaver per year. In summer beavers feed on succulents, too. Tree cutting and food cache construction by beaver reaches a peak in autumn (Hall 1960). Banfield (1977) estimated that about 200 aspen trees would support one beaver for 1 year.

igure 10.—A beaver dam and lodge in the pure aspen forest type, along a stream in Utah's mountains.

Figure 11.—An 8-inch diameter aspen felled by beavers during the previous week. The bark and twigs were eaten, and some branches were removed and used in the nearby lodge and dam.

Beaver cutting may extend a considerable distance from water, 100–650 feet (30 to 200 m), depending upon topography, food availability, and the behavioral characteristics of the colony. Therefore, potential beaver habitat in the aspen type would be a strip perhaps 650–1,000 feet (200–300 m) wide along each relatively placid perennial stream, with greater distances in bottomlands with a potential for extensive flooding by beaver dam construction. Greatest utilization of the aspen in this zone would be in dense stands of trees from 2 to 6 inches (5 to 15 cm) in diameter.

Porcupines

Porcupines are associated with a variety of woody vegetation types in the West, from conifers to sagebrush. Although this large rodent appears to have preference for some tree species, such as hemlock or basswood (Curtis 1941, Krefting et al. 1962), many species, including aspen (Lynch 1955), are commonly barked and appear to suffice as a winter food source (see the ANIMAL IMPACTS chapter) (fig. 12). During summer the porcupine also feeds on succulents, and then will readily eat aspen leaves if available (Banfield 1977). Because predation is not a serious consideration for this quill-covered animal, its use of cover probably is largely for physical comfort. It uses ground shelters (rocks, hollow logs, caves, etc.), especially in winter and for reproduction (Banfield 1977, Thomas 1979).

Pocket Gophers

Although the pocket gopher is seldom seen, evidence of this fossorial rodent is present in most aspen stands. This evidence consists of small soil mounds that are pushed to the surface during summer feeding and burrow building. In winter, mineral soil is deposited in elongated castings at the base of the snowpack. (See the ANIMAL IMPACTS chapter for more detail.)

Figure 12.—Porcupines feed on aspen and associated vegetation.

Pocket gophers perhaps are the most important member of the small mammal community in aspen forests in the West. Among the small mammals, they are comparatively large, 1/4 to 1 pound (100–500 gm), and often dominate the small mammal biomass (Andersen et al. 1980). Population densities of 36 or more individuals per acre (90 per ha) can be reached in very favorable habitats, such as meadows (Andersen and MacMahon 1981), beyond which intraspecific competition for territory may limit densities (Miller 1964). In the aspen type of northern Utah, Andersen and MacMahon (1981) found population densities varied from 1 to 13 gophers per acre (2 to 33 per ha) over a 4-year period. This was less than found in nearby meadows but markedly more than found in coniferous forest.

Forbs are the primary food of pocket gophers; indeed, forbs may be an essential food for the northern pocket gopher (Miller 1964). This may explain the abundance of gophers in the forb-rich aspen forest type. Gopher diets in summer consist of more than 75% aboveground plant parts; but their winter feeding activity is almost entirely restricted to roots and rhizomes (Ward and Keith 1962).

Population densities of gophers apparently are controlled by winter food supply and by soil conditions. When soils are not frozen solid nor saturated, gophers will burrow in the surface 6 inches (15 cm) of soil at a rate of 3/4 inch (2 cm) per minute and feed on whatever roots, especially forbs, are encountered (Andersen and MacMahon 1981). Andersen and MacMahon (1981) calculated that enough food material was present in the aspen forest to sustain pocket gophers with only 4 hours of feeding-burrowing per day. Hard frozen soil will stop all burrowing activity; but, aspen soils seldom freeze under the deep snowpacks typical in the mountainous West. However, when they do freeze, food caches may become critically important. Aspen soils seldom are too wet for burrowing, except during spring snowmelt, when portions of abandoned gopher burrows have been observed to carry runoff water (Andersen and MacMahon 1981).

Sites with well-drained and friable soils that are protected from freezing solid by topographic position or by deep snowpacks, and with abundant vegetation containing a large component of forbs, appear to be the best pocket gopher habitat (Andersen and MacMahon 1981, Miller 1964). Many aspen stands in the West fit this description perfectly. Only mountain meadows that are well drained and rich in forbs are better habitat.

Other Small Mammals

This composite category includes shrews, mice, voles, ground squirrels, tree squirrels, and chipmunks. There are five species of shrews, three of mice, five of voles, four of ground squirrels, two of tree squirrels, and four species of chipmunks in the aspen forests of the West (appendix). Some of these species are restricted to aspen stands that contain a substantial conifer component; others occur in pure aspen.

Rodents are the most numerous, large, primary consumers of plant energy. In the coniferous forest, deer mice, chipmunks, and red-backed voles are notable consumers of conifer seed (Radvanyi 1973). This probably is true in mixed aspen-conifer forests, too. Small mammals often have two or more litters per year, young mature in a couple months, and populations turn over rapidly. Population densities respond quickly to food availability, habitat changes, and weather. Small mammals are the most important food source for terrestrial carnivores (Halvorson 1981).

The deer mouse usually is the most abundant of all small mammals caught during trapping studies in aspen forests (Andersen et al. 1980, Hanley and Page 1982, Thammaruxs 1975). It is a generalist; 65-75% of its diet consists of seeds (Williams 1959); and it does well in the relatively open aspen forests. Another species, the least chipmunk, has similar habitat requirements, and often is found in near-equal abundance (Andersen et al. 1980, Hayward 1945, Thammaruxs 1975). The red-backed vole is restricted to forested habitats. It is quite abundant in dense aspen (Thammaruxs 1975), but probably most numerous in conifer forests (Halvorson 1982). Populations of this vole decline markedly if the forest is clearcut or burned[7] (Halvorson 1982). These declines often coincide with increases in deer mouse populations after forest removal.

On some aspen forest sites, the western jumping mouse is a common member of the small mammal population (Stinson 1977, Thammaruxs 1975). It, like the deer mouse and chipmunk, is a seed-eater. Voles, however, consume both seeds and succulent plant materials.

The flying squirrel, though seldom seen because of its nocturnal habits, also is present in the aspen forest. Andersen et al. (1980) estimated that it made up about 5% of the biomass of the seven most common mammal species found in the aspen type of northern Utah. Perhaps this mammal is even more important in mixed aspen-conifer stands. Flying squirrels are associated with coniferous forests, where they are dependent upon large snags for nesting cavities (Halvorson 1981), and where they may comprise 8–9% of the small mammal biomass (Andersen et al. 1980). At least in the East, both the flying squirrel and the red squirrel use abandoned sapsucker cavities in aspen (Kilham 1971).

The red squirrel is confined to coniferous trees for satisfactory habitat. Conifer cones and buds are its food source. Juvenile squirrels will disperse into the aspen forest; but mortality there is high (Rusch and Reeder 1978). These juveniles apparently either perish or find groves of conifers as habitat. Red squirrels often are found in isolated conifer groves amidst large stands of aspen. Mixed conifer-aspen stands will support good squirrel populations.

Predators and Other Mammals

Many different mammalian carnivores inhabit the aspen forest type (see the chapter appendix). The forest provides cover and protection from other predators and humans, but otherwise is not critical. The food base is their critical component. If suitable habitat is present in the aspen type for herbivores, and adequate and relatively stable populations of prey species are encouraged, the predators largely will take care of themselves, assuming that there is no human intervention.

Other animals in this group are omnivores; they may be as dependent upon the vegetation as they are upon a prey base for a food supply. The largest among these are bears. Black bears in Alberta, for example, prefer aspen, aspen-birch, and jack pine forests in summer and fall, presumably because of an abundance of berries in the deciduous forested uplands. Because they den near their fall feeding sites, most of the dens are also in the aspen and aspen-mixed stands (Fuller and Keith 1980, Tietje and Ruff 1980). Gullion (1977b) cited accounts of black bears feeding on aspen buds, leaves, and catkins (fig. 13). In Colorado and in Idaho, DeWeese and

Figure 13.—Black bears eat aspen buds and catkins, as is evident from the repeated climbing of this aspen tree in northern Colorado. (Photo by Gordon Gullion)

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[7] *Personal communications from Glenn L. Crouch, USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo., and H. Duane Smith, Brigham Young University, Provo, Utah.*

Pillmore (1972) reported several instances of black bears climbing aspen trees and robbing bird nests, including those of cavity nesting flickers.

Most predators are wide ranging and show limited affinity for any particular forest type. These species are listed in the appendix as being in the aspen type even though other types may provide equally good or better habitat. For example, the lynx probably prefers coniferous forest in some parts of its range. Other predators, such as the badger and the red fox, find open areas (grass and shrubs) more to their liking. They are found in aspen only incidentally.

Five species of bats are listed as being in the aspen type (see the chapter appendix). Perhaps the large insect populations in this forest type (MacMahon 1980; Winternitz 1980) attract these mammalian insectivores. Although bats may use the forest for feeding, many species use caves for roosting, resting, breeding, and hibernating. Bats, however, will crawl into hollow trees and under exposed flaps of bark for daytime roosting sites (Thomas 1979).

APPENDIX

Wild Mammals and Birds Found in Aspen and Aspen-Conifer Mixed Forests of Western United States and Adjacent Canada.

The mammal list was derived from Andersen et al. 1980; Armstrong 1972, 1977; Durrant 1952; Hanley and Page 1982; Hunt 1979; Jones et al. 1979 (nomenclature); Thammaruxs 1975; Weatherill and Keith 1969; from personal observations by the author; and from personal communications with Curtis Halvorson, U.S. Fish and Wildlife Service, Fort Collins, Colo.; and with H. Duane Smith, Brigham Young University, Provo, Utah. The bird list was derived from Behle and Perry 1975; DeByle 1981; Flack 1976; Smith 1982; Smith and MacMahon 1981; Winternitz 1976; Young 1973; from personal observations by the author; and from personal communications with Virgil E. Scott, U.S. Fish and Wildlife Service, Fort Collins, Colo.; Glenn L. Crouch, USDA Forest Service, Fort Collins, Colo.; Keith Dixon, Utah State University, Logan; and James Brown, USDA Forest Service, Missoula, Mont. Bird nomenclature follows latest AOU Checklist (The Auk 99(3), 1982).

MAMMALS

Scientific Name	Common Name
Sorex cinereus	Masked Shrew
Sorex vagrans	Vagrant Shrew
Sorex nanus	Dwarf Shrew
Sorex palustris	Water Shrew
Blarina brevicauda	Short-tailed Shrew
Myotis lucifugus	Little Brown Myotis
Myotis volans	Long-legged Myotis
Lasionycteris noctivagans	Silver-haired Bat
Eptesicus fuscus	Big Brown Bat
Lasiurus cinereus	Hoary Bat
Sylvilagus nuttallii	Nuttall's Cottontail
Lepus americanus	Snowshoe Hare
Lepus townsendii	White-tailed Jack Rabbit
Eutamias minimus	Least Chipmunk
Eutamias amoenus	Yellow-pine Chipmunk
Eutamias quadrivittatus	Colorado Chipmunk
Eutamias umbrinus	Uinta Chipmunk
Marmota flaviventris	Yellow-bellied Marmot
Spermophilus armatus	Uinta Ground Squirrel
Spermophilus tridecemlineatus	Thirteen-lined Ground Squirrel
Spermophilus variegatus	Rock Squirrel
Spermophilus lateralis	Golden-mantled Ground Squirrel

Scientific Name	Common Name
Tamiasciurus hudsonicus	Red Squirrel
Glaucomys sabrinus	Northern Flying Squirrel
Thomomys talpoides	Northern Pocket Gopher
Perognathus parvus	Great Basin Pocket Mouse
Castor canadensis	Beaver
Peromyscus maniculatus	Deer Mouse
Neotoma cinerea	Bushy-tailed Woodrat
Clethrionomys gapperi	Southern Red-backed Vole
Microtus pennsylvanicus	Meadow Vole
Microtus montanus	Montane Vole
Microtus longicaudus	Long-tailed Vole
Lagurus curtatus	Sagebrush Vole
Phenacomys intermedius	Heather Vole
Zapus princeps	Western Jumping Mouse
Erethizon dorsatum	Porcupine
Canis latrans	Coyote
Canis lupus	Gray Wolf
Vulpes vulpes	Red Fox
Ursus americanus	Black Bear
Ursus arctos	Grizzly Bear
Procyon lotor	Raccoon
Mustela erminea	Ermine
Mustela frenata	Long-tailed Weasel
Taxidea taxus	Badger
Mephitis mephitis	Striped Skunk
Felis concolor	Mountain Lion
Felis lynx	Lynx
Felis rufus	Bobcat
Cervus elaphus	Elk or Wapiti
Odocoileus hemionus	Mule Deer
Odocoileus virginianus	White-tailed Deer
Alces alces	Moose
Bison bison	Bison
Ovis canadensis	Mountain Sheep

BIRDS

Scientific Name	Common Name
Aix sponsa	Wood Duck
Bucephala clangula	Common Goldeneye
Bucephala islandica	Barrow's Goldeneye
Bucephala albeola	Bufflehead
Lophodytes cucullatus	Hooded Merganser
Mergus merganser	Common Merganser
Cathartes aura	Turkey Vulture
Accipiter striatus	Sharp-shinned Hawk
Accipiter cooperi	Cooper's Hawk
Accipiter gentilis	Northern Goshawk
Buteo platypterus	Broad-winged Hawk
Buteo swainsoni	Swainson's Hawk
Buteo jamaicensis	Red-tailed Hawk
Aquila chrysaetos	Golden Eagle
Falco sparverius	American Kestrel
Falco columbarius	Merlin
Falco peregrinus	Peregrine Falcon
Falco mexicanus	Prairie Falcon

Scientific Name	Common Name
Dendragapus obscurus	Blue Grouse
Bonasa umbellus	Ruffed Grouse
Tympanuchus phasianellus	Sharp-tailed Grouse
Meleagris gallopavo	Wild Turkey
Grus canadensis	Sandhill Crane
Columba fasciata	Band-tailed Pigeon
Zenaida macroura	Mourning Dove
Coccyzus erythropthalmus	Black-billed Cuckoo
Otus flammeolus	Flammulated Owl
Otus kennicottii	Western Screech-owl
Bubo virginianus	Great Horned Owl
Glaucidium gnoma	Northern Pygmy-owl
Asio otus	Long-eared Owl
Aegolius acadicus	Northern Saw-whet Owl
Chordeiles minor	Common Nighthawk
Phalaenoptilus nuttallii	Common Poorwill
Aeronautes saxatalis	White-throated Swift
Archilochus colubris	Ruby-throated Hummingbird
Stellula calliope	Calliope Hummingbird
Selasphorus platycercus	Broad-tailed Hummingbird
Selasphorus rufus	Rufous Hummingbird
Sphyrapicus varius	Yellow-bellied Sapsucker
Sphyrapicus ruber	Red-breasted Sapsucker
Sphyrapicus thyroideus	Williamson's Sapsucker
Picoides pubescens	Downy Woodpecker
Picoides villosus	Hairy Woodpecker
Picoides tridactylus	Three-toed Woodpecker
Colaptes auratus	Northern Flicker
Dryocopus pileatus	Pileated Woodpecker
Contopus borealis	Olive-sided Flycatcher
Contopus sordidulus	Western Wood-pewee
Empidonax flaviventris	Yellow-bellied Flycatcher
Empidonax traillii	Willow Flycatcher
Empidonax minimus	Least Flycatcher
Empidonax hammondii	Hammond's Flycatcher
Empidonax oberholseri	Dusky Flycatcher
Empidonax difficilis	Western Flycatcher
Myiarchus crinitus	Great Crested Flycatcher
Tyrannus tyrannus	Eastern Kingbird
Progne subis	Purple Martin
Tachycineta bicolor	Tree Swallow
Tachycineta thalassina	Violet-green Swallow
Stelgidopteryx serripennis	Northern Rough-winged Swallow
Hirundo pyrrhonota	Cliff Swallow
Perisoreus canadensis	Gray Jay
Cyanocitta stelleri	Steller's Jay
Nucifraga columbiana	Clark's Nutcracker
Pica pica	Black-billed Magpie
Corvus brachyrhynchos	American Crow
Corvus corax	Common Raven
Parus atricapillus	Black-capped Chickadee
Parus gambeli	Mountain Chickadee
Sitta canadensis	Red-breasted Nuthatch
Sitta carolinensis	White-breasted Nuthatch
Sitta pygmaea	Pygmy Nuthatch
Certhia americana	Brown Creeper
Troglodytes aedon	House Wren
Regulus satrapa	Golden-crowned Kinglet
Regulus calendula	Ruby-crowned Kinglet

Scientific Name	Common Name
Sialia mexicana	Western Bluebird
Sialia currucoides	Mountain Bluebird
Myadestes townsendi	Townsend's Solitaire
Catharus fuscescens	Veery
Catharus ustulatus	Swainson's Thrush
Catharus guttatus	Hermit Thrush
Turdus migratorius	American Robin
Ixoreus naevius	Varied Thrush
Dummetella carolinensis	Gray Catbird
Toxostoma rufum	Brown Thrasher
Bombycilla garrulus	Bohemian Waxwing
Bombycilla cedrorum	Cedar Waxwing
Sturnus vulgaris	European Starling
Vireo solitarius	Solitary Vireo
Vireo gilvus	Warbling Vireo
Vireo olivaceus	Red-eyed Vireo
Vermivora peregrina	Tennessee Warbler
Vermivora celata	Orange-crowned Warbler
Vermivora virginiae	Virginia's Warbler
Dendroica petechia	Yellow Warbler
Dendroica coronata	Yellow-rumped Warbler
Setophaga ruticilla	American Redstart
Seiurus aurocapillus	Ovenbird
Oporornis agilis	Connecticut Warbler
Oporornis philadelphia	Mourning Warbler
Oporornis tolmiei	MacGillivray's Warbler
Wilsonia pusilla	Wilson's Warbler
Piranga ludoviciana	Western Tanager
Pheucticus ludovicianus	Rose-breasted Grosbeak
Pheucticus melanocephalus	Black-headed Grosbeak
Guiraca caerulea	Blue Grosbeak
Passerina amoena	Lazuli Bunting
Pipilo chlorurus	Green-tailed Towhee
Pipilo erythrophthalmus	Rufous-sided Towhee
Spizella arborea	American Tree Sparrow
Spizella passerina	Chipping Sparrow
Spizella pallida	Clay-colored Sparrow
Spizella breweri	Brewer's Sparrow
Pooecetes gramineus	Vesper Sparrow
Chondestes grammacus	Lark Sparrow
Passerella iliaca	Fox Sparrow
Melospiza melodia	Song Sparrow
Melospiza lincolnii	Lincoln's Sparrow
Zonotrichia albicollis	White-throated Sparrow
Zonotrichia leucophrys	White-crowned Sparrow
Junco hyemalis	Dark-eyed Junco
Euphagus cyanocephalus	Brewer's Blackbird
Quiscalus quiscula	Common Grackle
Molothrus ater	Brown-headed Cowbird
Icterus galbula	Northern Oriole
Pinicola enucleator	Pine Grosbeak
Carpodacus purpureus	Purple Finch
Carpodacus cassinii	Cassin's Finch
Carpodacus mexicanus	House Finch
Loxia curvirostra	Red Crossbill
Carduelis pinus	Pine Siskin
Carduelis tristis	American Goldfinch
Coccothraustes vespertinus	Evening Grosbeak

WATER AND WATERSHED

Norbert V. DeByle

Quaking aspen dominates several million acres on mountainous watersheds in the West. The sites occupied receive enough precipitation to yield water to lower elevations. Most aspen areas receive 16 inches (40 cm) or more precipitation annually; many receive more than 39 inches (100 cm) (see the CLIMATES chapter), well in excess of on-site loss from evapotranspiration. The distribution of aspen in the West coincides well with areas that have deep winter snowpacks and that produce runoff (fig. 1) (see the DISTRIBUTION and CLIMATES chapters). The recharge of soil with snowmelt water during April and May is especially important to aspen and associated vegetation types (see the EFFECTS OF WATER AND TEMPERATURE chapter). Summer rains augment this stored water supply.

In the relatively arid western United States, water is a very important resource yielded from the aspen type. The importance of water increases as human populations grow and make greater demands on a limited, and mostly fixed water supply. The mountains of the interior West supply most of the water needed by arid and semiarid valleys. These water-yielding lands are covered with many vegetation types: mountain brush, spruce-fir, pine, sagebrush-grass, mountain meadows, and alpine tundra, as well as aspen. Aspen provides excellent protective cover on mountain sites that yield much high-quality water. For reasons discussed later, sites occupied by aspen provide more water than many other sites.

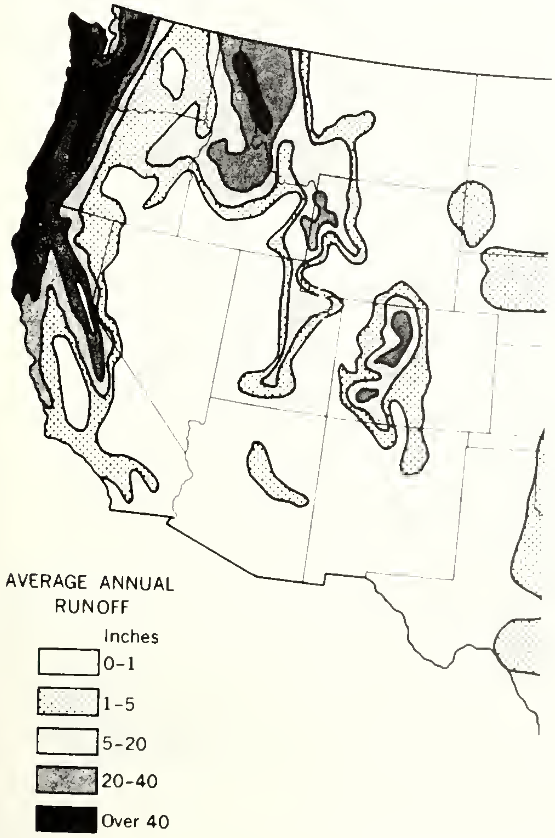

Figure 1.—Average annual runoff in the western United States.

Aspen Influences

Snow

During winter and early spring (typically for 4 to 6 months), most aspen sites in the West are snow-covered. The depth and ablation (snowmelt and evaporation) rates of the snowpack are affected by the aspen forest. In both Minnesota and New Mexico, for example, more snow accumulated under aspen; but it melted faster and disappeared earlier than from under conifers, primarily on southerly exposures (Gary and Coltharp 1967, Weitzman and Bay 1959). Swanson and Stevenson (1971) found that isolated leafless aspen and willow stands in Alberta retained a snowpack during chinook winds that melted all snow from large open areas. Small openings within these stands were effective snow traps, accumulating one-third more snow than elsewhere in the stand. They found that snow ablated 30% more slowly in these openings, extending the snowmelt runoff or groundwater recharge later into the spring.

Aspen forests intercept only minimal amounts of snow, especially compared to coniferous forests, where much of the snow may never reach the ground. In central Utah, Harper found 5% to 70% less water in the snowpack under mixed aspen-conifer stands than under pure aspen.[1] Dunford and Niederhof (1944) found 12% more snow under aspen than in the open. Nearby lodgepole pine contained 12% less snow than the open area, which was approximately 75% of the amount found under aspen. Intercepted snow may evaporate more readily than snow on the ground because of greater surface area exposure to radiation and wind. However, much of what is intercepted by tree crowns later may be transferred elsewhere within the forest (Miller 1962). Crown shape, crown closure, aspect and exposure, and climatic conditions during and after snowfall all affect the amount of snow intercepted and its later disposition.

In the Rocky Mountain West, the snow surface under a leafless aspen canopy is exposed to a high evaporation potential because of a relatively dry atmosphere, much direct solar radiation, and only partial shelter from wind. Some snow evaporates or sublimates. Doty and

[1] *Personal communication with Kimball Harper, Brigham Young University, Provo, Utah.*

Johnston (1969) measured losses from the snowpack under aspen, under conifers, and in the open, on a typical aspen site in Utah. They found twice as much evaporative loss from the snowpack in the open than they did under conifers. Losses under aspen were intermediate, averaging about 1 inch (2.5 cm) of water loss from the snowpack during a typical winter (fig. 2). However, these measurements were made when winds were less than 7 miles per hour (3 m/sec). When winds are greater, snow becomes airborne. Sublimation from these airborne snow particles is greater than from the snowpack surface because of more exposed surface area and the lack of a saturated air boundary layer. Thus, wind increases evaporative loss. In Doty and Johnston's (1969) study, air movement under the leafless aspen stand was only two-thirds that found in the open; snow drifting was less, and water loss from airborne snow, therefore, would be less than in the open. However, evaporative losses will vary with aspect and degree of protection provided by the vegetation.

Rain

The aspen canopy potentially intercepts much more rain in summer than snow in winter. For example, 10.3% of gross summer rainfall did not reach the ground in a dense Utah aspen stand (Johnston 1971). Because summer is the driest season in much of the West, this loss becomes much less important when converted to actual rainfall. In the Utah stand, the average summer rainfall was 4.5 inches (11 cm), of which only ½-inch (1.2 cm) was caught in and evaporated from the foliage. This corroborated earlier findings by Dunford and Niederhof (1944) in Colorado. They measured 15.7% interception of the 5 inches (13 cm) of summer rainfall—or an average summer season loss of 3/4 inch (2 cm).

Stemflow redistributes precipitation, and may be a significant influence in eastern aspen forests by funneling rain and nutrients to the feeding roots at the tree base (Clements 1971). However, both Johnston (1971) and Dunford and Niederhof (1944) found negligible stemflow in aspen stands in the West—only 1.4% and 1.1%, respectively, of the summer season rainfall. This small trickle down aspen boles is not likely to measurably influence the forest or its hydrology.

Wind

Wind during the growing season will increase evapotranspiration rates. Compared to an adjacent opening, air movement during summer was only one-sixth as much under a dense Utah aspen stand (Marston 1956), where the aspen cover reduced air velocities an average of 2.6 miles per hour (1.2 m/sec). This reduction, and the absorption of solar radiation by the overstory, reduces potential evapotranspiration under the canopy.

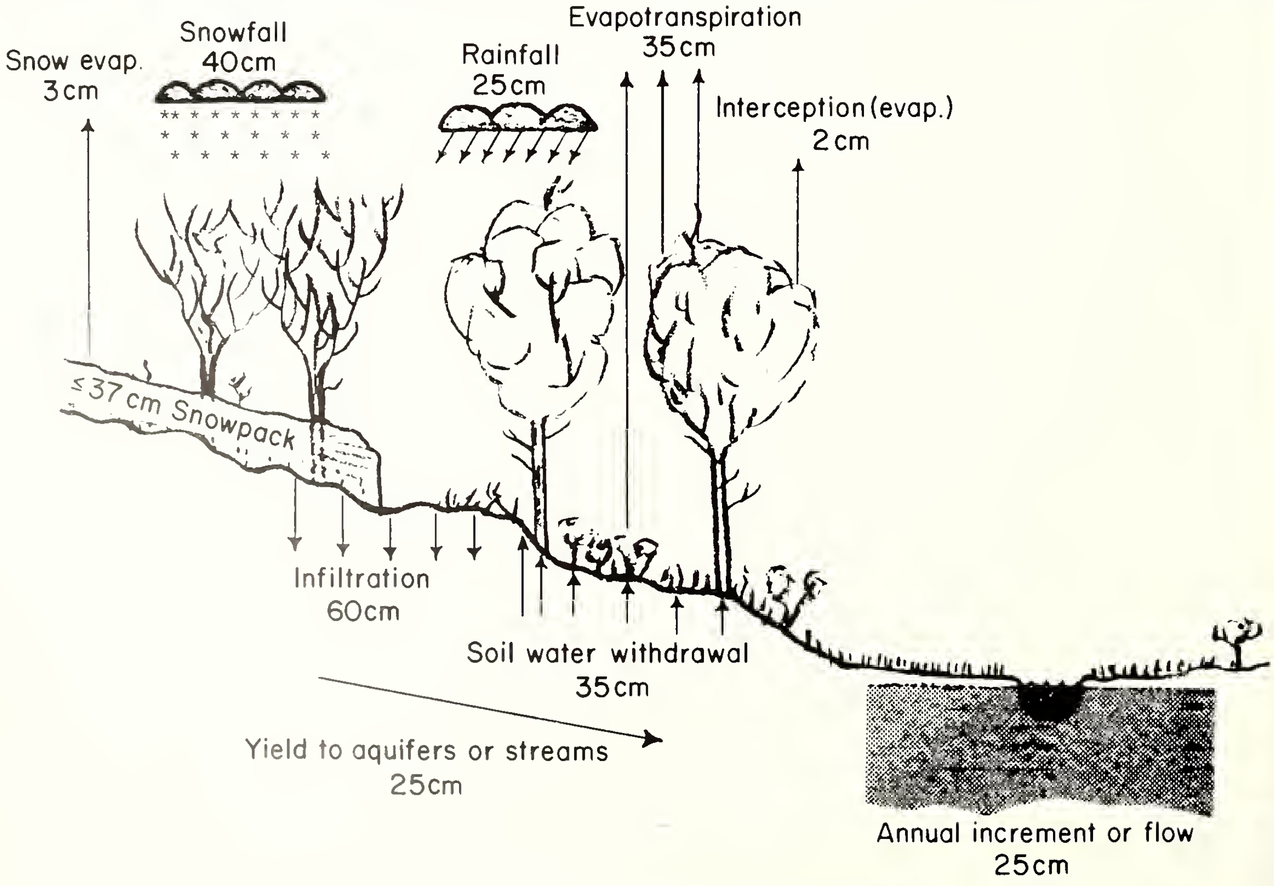

Figure 2.—Water balance in a typical western aspen catchment.

As noted previously, during winter, wind affects distribution and depth of snow, as well as its rate of evaporation. During this dormant season, air movement is greatest in large openings, less in aspen or other deciduous hardwood stands, and least in dense conifer stands.

Aspen-Soil-Water Relations

Sucoff (1982) provided a broad review of water relations in the aspens. Physiologically, aspen differs from its coniferous counterparts in the West. Transpiration from aspen, as from other deciduous hardwoods, is negligible during the dormant season. In contrast, evergreen coniferous trees in the same environment transpire in the spring, before aspen develops leaves, and continue to transpire in the autumn, after the aspen leaves drop. Because of this, conifers may use 3 to 7 inches (7 to 18 cm) more water per year than does aspen (Gifford et al. 1983, 1984; Jaynes 1978). While in leaf, however, aspen is a good wick, withdrawing water by the roots and transpiring it from the crowns. Aspen readily withdraws most available water from the soil to the depth of effective rooting, commonly 3–10 feet (1–3 m) (Berndt and Gibbons 1958, Gifford 1966).

Aspen forests transpire water throughout the growing season; but most is lost immediately after full leaf development in the spring and early summer (fig. 3) (Kramer and Kozlowski 1960, Tew 1967). Early in the growing season, the soil contains a full charge of available water. Daily periods of transpiration are longest on these long days. As the season progresses, decreasing soil water potentials, shorter days, and aging leaves all cause a decrease in water-use rates.

Summer rains wet the vegetation (interception), and, if more than 0.2 inch (5 mm) falls, enough reaches the ground to recharge the surface soil. The forest then transpires at or near its potential rate for a short period after each storm. However, within a few days, this added water supply is exhausted, and transpiration declines. These summer storms are frequent in the southern part of the aspen range (see the CLIMATES chapter).

The stems of aspen clones, in part, are interconnected on a common parent root system (DeByle 1964, Tew et al. 1969) (see the MORPHOLOGY and the VEGETATIVE REGENERATION chapters). Root-connected groups (2 to 43 stems) potentially can function as individual units for water transport, especially during times of moisture stress (fig. 4).

Soil water depletion during the growing season has been measured on a variety of aspen sites in Utah (Croft and Monninger 1953; Johnston 1969, 1970; Johnston et al. 1969; Tew 1967).[2] In all instances, the available water was extracted by aspen fully occupying the site from the upper 6–7 feet (2 m) of soil during the growing season (June through mid-September). Soil water potentials in these profiles at the end of summer often were near −15 bars. In Arizona, New Mexico, and Colorado, where summer rain is much more frequent and abundant, soils may not dry out so thoroughly.

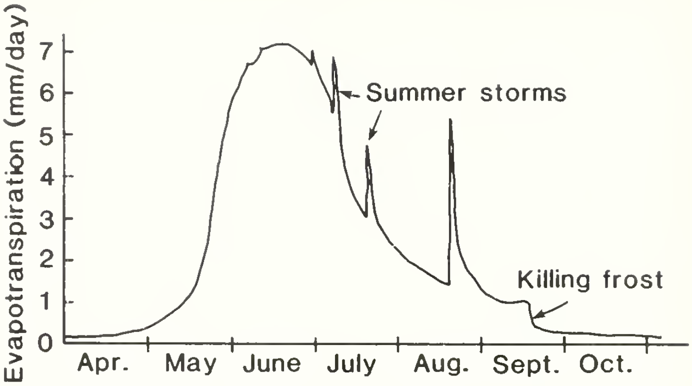

Figure 3.—Approximate evapotranspiration from the aspen forest during a typical growing season in the interior western United States.

Water begins to be extracted in significant quantities in the spring, when vegetative buds burst and new leaves emerge. It has not been possible to make valid soil water depletion measurements in the aspen forest in the spring until snowmelt ends and the soil profile ceases draining rapidly. By that time, many high-elevation aspen already are partially leafed out, and have transpired water. Therefore, the measurements in the cited Utah studies are conservative.

Precipitation during the growing season seldom recharges more than the surface 8 to 16 inches (20 to 40 cm) of soil under most aspen in the West. Because it, too, is lost to evapotranspiration, this precipitation increment is added to the measured soil water depletion to provide an estimate of evapotranspiration by the aspen community.

In Utah, estimated evapotranspiration using this method averaged 2.3 inches per foot (19 cm/m) of soil depth from mature aspen. It varied from 5.5–11 inches (14 to 28 cm), depending upon amounts of summer precipitation received and the soil physical properties that controlled the amount of available water held in the profile (Johnston et al. 1969). Based on an assumed average effective aspen rooting depth of 8 feet (2.5 m) and an average amount of summer precipitation of 4.7 inches (12 cm), a rough estimate of evapotranspiration from mature aspen in Utah is 17 inches (44 cm) per year. From similar work in southern Alberta, Singh estimated 16.5 inches (42 cm) of evapotranspiration from aspen during a 122-day growing season.[3] In contrast, Kaufmann more conservatively estimated evapotranspiration from aspen in Colorado to be less than 8 inches (20 cm) per year.[4]

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[2] *DeByle, Norbert V., Robert S. Johnston, Ronald K. Tew, and Robert D. Doty. 1969. Soil moisture depleton and estimated evapotranspiration on Utah watersheds. 14 p. [Paper presented at International Conference on Arid Lands in a Changing World, June 3-13, 1969, Tucson, Ariz.] [Abstracts]*

[3] *Personal communication with Teja Singh, Canadian Forestry Service, Edmonton, Alberta.*

[4] *Personal communication from Merrill R. Kaufmann, USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo.*

Most soil water is withdrawn early in the growing season—when it is held under least tension and, therefore, is readily available to the rapidly transpiring trees. Tew (1967) found that more than 80% of the seasonal depletion took place in the first 49 days (40%) of the growing season. Later, water is withdrawn from deeper within the rooting zone. Because most roots are near the surface, available water is taken from the upper portion first. Once water is depleted from the upper zones, the roots near the bottom of the profile more slowly withdraw water and bring the trees through any late-summer drought. As noted previously, whenever summer rains recharge the surface soil, rapid uptake by surface roots resumes and transpiration temporarily increases.

Data from Utah indicate that most evapotranspirational demand is satisfied by water from the upper portion of the soil profile (Johnston 1970, Johnston et al. 1969). Unless the season is exceptionally dry, the lower portion will not lose all of its available water. Aspen roots typically do not fully occupy these lower depths, and water movement through the soil to the sparsely scattered root-absorbing surfaces is very slow at lower water potentials. Despite low water potentials within the tree, movement of the remaining water into the roots progresses slowly at the lower limits of the rooting zone.

Dense stands of aspen root suckers quickly replace aspen trees that are clearcut, burned, or otherwise quickly killed. These sucker stands use less water than the mature forest; in Utah they used from ½ to 5 inches (1 to 13 cm) less water from the surface 6–7 feet (2 m) of soil during the growing season (Johnston et al. 1969). Most of this savings is in the lower half of the soil profile; evapotranspiration from the upper half remains about the same as before. These differences diminish rapidly as sprout stands mature and transpiration accelerates. Within 10 or 20 years, the sprout stand probably will consume as much water as its parent trees did.

Water returned to the atmosphere by evapotranspiration is a loss to either streamflow or groundwater. The deficit in maximum soil water content at the end of each growing season, caused by evapotranspiration, first must be satisfied by autumn precipitation or by snowmelt before significant amounts of water will drain through the soil and be yielded from the watershed. Autumn rains usually do not recharge the mantle sufficiently to produce significant water yields. Instead, on most aspen watersheds in the West, spring snowmelt produces most of the streamflow or aquifer recharge. Water evaporated or transpired during the growing season from these sites is expressed as reduced water yields during the following spring and summer.

Overland Flow and Erosion

Aspen has a measurable influence on the underlying soil. Tew (1968) found the surface 6 inches (15 cm) of soil under Utah aspen stands had 4% more organic matter, higher water holding capacity, slightly higher pH, and more available phosphorus than adjacent stands of shrubs and herbaceous vegetation. Aspen produces

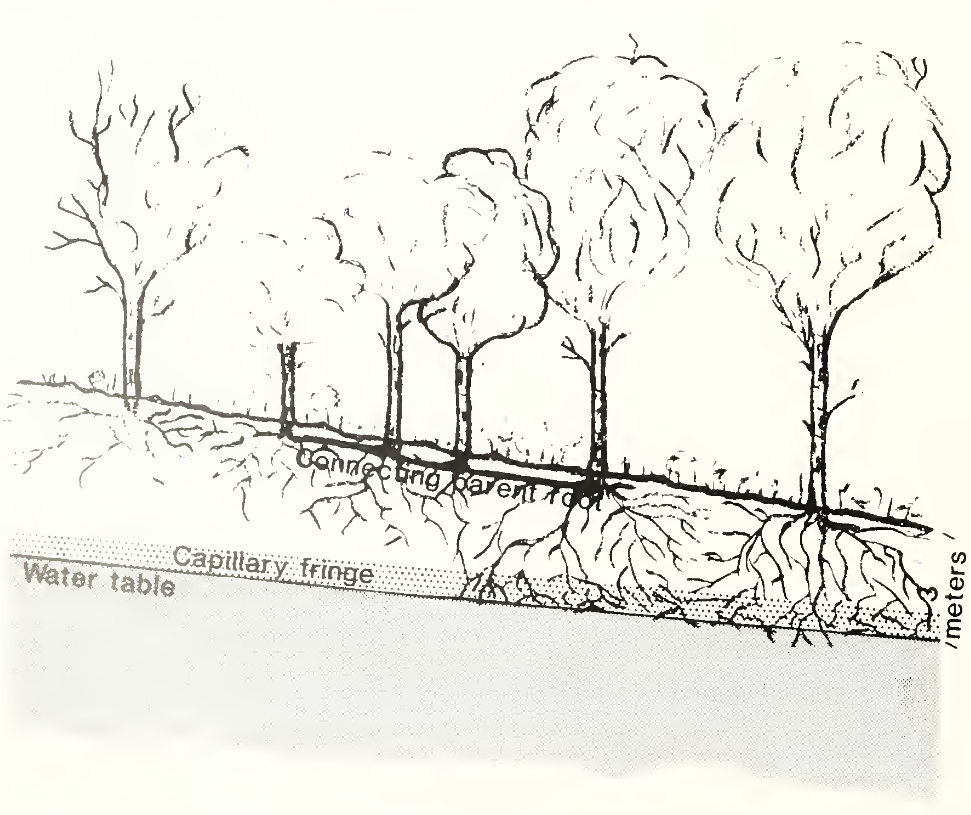

Figure 4.—Roots of an aspen clonal group, with four interconnected trees, tapping a water table.

nutrient-rich litter that decays rapidly (Bartos and DeByle 1981, Daubenmire 1953, Daubenmire and Prusso 1963). A thin surface organic soil horizon is typically underlain by thick A_1 horizon—high in organic matter content and available nutrients. Aspen are efficient nutrient pumps that enrich the surface soil horizons. (See the SOILS chapter.)

A well-stocked aspen stand provides excellent watershed protection. The trees, the understory of brush or herbaceous species, and the litter furnish virtually 100% soil cover. A mixture of herbaceous and woody root systems penetrate and anchor the soil. Erosion-producing overland flow is almost nonexistent under stands like these—even storms with 5-minute intensities approaching 6 inches (15 cm) per hour infiltrate the porous, humus-rich soil (Marston 1952). Snowmelt is never this rapid; large frontal systems usually provide gentle rains; only intense summer storms produce rainfall at rates approaching the infiltration capacity of aspen forested soils.

However, erosion in the form of mass movement or slumping takes place on many aspen-forested mountainsides in the West. This usually is the natural geologic rate of erosion on unstable landforms. Bailey[5] identified and described these landforms and associated hazards in northwest Wyoming; the principles apply elsewhere. Aspen is one of only a few tree species that colonize these unstable slopes. This erosion does not occur because of poor aspen cover; instead these landforms are covered with aspen, brush, and herbaceous species because of their instability. Under these conditions, aspen provides the best natural protection possible on soils that frequently have a high clay content, are plastic, and are often quite wet.

Erosion on otherwise stable aspen-covered slopes may occur if excessive use or abuse reduces the cover of vegetation and litter to 65% or less (Marston 1952). This usually results from excessive grazing and browsing by ungulates (Bailey et al. 1934, 1947).

In the aspen type of northern Utah, Marston (1952) found that less than 1% of any storm ran off the surface of well-vegetated plots. Erosion was negligible if less than 5% of the rainfall ran off as overland flow. The ground cover required to keep overland flow at 5% or less increased from 5% of the plot area at a rainfall intensity of 1.5 inches (4 cm) per hour to 65% at an intensity of nearly 3 inches (8 cm) per hour.

Meeuwig (1970) concluded that the proportion of the soil surface protected from raindrop impact by vegetation, litter, and stone was the most important factor in erosion control. Slope gradient and bulk density of the surface mineral soil varied directly with amount of erosion measured. Soil organic matter favored stability of fine textured soils but apparently increased erodibility of sandy soils.

Water Quality

Ungrazed aspen watersheds yield excellent quality water, within the limits imposed by geologic conditions. A pair of such watersheds in northern Utah, for example, yielded streamflow with less than 60 ppm suspended sediment, nitrate concentrations seldom exceeded 0.1 ppm; conductivity ranged from 70 to 342 μmhos (varying inversely with volume of streamflow); bicarbonate and calcium comprised the bulk of the dissolved chemical load; pH averaged 7.5; and there were very low but variable counts of bacteria (0 to 250 per 100 ml) (Johnston and Doty 1972). In Alberta, Singh (1976) found that dissolved solids concentration in streamflow from an aspen-grassland catchment averaged 270 ppm with a range of 148 to 331 ppm.

Bacterial counts, which include enteric bacteria, were high enough in streamwater to require treatment to meet potability standards, even counts from the virtually undisturbed Utah watersheds. Bacterial concentrations on these watersheds were highest during rising stages of streamflow—indicating a flushing action from the banks, from overland flow directly into the streams, and from beaver dams. Wildlife was the only known source of enteric bacteria in these Utah drainages (Johnston and Doty 1972).

Darling and Coltharp (1973) sampled stream water quality from three small watersheds in which aspen was a major vegetation component. Total coliform, fecal coliform, and fecal streptococci counts were higher in streams below the two grazed areas than the ungrazed area. Maximum counts were reached during snowmelt runoff and during the grazing period; minimum counts occurred in winter. There were no significant impacts from grazing on pH, temperature, turbidity, nitrate content, or phosphate content of the streamwater.

Clearcutting the aspen forest potentially could alter water quality, because this practice interrupts nutrient cycling, increases insolation at the forest floor, increases water yields, and even may cause some overland flow. Despite this potential, limited studies have not shown any appreciable change in water quality attributable to aspen harvest (Richardson and Lund 1976, Verry 1972). No major changes in water quality after clearcutting were evident in data from a Utah study, either (Johnston 1984).

Vegetation Type Comparisons

Aspen is not entirely unique; other vegetation types growing in the same environment also use water, protect the soil from erosion, and influence the hydrologic system.

The following comparison of vegetation types assumes all other factors are held constant—that elevation, soil

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[5] *Bailey, Robert G. 1971. Landslide hazards related to land use planning in Teton National Forest, northwest Wyoming. 131 p. USDA Forest Service, Intermountain Region. Ogden, Utah.*

type and depth, topography, climate, and geological conditions are identical across all vegetation types. Use by ungulates and by people are not considered. These conditions seldom, if ever, are present in the real world. Nevertheless, at least qualitative differences among aspen, conifers, mountain brush, and grass-forb communities are attempted in table 1. Comparisons can be made only horizontally across types, not vertically among parameters.

The amount of solar radiation that penetrates the vegetation and reaches the soil or snow surface is controlled by canopy density. Air movement within the stand or near the ground is similarly affected by the canopy. Conifers are dense throughout the year; aspen and mountain brush in winter generally provide only limited screening to wind or sunlight, although this can be greatly influenced by aspect and slope; and grass-forb cover has no effect when buried under snow.

The effect of vegetation on amounts of precipitation reaching the ground and its disposition (runoff, snowmelt, etc.) is hydrologically important. Perhaps the mountain brush, and definitely the grass-forb type intercepts less incoming precipitation than does aspen. Winter snowpacks likely are greatest under aspen, and their melt rates in the spring should be similar to those in the open grass-forb community.

The amount of water used by each of these vegetation types depends on the site. As a result, available data are more difficult to interpret than climatic data. Aspen, deciduous brush, and the grass-forb communities transpire significantly only in late spring and summer, whereas the conifers and evergreen brush species may transpire whenever water is available and leaf temperatures permit. Therefore, as noted previously, conifers most probably transpire more water per year (Gifford et al. 1983, 1984).

Table 1.—Comparative influences of four vegetation types in the western United States and southwestern Canada on several climatic and hydrologic parameters.[1]

Physical Parameter	Vegetation type			
	Aspen	**Conifers**	**Mountain brush**	**Grasses and forbs**
Climatic variables				
Solar radiation to ground				
Summer	----	----	---	--
Winter	--	----	-	0
Wind				
Summer	---	----	--	-
Winter	-	----	-	0
Interception				
Rain	+ +	+ + + +	+ +	+
Snow	+	+ + + +	+	0
Snowpack				
Water content	+ + +	----	+ +	+
Rate of melt	-	----	-	0
Water Use				
Transpiration season	Late spring and summer	Sp, Su, Au	*Deciduous* Late spring and summer *Evergreen* Sp, Su, Au	Late spring and summer
Amount	+ + +	+ + + +	+ + +	+ +
Rooting depth	+ + +	+ + +	+ + +	+ +
Soil water use				
Amount	+ + +	+ + + +	+ + +	+ +
Depth	+ + +	+ + +	+ + +	+ +
Water Yields				
Quantity	---	----	---	--
Timing	Intermediate	Latest	Intermediate	Earliest
Quality				
Chemical absence	+ + + +	+ + +	+ + + +	+ + + +
Sediment absence	+ + + +	+ + + +	+ + +	+ + +
Other				
Litter depth	+ +	+ + + +	+ +	+
Infiltration	+ + + +	+ + +	+ + +	+ +
Surface runoff	----	---	---	--
Erosion	----	---	---	--

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[1] – = *relative decrease;* + = *relative increase;* 0 = *no likely change from that found in a hypothetical, large, open area without vegetation.*

Depth of rooting and amount and depth of soil water consumption during the monitored growing season are somewhat similar for the tree and brush species studied (Johnston et al. 1969). In contrast, the grass-forb type sends roots to less than one-half the depth and, consequently, uses much less water than its woody counterparts on deep, well-drained soils. All use more water than evaporates from bare soils (fig. 5).

Water yield is the residual after losses by evapotranspiration. Because the coniferous type has the potential of using the most water, yields from it presumably would be least. The converse is true for the grass-forb type. Although aspen and deciduous brush transpire during a shorter season and intercept less snow than the conifers, they withdraw water from just as great a depth as the conifers; therefore, yields from aspen and brushlands are estimated to be intermediate.

Snowmelt is earliest in the montane grass-forb community; therefore, peak spring streamflow is earliest, and it perhaps has the sharpest and highest peaks. Rate of snowmelt under conifers is slowest; but less snow is present on the ground under dense coniferous stands. As a result, the ground often is bare under these stands almost as early as in the aspen. To produce latest timing of peak spring flows and to sustain snowmelt flows well into summer (table 1), there would have to be many, relatively small, partially shaded openings to trap snow in the conifer forest.

If all other factors are held constant, quite similar quality water will be yielded from all four vegetation types. Streamflow from all types will be of markedly better quality than from any denuded area. The aspen type appears to have the potential of yielding the highest quality water because the soil that develops under it is porous, essentially neutral, high in incorporated organic matter, and biologically active. Conifers develop acid, nutrient-leached soils that have the potential of yielding dissolved materials to percolating water; some grass-forb types do not provide as good a protective cover from erosion as do forests; and water repellent materials are produced in both conifer and some brush types that can encourage overland flow.

Litter depths (surface organic soil horizons) are greatest under conifers and least under many grass-forb communities. This directly controls the amount of water that can be stored in or intercepted by this layer. In turn, infiltration, runoff rates, and other hydrologic variables are affected.

For reasons already stated, infiltration probably is best under aspen. It may be poorest under grass-forb cover, because this type often has shallow litter depths and high soil bulk densities. Therefore, the potential for surface runoff and erosion on the grass-forb type would be greater. The differences among vegetation types, however, are likely to be minor. Again, good data for undisturbed stands on like sites are not available.

All four types compared here seldom occur on truly similar sites. For example, conifers are able to occupy higher elevations than aspen; therefore, they often grow on sites that receive more precipitation. Thus, water yields from these conifer sites usually are greater, and, because of dilution, chemical water quality may be better than from nearby, but lower, aspen sites (Singh 1976).

Water Use and Yield

Irrigation has been the major consumptive use of water in the West. Domestic and industrial uses have grown, often at the expense of irrigation water where supplies already are fully allocated. Some water also is used to maintain fisheries and aquatic habitats. In addition, marshes and waterfowl refuges receive water in the form of irrigation flows and other "used" water, particularly in the Great Basin province.

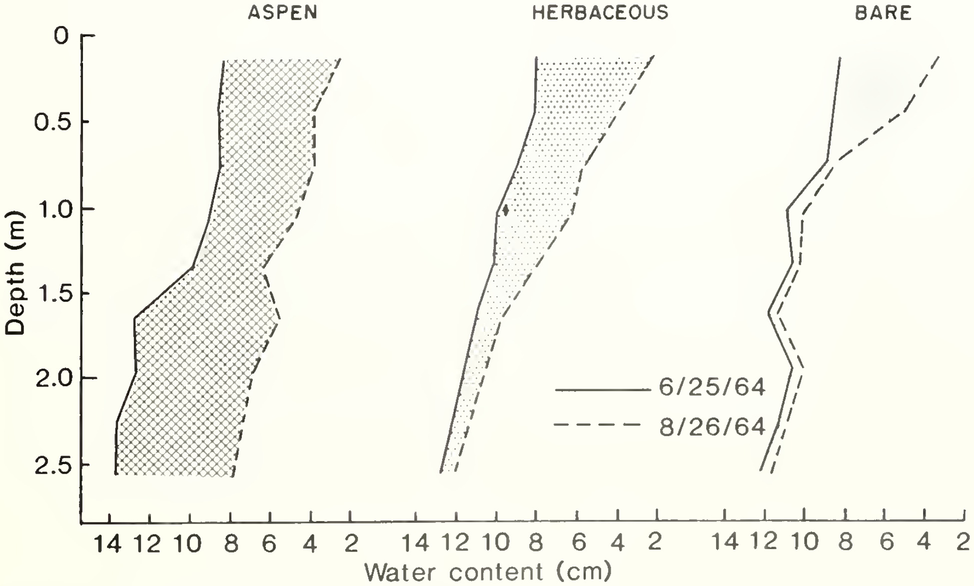

Figure 5.—Soil moisture profiles under three cover conditions on one site at beginning and end of growing season.

Water has long been an important commodity, vital to the growth and development of the West. However, the price paid for water usually does not reflect its value. What is paid for it in the marketplace usually reflects the costs to the processor (e.g., the municipality or irrigation company), not what the consumer would be willing to pay. The value of water varies with its use, as well as other factors. For example, water consumed by domestic and industrial users has a much higher value than that used for irrigation.

It may be useful to provide an estimate of the amount of water yielded by aspen lands in the mountainous West. Using averages from across the West, the aspen type receives about 24 inches (60 cm) of precipitation annually in the interior mountains. About 14 inches (35 cm) of this is lost by evapotranspiration (Johnston et al. 1969). The difference of 10 inches (25 cm) is potential water yield that could contribute to streamflow or groundwater aquifers. This is equivalent to a yield of approximately 4.8 million acre-feet of water per year from the aspen lands. (Options for improving water yield from aspen lands are discussed in the MANAGEMENT FOR ESTHETICS AND RECREATION, FORAGE, WATER, AND WILDLIFE chapter.)

WOOD RESOURCE

John R. Jones, Norbert V. DeByle, and Robert P. Winokur

Aspen has not been cut extensively in the West; in fact, it has been grossly underutilized. For example, as recently as 1975, the aspen harvest from National Forests in four Forest Service regions in the Rocky Mountain area was 7.64 million board feet.[1] Additional minor volumes were cut on special-use permits for products such as fuel and corral poles. The total amount cut represented only 0.1% of the net volume available in these aspen forests.

Supply

There are 4.4 million acres of commercial aspen forest in the West (Green and Van Hooser 1983). More than one-half is in Colorado (table 1). Commercial forest land is that on which cutting is permitted, and which can produce, under management, at least 20 cubic feet of industrial wood per acre annually.

Earlier publications (Choate 1963, 1965, 1966; Miller and Choate 1964; Spencer 1966), reported more acreage of commercial aspen forest. The change is a result of reclassification of aspen acreage from commercial to noncommercial after site productivity was reevaluated and after harvesting on some lands was prohibited.

The net bole volume of aspen growing stock[2] in the interior West was nearly 4.25 billion cubic feet in 1977 (table 2). More than 70% was in Colorado and Utah. It included pure aspen stands as well as aspen mixed with conifers, even though the latter are not classed as aspen. The net volume of sawtimber on commercial forest land in the West is shown in table 3. These data emphasize the relatively small diameter of most aspen sawtimber.

Basal Area

Basal area is a measure of how densely a stand of trees occupies an area. It is better than tree population as a measure of site occupancy, because it is less dependent upon tree size. Basal area and number of trees together are better than either considered alone.

Baker (1925) showed basal area increasing both with age and with site quality. His tables were based on a large, but localized sample. The relationships are somewhat exaggerated, because the tables included only

Table 1.—Area (in thousands of acres) of aspen forest type by stand size class on commercial timberland[1] in the West (Greene and Van Hooser 1983).

	Sawtimber	Poletimber	Stand size class[2] Saplings	Nonstocked	All classes
Colorado	664.1	1,447.7	378.5	363.4	2,853.7
Utah	235.6	352.6	98.7	30.1	717.0
New Mexico	168.6	138.8	31.0	—	338.4
Wyoming	67.5	79.8	39.3	23.7	210.3
Arizona	41.6	34.9	35.6	—	112.1
Idaho	23.0	39.1	36.4	—	98.5
Montana	0.6	21.6	21.8	0.3	44.3
Nevada	6.5	—	—	—	6.5
Western South Dakota	14.7	4.0	2.0	—	20.7
Total	1,222.2	2,118.5	643.3	417.5	4,401.5

[1]*Commercial timberland is forest land capable of producing at least 20 cubic feet of industrial wood per acre per year and not reserved for uses which are not compatible with timber production.*

[2]*Stand size class is determined by the predominant size in the stand. Aspen trees in the West classed as sawtimber are 11 inches d.b.h. or larger; poletimber trees are 5 to 11 inches d.b.h.; and saplings are 1 to 5 inches d.b.h. Sawtimber stands are at least 10% stocked with growing stock trees, with 50% or more in sawtimber or poletimber, and with sawtimber at least equal to poletimber. Poletimber stands have the same stocking requirements, except poletimber stocking exceeds sawtimber. Sapling/seedling stands have the same stocking requirements, except more than 50% of the stocking is in saplings and/or seedlings.*

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[1] *Information provided by USDA Forest Service Intermountain, Northern, Rocky Mountain, and Southwestern Regional Offices.*

[2] *Growing stock trees are live trees in all size classes that meet the standards of quality and vigor. Cull trees, because of decay or poor form, or trees of very poor vigor are not included. Growing stock volume is the bole volume, in cubic feet, of those trees from the stump to a 4-inch (10-cm) diameter, with deductions for rot (Green and Van Hooser 1983).*

Table 2.—Net volume[1] (in millions of cubic feet) of aspen growing stock on commercial timberland in the West (Greene and Van Hooser 1983)

	Diameter class (*inches*)										
	5.0–6.0	7.0–8.0	9.0–10.9	11.0–12.0	13.0–14.9	15.0–16.9	17.0–18.9	19.0–20.9	21.0–22.9	23.0–24.9	≥ 25	All classes
Colorado	338.9	640.6	567.1	351.8	200.8	108.2	59.9	30.5	5.9	6.2	0.3	2,310.2
Utah	155.3	179.4	133.8	119.8	72.5	43.0	22.8	6.1	4.7	3.2	1.6	742.2
New Mexico	101.9	120.0	108.7	95.0	65.6	48.4	32.2	17.8	9.5	0.1	0	599.2
Wyoming	56.3	51.1	51.8	10.7	19.1	7.7	2.3	0.1	0	0	0	199.1
Arizona	27.8	32.2	33.7	39.0	32.0	21.2	16.3	9.2	6.0	1.0	1.2	219.6
Idaho	16.0	20.6	15.3	16.1	7.9	1.2	0.6	0	0	0	0	77.7
Montana	13.0	18.2	13.8	9.4	2.7	2.6	1.1	1.1	0	(2)	0	61.9
Nevada	3.0	2.1	2.1	3.4	1.5	0.1	0.1	0.1	(2)	0	0	12.4
Western South Dakota	4.6	2.3	1.2	0.3	0	0	0	0	0	0	0	8.4
Total	716.8	1,066.5	927.5	645.5	402.1	232.4	135.3	64.9	26.1	10.5	3.1	4,230.7

[1] *After deduction for rot and defect. To a 4-inch (10-cm) top diameter.*

[2] *Less than 0.05 million cubic feet.*

Table 3.—Net volume (in millions of cubic feet) of sawtimber on commercial forest land in 1977, International 1/4 inch rule (Green and Van Hooser 1983)

	Diameter class (*inches*)								
State	12	14	16	18	20	22	24	≥ 25	All classes
Colorado	1,780.3	1,027.5	570.2	325.9	168.6	32.0	34.9	2.1	3,941.5
New Mexico	533.0	387.0	288.3	193.9	110.6	59.9	0.7	0	1,573.4
Utah	555.4	342.5	211.2	112.4	29.9	24.1	16.7	9.1	1,301.3
Arizona	194.8	163.4	109.4	86.9	50.3	31.9	5.1	5.9	647.7
Wyoming	62.2	135.0	56.9	13.5	0.6	0	0	0	268.2
Idaho	76.5	37.1	5.4	2.4	0	0	0	0	121.4
Montana	47.0	14.8	13.0	5.3	6.3	0	0.2	0	86.6
Nevada	14.9	6.6	0.4	0.4	0.2	0.1	0	0	22.6
Western South Dakota	1.5	0	0	0	0	0	0	0	1.5
Total	3,265.6	2,113.9	1,254.8	740.7	366.5	148.0	57.6	17.1	7,964.2

trees 4 inches (10 cm) d.b.h. and larger; the proportion of these trees in the stand also increased with both age and site quality. However, his data for stands of 90 years and older, on site classes 1 through 3 were essentially free of bias, because even-aged, mature stands on such sites have very few trees smaller than 4 inches (10 cm) d.b.h. His basal area (in square feet per acre) data for these site classes follow.

Age (*years*)	Site class 1	2	3
90	161	146	128
110	172	158	138
130	181	166	146

Extensive sampling in Saskatchewan, showed a similar correlation of basal area with site and age (Kirby et al. 1957).

Basal areas vary widely among stands, even among clones within a stand (Jones and Trujillo 1975a, Wall 1971). Basal areas tended to be greater in Newfoundland and Alaska than in central Canada, and greater in central Canada than in the Lake States (Page 1972). Basal areas in Saskatchewan (Kirby et al. 1957) were substantially less than those of central Utah stands with similar height growth rates (Baker 1925).

Basal areas encountered while sampling hundreds of aspen stands in Utah and Idaho ranged from about 30 to 250 square feet per acre.[3] In Colorado, southern Wyoming, and northeastern Utah, basal areas in sampled pure aspen stands ranged from 10 to 380 square feet per acre.[4] In mixed stands in Arizona, Reynolds (1969) found 299 square feet of aspen in an aspen-ponderosa pine mix that had a total basal area of 460 square feet per acre. In general, before an aspen stand deteriorates in old age, most single-storied aspen stands in the West seem to be near maximum stocking for the particular combination of age, site, and clone.

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[3] *Unpublished data on file at the Intermountain Forest and Range Experiment Station's Forestry Sciences Laboratory, Logan, Utah.*

[4] *Unpublished data collected by H. Todd Mowrer, and Wayne D. Shepperd, on file at the Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo.*

Measuring and Predicting Volume and Growth

Biomass is a useful concept for expressing ecosystem productivity, especially in ecosystem modeling. In the strictest sense, biomass is the total weight of organic matter per unit of space in an ecosystem. Commonly, however, it is used with respect to a single component of the vegetation (Ford-Robertson 1971). Too frequently, because of the difficulty of determining the dry weight of root systems, biomass data do not include roots. When only the aboveground standing crop of trees is considered, without regard to other parts of the biotic community, the concept of biomass is compromised. In such cases, "aboveground dry weight of trees" is the correct term.

Equations have been developed for estimating the ovendry weight of various aboveground components of aspen trees using simple measurements of height and diameter (Bartos and Johnston 1978, Bella 1968, Schlaegel 1975a, Zavitkovski 1971). Some, such as Bartos and Johnston (1978), found diameter alone to be the dominant variable. They developed exponential curves, with R^2 values of 0.997, of above-ground tree "biomass" as a function only of diameter at breast height.

Using Schlaegel's equations, the aboveground dry weight per acre of each diameter class and of entire overstory stands also can be estimated. In addition, Schlaegel (1975a) presented equations for cubic volume and green weight, and tables for each of those variables.

The aboveground dry weight per acre has been estimated for a few stands and sites in the West and elsewhere (table 4). Extremely high values, probably near maximum, of basal area and biomass are illustrated in figure 1.

Volume

The volume of usable wood in a stand, called "net volume," strongly influences what management operations are economically feasible. On a regional basis, it also is important for determining what manufacturing facilities are feasible in the area (see the WOOD UTILIZATION chapter). Therefore, efficient and accurate methods of estimating net volume of standing trees are important.

Usually, net volume estimates are obtained in two steps. First, the gross volume of that portion of the bole large enough for the products of interest is estimated. Second, the gross volume is reduced by a factor, based on observable defects such as crooks, external indications of decay, and local experience. For example, Hinds (1963) produced a guide for estimating cull caused by heartrot of aspen that is based on the number and location of *Phellinus tremulae* conks.

Gross volume estimates usually are based upon measurements of diameter and tree height. Depending upon the system used, height is expressed as total tree height or as the number of log lengths that can be cut from a tree to a specified top diameter, assuming no defects.

Table 4.—The aboveground ovendry weight of aspen in various stands.

Location	Description		Weight (*lb/acre*)	Reference
Northern Utah	Includes leaves and dead wood.			
	Average age 48 years, height 23 feet, 4.6 inches d.b.h.		55,000	Bartos and Johnston (1978)
	47 years, 36 feet, 5.3 inches		83,000	
Western Wyoming	116 years, 42 feet, 8.7 inches		78,000	
Manitoba	13 years old, 25 feet tall, no leaves.		31,800	Bella and Jarvis (1967)
Minnesota	Trees with leaves, down timber, undergrowth.		203,590	Bray and Dudkiewicz (1963)
	Standing overstory trees only.		184,470	
Escudilla Mt., Arizona	Standing live trees including leaves	*Dominant height*		Jones and Trujillo (1975a)
	All stands 22 years old, heavily stocked.	39 feet	113,900	
		35 feet	68,900	
		31 feet	48,400	
Alberta	Stand 55 years old.		259,000	Peterson et al. (1970)
Ontario	Site index 90 at base age 50.	*Stand age*		Pollard (1971)
	Live trees, not including leaves.	4 years	15,300	
		5 years	21,500	
		6 years	28,200	
		7 years	30,500	
Ontario	Site index 75 at base age 50. Stand 50 years old. Apparently live trees only, no leaves.		81,900	Pollard (1972a)

Kemp[5] developed equations in 1958 that are used by the Forest Service to estimate gross volumes of standing aspen in the northern portion of the interior (table 5) West. Table 6 is one of several tables derived from those equations. Equations and tables developed by Hatch[6] have been used for the aspen in northern Utah. Although they have not been published, the tables by Kemp and by Hatch probably are the best currently available for the areas in which they are used for inventory purposes.[7]

Edminster et al. (1982) developed volume tables from a very large and widely distributed sample of aspen in Colorado. A useful one for sawtimber volume estimation is shown as table 7. Hann and Bare (1978a) developed a more versatile system for estimating the volumes of aspen based on data from northern New Mexico. It allows for forked and damaged trees, separately, and accommodates various standards of top utilization as well as different log rules. A companion publication (Hann and Bare 1978b) gives volume tables for unforked trees. However, because of sample size limitations, the equations should be used with caution for larger trees (greater than 10 inches d.b.h.).

Shepperd and Mowrer (1984) developed whole stand volume tables from the equations in Edminster et al. (1982), which predict stand volumes for aspen, given average stand basal area and average stand height. These tables allow quick stand volume estimates to be made from simple cruise data.

Figure 1.—A 0.1-acre plot selected to represent maximum stocking for aspen. Age 162 years, tallest trees 121 feet. Not including understory conifers, the stocking was: basal area 411 square feet per acre; dry weight (without leaves or roots) 700,800 pounds per acre; gross volume (International 1/4 inch rule) 115,500 board feet per acre. Site index was 78 feet at 80 years, which is good but not exceptional in the Southwest. Apache National Forest, Arizona.

Yield Equations and Tables

Yield equations and tables are used to predict the wood producing capacity of forest sites. Empirical yield tables are made with data from plots selected with few criteria of stocking or condition except that the site be considered forested. An empirical table represents approximately average conditions for the area.

Baker (1925) provided an empirical yield table for even-aged stands of aspen in the West (table 8). It shows gross volumes expected at different ages on sites of different qualities. Because aspen trees are relatively small, and because defects such as cull and crook are common, aspen stands that have a net yield of 12,000 board feet per acre (29,650 board feet per ha) are considered good.

Baker collected his data over several years, beginning in 1912. They are from a single area largely in central Utah, with a working radius feasible for the primitive travel common at the time.[8] His values seem too low for similar site classes in Colorado, Arizona, and New Mexico. A more recent study of volume production and decay losses in Colorado, on site classes 1 and 2, showed considerably more volume production (Hinds and Wengert 1977).

Yield tables and equations usually are keyed to site classes or indexes, defined by the heights of dominant trees at a given age. Baker made his site class table using early techniques. The site index curves that result from graphing these tabular values look rather unusual. Therefore, new site index curves and a table were made from stem analysis on widely distributed plots in Colorado and New Mexico (Jones 1966, 1967a). However, new yield data were not taken. Use of Jones's site index curves with Baker's yield tables result in predicted yields that appear too low for Colorado or New Mexico. Edminster et al. (1985) developed new site index curves for aspen in the central Rocky Mountains (fig. 2), which are more compatible with current forest inventory procedures.

Empirical yield equations made with data from unmanaged stands usually are not well suited for characterizing yield capacity of managed stands. The stocking and structure of mature unmanaged stands, especially overmature stands, are too irregular. Judging from tables in Green and Setzer (1974), the rough corrections used to adjust for this are not satisfactory. Because of the impacts of diseases and subsequent mortality in partially cut aspen stands (see the INTERMEDIATE TREATMENTS chapter), artificial density control actually may decrease yields (Walters et al. 1982).

More accurate yield equations and tables need to be developed with better data over the range of variability of aspen in the West. A better measure of net volume in aspen needs to be made for the western States. A new system also is needed to characterize sites and predict

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[5] *Kemp, P. D. 1958. Volume tables for western tree species. (Unpaged.) Intermountain Forest and Range Experiment Station, Ogden, Utah.*

[6] *Hatch, Charles. Volume equations for several species, including aspen, on the Salmon and Ashley National Forests; on file at the Intermountain Forest and Range Experiment Station, Ogden, Utah.*

[7] *Personal communication with David C. Chojnacky, Renewable Resources Evaluation Unit, Intermountain Forest and Range Experiment Station, Ogden, Utah.*

[8] *Correspondence with F.S. Baker, on file at the Rocky Mountain Forest and Range Experiment Station's Forestry Sciences Laboratory, Flagstaff, Ariz.*

Table 5.—Equations for estimating gross cubic feet and board feet of standing aspen boles in the West.[1]

Volume Statistic	Equations[2]
Cubic feet, trees up to 20.9 inches d.b.h.	$V = -0.343 + 0.224 (D^2H/100)$
Cubic feet, trees 21 inches d.b.h. or larger	$V = 1.071 + 0.217 (D^2H/100)$
Board feet, International 1/4-inch rule, trees up to 20.9 inches d.b.h.	$V = -9.547 + 1.309 (D^2H/100)$
Board feet, International 1/4-inch rule, trees 21 inches d.b.h. or larger	$V = -12.441 + 1.325 (D^2H/100)$
Board feet, Scribner rule, trees up to 20.9 inches d.b.h.	$V = -18.544 + 1.197 (D^2H/100)$
Board feet, Scribner rule, trees 21 inches d.b.h. or larger	$V = -21.309 + 1.216 (D^2/H/100)$

[1] *Kemp, P. D. 1958. Volume tables for western tree species. (Unpaged.) Intermountain Forest and Range Experiment Station, Ogden, Utah.*

[2] *V = volume to a variable top diameter*
D = diameter breast high (inches)
H = total tree height (feet).

Table 6.—Board-foot volumes for aspen to a variable top, Scribner rule.[1]

	Total height (*feet*)									
d.b.h.	**40**	**50**	**60**	**70**	**80**	**90**	**100**	**110**	**120**	**130**
(inches)										
11	39	54	68	83	97	112	125			
12	50	68	85	102	119	137	154	171		
13	62	83	103	123	143	164	184	204		
14		99	122	146	169	193	216	240	263	
15		116	143	170	197	224	251	278	305	
16			165	196	227	257	288	319	349	
17			189	224	258	293	327	362	397	431
18			214	253	292	331	369	408	447	486
19				284	327	370	414	457	500	543
20				317	364	412	460	508	556	604
21				354	408	461	515	569	622	676
22				391	450	508	567	626	685	744
23				429	493	558	622	686	751	815
24				469	539	609	679	749	819	889
25				511	587	663	739	815	891	967
26					636	719	801	883	965	1,047
27					687	777	865	954	1,042	1,131
28					741	837	932	1,027	1,122	1,218
29					797	899	1,001	1,104	1,206	1,308
30					854	964	1,073	1,183	1,292	1,401

[1] *Kemp, P. D. 1958. Volume tables for western tree species. (Unpaged.) Intermountain Forest and Range Experiment Station, Ogden, Utah.*

yield on aspen land in the West. The system should accommodate stands managed at different stocking levels, as well as stands receiving no management other than periodic clearcutting and controlled livestock use. A recently completed whole stand model for even-aged aspen stands should provide growth and yield information for a wide variety of stand densities and site index classes.[9]

Counting Aspen Growth Rings

One of the fundamental activities required to collect new or updated inventory information is estimating tree ages, even though aspen rings are notoriously difficult to count. For this reason, different methods are discussed here briefly.

Increment cores usually are used to determine aspen age. However, increment coring can cause discoloration and decay of the tree in the vicinity of the core, especial-

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[9] *Edminster, Carleton B., and H. Todd Mowrer. 1985. Growth and yield relationships for aspen in the central Rocky Mountains. Manuscript in preparation, intended for publication by the Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo.*

Table 7.—Board-foot volume, Scribner rule, to a 6-inch top diameter inside bark, for aspen in Colorado (Edminster et al. 1982).

d.b.h.	Total height (*feet*) above ground 30	40	50	60	70	80	90	100	Basis: trees
(*inches*)									
7	8	8	12	18	24	31			94
8	8	12	21	29	37	45			84
9	10	21	31	41	51	62			107
10	17	30	42	55	67	80	91		96
11	25	40	55	70	84	98	112		82
12	33	51	68	86	102	118	134		92
13		63	83	102	121	140	158	177	78
14		75	97	119	141	163	184	206	56
15		88	113	138	163	188	212	237	50
16		101	130	158	186	214	242	270	37
17			147	179	210	242	274	306	27
18			166	201	237	272	307	343	17
19			185	225	264	303	343	382	14
20			206	250	293	336	380	423	8
21			228	276	323	371	419	467	5
22				303	355	408	460	512	3
23				331	389	446	503	560	2
24				361	423	485	548	610	0
25					460	527	594	661	0
Basis: trees:	1	16	88	253	319	138	31	6	852

Block indicates extent of data.

Computed from: $V = 8$ *for* D^2H *to 2,500;*
$V = 0.011389D^2H - 20.5112$ *for* D^2H *larger than 2,500 to 8,850;*
$V = 0.010344D^2H - 11.2615$ *for* D^2H *larger than 8,850.*

Standard errors of estimate: ± 7.1 board feet (± 16.73% of mean); ± 27.9 board feet (± 19.33% of mean).

Coefficients of determination: 0.9021; 0.8696.

Diameter classes full-inch (e.g., 20-inch class includes 20.0 to 20.9 inches d.b.h.)

Table 8.—Empirical yield table for even-aged aspen stands (Baker 1925).[1]

	SITE 1 Volume per acre			SITE 2 Volume per acre			SITE 3 Volume per acre			SITE 4 Volume per acre		
Age	Basal area (*ft*²)	Total (*ft*³)	Saw-timber[2] (*bd ft*)	Basal area (*ft*²)	Total (*ft*³)	Saw-timber[2] (*bd ft*)	Basal area (*ft*²)	Total (*ft*³)	Saw-timber[2] (*bd ft*)	Basal area (*ft*²)	Total (*ft*³)	Saw-timber[2] (*bd ft*)
30	76	300	--	14	--	--	--	--	--	--	--	--
40	124	1,350	--	78	500	--	--	--	--	--	--	--
50	136	2,250	600	114	1,350	--	72	500	--	--	--	--
60	144	3,000	2,600	124	2,100	600	104	1,300	--	70	400	--
70	148	3,550	4,800	132	2,750	2,000	114	1,950	150	92	1,000	--
80	154	4,050	6,800	140	3,250	3,400	122	2,500	1,000	104	1,600	200
90	161	4,500	9,000	146	3,650	4,800	128	2,950	1,600	110	2,050	300
100	166	4,850	11,000	152	4,000	6,200	134	3,300	2,200	116	2,400	400
110	172	5,100	13,200	158	4,300	7,600	138	3,600	2,800	120	2,700	600
120	177	5,350	15,400	162	4,550	9,000	142	3,850	3,600	124	2,950	800
130	181	5,600	17,400	166	4,750	10,400	146	4,050	4,200	--	--	--
140	184	5,950	19,600	170	4,900	11,800	--	--	--	--	--	--
150	186	6,100	21,600	--	--	--	--	--	--	--	--	--

[1] *Includes only trees more than 4 inches (10 cm) d.b.h. All volumes are gross, without deductions for cull or form.*
[2] *Includes all trees 10 inches (25 cm) d.b.h. and larger. Merchantable length taken to a 9-inch top diameter.*

ly if the wound does not heal (LaFlamme 1979). Cross sections are better but usually are not practical to obtain.

Lynn (1964) heated cores in aluminum foil holders until the cores turned brown. Brace (1966) and Maini and Coupland (1964) reported that soaking cores in water made the rings more visible. Svoboda and Gullion (1972) used an inexpensive but satisfactory technique to underlight cores, using transmitted light rather than reflected light to count the rings. Rose (1957) soaked cores in light-weight penetrating oil for 1 week; the oil-impregnated cores became translucent, and the rings were easily counted using transmitted light. He found that a vacuum decreased the time required for oil impregnation to minutes. Jones (1967b) experimented with several wetting agents including benzidine, kerosene, light machine oil, water, and saliva.

A properly shaved surface will accentuate the rings. Trujillo (1975) found a vise attached to the tailgate of a pickup truck was a convenient accessory for shaving cores in the field. A sharp utility knife gave good results. Then the cores were oven-dried for 48 hours at 212°F (100°C). A cloth moistened with a 4% solution of pentachlorophenol in kerosene or mineral spirits was wiped lightly on the shaved side of the oven-dried cores, which were then redried at 212°F (100°C) for 4 hours. Counting was done with a binocular microscope using top lighting. After 1 year of storage, the rings still could be easily counted.

Campbell (1981) suggested three main sources of error for age determination of aspen cores: (1) narrow rings, (2) pith and central rings not present in the core, and (3) estimating the tree's age at core height. Generally, the margin of error for each of the three sources can be reduced substantially by boring the tree close to the ground on the uphill or concave side of any butt sweep. The resulting core will contain the tree's widest rings, will usually contain the pith or lack only a few central rings, and will have fewer years to estimate for the age at core height. Cores are stored in plastic drinking straws.

For laboratory analysis, Campbell (1981) recommended first soaking an aspen core in a wetting solution of water, methanol, and detergent. Next, clamp the core in a vise and shave it transversely across the vessel elements with a razor blade. Then illuminate the translucent core with fluorescent lighting from above and below and use a dissecting scope to count the rings. The tree's total age equals the sum of the rings actually counted, the years estimated to reach core height, and if the pith is absent, the estimated number of missing rings to the center.

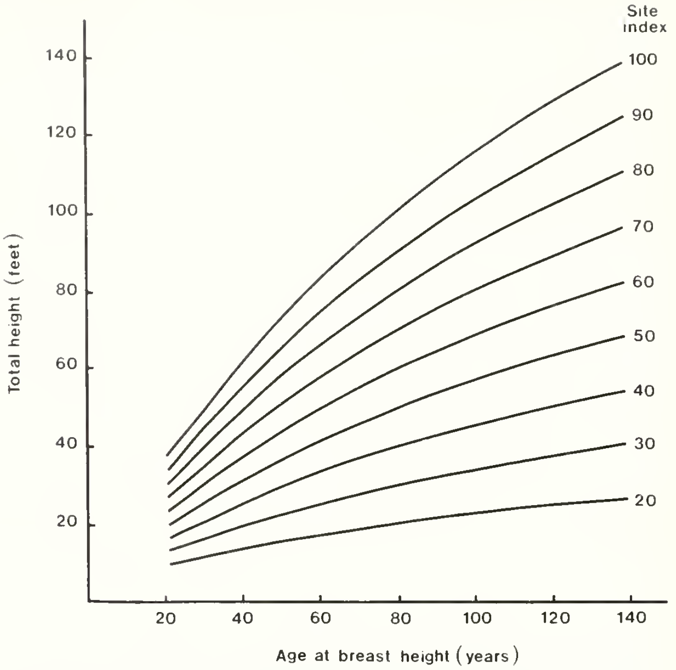

Figure 2.—Site index curves for aspen in the central Rocky Mountains. Base age 80 years after reaching breast height (Edminster et al. 1985).

If stem cross sections are available, they may be split through the pith, and one or more radii beveled with a sharp utility knife to facilitate ring counts. Normally, it is impossible to determine the age of decayed sections by ordinary methods, even when they are carefully prepared (Kirby 1953). Some will fall apart if they are oven-dried. Ghent (1954) described a way of impregnating decayed cross sections with paraffin wax before counting.

The only false rings Jones has observed probably resulted from outbreaks of the western tent caterpillar or other defoliating insects.[10] Maini and Coupland (1964) found false rings in aspen in the Canadian prairie-forest transition; false rings might be anticipated in similar fringe habitats of the interior western United States.

[10] *Personal observations by John R. Jones, Rocky Mountain Forest and Range Experiment Station, Forestry Sciences Laboratory, Flagstaff, Ariz.*

WOOD UTILIZATION

Eugene M. Wengert, Dennis M. Donnelly, Donald C. Markstrom, and Harold E. Worth

In the past, markets for quaking aspen timber from the Rocky Mountains have been insufficient to support significant harvesting. This shortage of markets severely restrained the potential for aspen management. As a result, many stands protected from wildfire gradually reverted to conifers (see the VEGETATIVE REGENERATION and FIRE chapters).

Significant markets for aspen products have not developed in the West because of a plentiful supply of coniferous woods and, to some extent, because the technical factors related to utilization of quaking aspen have not been well understood. Unfavorable economic factors, such as harvesting costs that are high relative to product values, also have inhibited aspen use. Resource managers and wood processors in the West have found it difficult to identify and evaluate viable utilization opportunities. A major barrier to utilization has been not knowing the volume and location of aspen available on a sustained yield basis.

To provide some of the needed information, this chapter examines aspen tree and wood characteristics, and products that can be made from quaking aspen. It also discusses the utilization outlook, and presents technical and economic requirements for beginning or changing to a wood products business featuring products made of aspen wood. The WOOD RESOURCE chapter presents supply and yield information for aspen in the West.

UTILIZATION CHARACTERISTICS

Each tree species has genetic and growth peculiarities that make it unique for utilization purposes. Some utilization characteristics of quaking aspen (*Populus tremuloides* Michx.) are very similar to other species, particularly to other *Populus* species. The technological and economic tasks of utilization are to mesh species characteristics as closely as possible with the properties desired in the end products.

The Tree

In the West, a typical aspen sawtimber tree, at maturity, is 80–100 years old, 60–80 feet (18–24 m) tall, and 11 inches (28 cm) d.b.h. or larger (Baker 1925). A few are older than over 200 years, taller than 100 feet (30 m), or larger than 20 inches (52 cm) d.b.h. One tree in Utah was reported to be 120 feet (36.6 m) tall and 4 feet (1.2 m) in diameter (Jones and Markstrom 1973).

The fungus *Phellinus tremulae* (= *Fomes igniarius*) frequently attacks the center of mature trees; fungal conks on the tree bole are its surficial evidence (Davidson et al. 1959) (see the DISEASES chapter). Defect deductions are typically up to 20% of the gross scale (Scribner Decimal C log rule) (Hinds and Wengert 1977). Aspen stems are often crooked or sweepy and may have numerous branches at mid-length. (See the MORPHOLOGY chapter for a discussion of general characteristics of aspen tree form.)

Published information on the characteristics of aspen trees and logs in the West is extremely scarce. Wengert sampled 282 logs—approximately every third tree-length log on 14 truckloads harvested from a southwestern Colorado timber sale.[1] These trees were considered to be fairly typical of sawtimber from pure aspen stands in the area. However, no statistically valid general inferences can be made from these data for the aspen resource in the Rocky Mountains. Measurements included log diameters at both ends (inside and outside the bark), log lengths, and gross and net scale (Scribner Decimal C log rule). Log taper averaged 0.114 inch per foot of length (0.97 cm/m). Scalable defect amounted to about 25% of the gross log scale, approximately one-half of which was attributable to crook and sweep. Bark volume averaged about 17% of the gross log volume, as contrasted with 12% reported for Minnesota aspen (Marden et al. 1975).

Relationships between gross merchantable volume of the tree, diameter at breast height, and its height were determined for aspen in Colorado (Edminster et al. 1982). These relationships can be expressed by the following equations—[1] for board feet and [2] for cubic feet:

$$\begin{aligned} V &= 8 \text{ for } D^2H \text{ to } 2{,}500; \\ V &= 0.011389D^2H - 20.5112 \text{ for } D^2H \text{ larger than } 2{,}500 \text{ to } 8{,}850; \\ V &= 0.010344D^2H - 11.2615 \text{ for } D^2H \text{ larger than } 8{,}850. \end{aligned} \qquad [1]$$

where:

V = gross volume, in board feet, inside bark Scribner Rule, merchantable stem excluding stump and top. Top diameter is 6 inches inside bark, and stump height is 1 foot.

D = d.b.h. outside bark, in inches.

H = total height, in feet.

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[1] *Personal observations and field data collected by Eugene M. Wengert, formerly Research Wood Technologist at the USDA Forest Service, Forest Products Laboratory, Madison, Wisc., on assignment to the Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo.*

$V = 0.002195D^2H - 0.9076$ for D^2H to 11,800;

$V = 0.001837D^2H + 3.3075$ for D^2H larger than 11,800. [2]

where:

V = gross volume, in cubic feet, inside bark merchantable stem excluding stump and top. Top diameter is 4 inches inside bark, and stump height is 1 foot.

D = d.b.h. outside bark, in inches.

H = total height, in feet.

The Log

The size and geometry of trees and logs strongly influence utilization and the efficiency of converting timber into products. Product yield often can be greatly improved by selectively cutting tree-length logs into two or more short logs. This is particularly important for quaking aspen because of the high incidence of crook, sweep, and rot in typical mature trees. By judicious logmaking, straighter and less defective logs can be obtained from aspen boles that are crooked or contain rot. Generally, the shortest possible aspen logs produce the best yields of aspen lumber. Nominal 8-foot logs are the most common length used in Rocky Mountain sawmills. Also, this length is usually appropriate for pulpwood or veneering operations.

The Wood

The wood of quaking aspen in the West is classified as a "soft hardwood." It is virtually identical to the wood of quaking aspen and bigtooth aspen (*Populus grandidentata* Michx.) in the eastern U.S. and Canada. However, it differs substantially from the wood of most eastern hardwoods and from the woods of conifers, with which aspen is associated and processed in the West.

Anatomical Structure

The sapwood is whitish to creamy colored and generally merges into similarly colored heartwood without clear demarcation. Surfaces have a pronounced silky luster. The wood has a characteristic odor and taste only when green (Panshin and Zeeuw 1980). In addition, a condition called "wetwood," probably bacteria-caused (Ward 1976), often is present in aspen, and may be the source of the odor associated with green wood. Discolorations around knots and in the center of the tree are associated with wetwood or early stages of decay.

The darker color of the summerwood makes the growth rings in aspen distinguishable, but not conspicuous. The wood has numerous small pores (vessels) that are visible only with a hand lens on a cleanly cut cross-section. The pores are largest in the springwood and decrease gradually in size through the summerwood. The rays are so fine that they are scarcely visible, even with a hand lens. These anatomical characteristics of quaking aspen are indistinguishable from those of bigtooth aspen, and are similar to those of other *Populus* species, such as cottonwood. However, cottonwood is coarser in texture, somewhat darker in color (never creamy), and without luster.

The basic anatomical properties of aspen are unusual enough to make it a good choice for certain uses. For example, because properly dried aspen wood is practically without odor or splinters, food service manufacturers often supply containers and utensils made of aspen to avoid transmittal of odor from the wood.

Moisture Content and Shrinkage

The moisture content of wood in standing aspen trees varies considerably, depending upon the season and upon the presence of bacterial wetwood. No extensive study has been made of seasonal moisture content variation in aspen in the West. However, in the Lake States, Marden et al. (1975) found that the moisture content (as a percentage of ovendry weight) of 239 loads of freshly cut aspen pulpwood varied from 80% in summer to 111% in winter. In the Black Hills, Yerkes (1967) measured the seasonal change in 10 live aspen trees from an autumn low of 82% to a winter (February) high of 102%, which compares closely with the Lake States findings. The wetwood moisture content can be as high as 160% (Bois 1974, Knutson 1968). In summer, an average heartwood moisture content of 74% and sapwood moisture content of 91% were measured in the southwestern Colorado log sample described previously.[1] Bark moisture content is lower and less variable than that of wood (Marden et al. 1975).

Shrinkage characteristics are important for most wood products. Aspen has a fairly low green-to-ovendry shrinkage—3.5% radial, 6.7% tangential, and 11.5% volumetric (USDA Forest Service 1974b). The large tangential-to-radial ratio indicates that aspen will be subject to cupping and diamonding during the drying process, or during use if the moisture content changes significantly. Longitudinal shrinkage, which can be ignored for most species, is more significant for aspen. This unusually high longitudinal shrinkage results in lumber that has a tendency to bow, twist, and crook in drying and use, and veneer that may buckle if it is not properly dried.

Specific Gravity and Weight

Specific gravity is related to several wood properties and is frequently used as a relative measure of these properties within or between species. Specific gravity is an index of weight and density. It is based upon green volume and oven-dry weight.

The limited specific gravity measurements made for aspen in the West compare closely with data from Lake States and Canadian aspen. From the limited data available, it has been estimated that the specific gravity of quaking aspen in the West averages about 0.38, with a variation of about ± 0.08.[1] This specific gravity value is similar to the 0.367 value for Upper Michigan aspen (Erickson 1972) and to the 0.37 value for several sources of Canadian aspen (Kennedy 1965), but is slightly higher than the 0.35 value reported by the USDA Forest Service (1974b).

Specific gravity of bacterial wetwood is 0.03 to 0.04 lower than that of normal wood (Haygreen and Wong 1966, Kennedy 1974). The impacts of this difference on utilization have not been determined; but, factors such as pulp yield and wood strength, where the density of wood fibers is important, may be affected.

The specific gravity of aspen bark is higher than that of wood. Based on limited unpublished data for aspen in the West, bark specific gravity appears to average about 0.45, with a range of 0.38 to 0.57.[1] This compares with a range of 0.37 to 0.52 for Minnesota aspen bark (Lamb and Marden 1968), and 0.446 to 0.602 for aspen bark in Michigan (Erickson 1972).

Table 1 summarizes several weight, volume, and moisture characteristics of aspen in the West.[1]

Mechanical Properties

Aspen lumber sometimes is used for structural purposes, including aspen studs for light frame construction (Thompson 1972). Aspen 2x4's, produced in limited quantities in the Lake States, have been marketed under the grading rules of the Northern Hardwood and Pine Manufacturers Association. Design values for aspen used in light framing, as published by the National Forest Products Association, are listed in table 2. Aspen

Table 1.—Properties of wood and bark of quaking aspen in the West.[1]

	English	S.I. units
Specific gravity		
(Based on volume green; weight O.D.)[2]		
Wood	0.38	
Bark	0.45	
Density		
(Based on volume green)		
Wood (O.D.)[2]	24 lb/ft^3	0.38 g/cm^3
Bark (O.D.)[2]	28 lb/ft^3	0.45 g/cm^3
Wood at 12% water content	27 lb/ft^3	0.43 g/cm^3
Green sapwood	45 lb/ft^3	0.73 g/cm^3
Green heartwood[3]	41 lb/ft^3	0.66 g/cm^3
Green bark	55 lb/ft^3	0.88 g/cm^3
Moisture content (summer harvest)		
(Based on weight O.D.)[2]:		
Sapwood	91%	
Heartwood	74%	
Bark	96%	
Cord volume and weight		
Green wood per rough cord[4]	79 ft^3	2.2 m^3
Green wood per peeled cord[5]	94 ft^3	2.7 m^3
Green wood and bark per rough cord[4]	4,400 lbs	2,000 kg
Green wood and bark per rough cord assuming 33% bark loss in skidding[4]	4,100 lbs	1,900 kg
Lumber weight per MBF at 12% water content		
Thickness of 25/32 inch (1.98 cm)	1,800 lbs	800 kg
Bolt volume and weight[6]		
Green wood per bolt	4.9 ft^3	0.14 m^3
Green bark per bolt	0.79 ft^3	0.022 m^3
Wood (ovendry)[2] per bolt	117 lb	53 kg
Bark (ovendry)[2] per bolt	22 lb	10 kg
Green bark weight per bolt	44 lb	20 kg

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[1] *Information based on personal observations and field data collected by Eugene M. Wengert, formerly Research Wood Technologist at the Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo.*

[2] *O.D. = Ovendry; no further weight loss at 215°F (102°C).*

[3] *Wetwood may increase this value by 10% or more.*

[4] *Based on 16 rough bolts per cord.*

[5] *Based on 19 peeled bolts per cord.*

[6] *Based on bolt 100 inches (2.5 m) long and 10 inches (25 cm) diameter inside the bark at small end.*

Table 2.—Design values[1] (in pounds per square inch) for aspen lumber graded under Western Wood Products Association rules.[2]

Commercial grade	Size classification	Extreme fiber in bending "F_b"		Tension parallel to grain "F_t"	Horizontal shear "F_v"	Compression		Modulus of elasticity "E"
		Single-member uses	Repetitive member uses			Perpendicular to grain "$F_{c\perp}$"	Parallel to grain "F_c"	
Select structural		1,300	1,500	775	60	265	850	1,100,000
No. 1	2-4 inches	1,100	1,300	650	60	265	675	1,100,000
No. 2	thick	925	1,050	525	60	265	550	1,000,000
No. 3	2-4 inches	500	575	300	60	265	325	900,000
Appearance	wide	1,100	1,300	650	60	265	825	1,100,000
Stud		500	575	300	60	265	325	900,000
Construction	2-4 inches	650	750	400	60	265	625	900,000
Standard	thick	375	425	225	60	265	500	900,000
Utility	4 inches wide	175	200	100	60	265	325	900,000
Select structural		1,150	1,300	750	60	265	750	1,100,000
No. 1	2-4 inches	950	1,100	650	60	265	675	1,100,000
No. 2	thick	775	900	425	60	265	575	1,000,000
No. 3	5 inches	450	525	250	60	265	375	900,000
Appearance	and wider	950	1,100	650	60	265	825	1,100,000
Stud		450	525	250	60	265	375	900,000

[1] *These design values apply to lumber when used at a maximum moisture content of 19%.*

[2] *Source: Table 4A, Design Values for Wood Construction, Supplement to the 1982 Edition, National Design Specification for Wood Construction, National Forest Products Association, 1619 Massachusetts Ave. N.W., Washington, D.C., March 1982. 32 p. See Table 4A footnotes when using design values.*

[3] *Tabulated tension parallel to grain values for all species 5 inches and wider, 2-4 inches thick (and 2½-4 inches thick) size classifications apply to 5-inch and 6-inch widths only, for grades of Select Structural, No. 1, No. 2, No. 3, Appearance, and Stud (including dense grades). For lumber wider than 6 inches in these grades, the tabulated "F_t" values shall be multiplied by the following factors:*

Grade (2-4 inches thick, ≥5 inches wide) (2-4.5 inches thick, ≥5 inches wide) (Includes "Dense" grades)	Multiply tabulated "F_t" values by		
	5-6 inches wide	8 inches wide	≥10 inches wide
Select Structural	1.00	0.90	0.80
No. 1, No. 2, No. 3, and Appearance	1.00	0.80	0.60
Stud	1.00	--	--

also has been used in the Rocky Mountains for mine timbers, where bending and resiliency are important considerations. In addition, there are many other uses and potential uses of aspen wood where mechanical properties are important, such as pallets or matchsticks.

Although there is little specific knowledge of the mechanical properties of aspen in the Rocky Mountains, it appears to be very similar to the wood of aspen from Lake States and Canadian sources. Therefore, some of the more important mechanical property values reported by various investigators for Lake States and Canadian aspen are summarized in table 3.

Aspen is roughly comparable to hardwoods such as basswood (*Tilia* spp.) and butternut (*Juglans cinerea* L.), ranking it at the low end of North American hardwoods in terms of strength. In relation to the softwoods, its mechanical properties are in the same general range as eastern white pine (*Pinus strobus* L.) and ponderosa pine (*Pinus ponderosa*), although there are major differences in some properties. Somewhat ironically, it is the modest level of aspen's mechanical properties that give it unique advantages in terms of utilization. It is strong enough to serve many functions adequately, and yet, is light in weight, which is sometimes an overriding consideration. Strength adequate for many purposes is combined with straight grain and freedom from splintering. Its soft texture permits the wood to be worked easily and provides an excellent surface for printing or painting. These properties make aspen especially attractive for crating and packaging lumber, matchsticks, and excelsior.

Fastener Withdrawal Resistance

The resistance of metal fasteners to withdrawal is strongly related to the density of the wood. Low density woods, such as aspen, do not perform as well as denser woods in applications where tight fasteners are important. Further, if nails are driven into green wood, they will lose withdrawal resistance as the wood dries. For example, a seven-penny cement-coated nail driven into the side grain of dry aspen should have a withdrawal resistance of about 194 pounds (88 kg). The same nail driven into green aspen that subsequently dries would retain a withdrawal resistance of only 20 pounds (9 kg) (Johnson 1947). Because the nail withdrawal resistance of aspen is comparatively low, more nails, larger diameter nails with large heads, or special withdrawal-resistant nails are required. However, aspen has little tendency to split when nailed, which partially compensates for its otherwise low nailholding properties.

Processing and Fabrication Characteristics

Machining.—Machining is a broad term that includes sawing, planing, shaping, sanding, and boring. Aspen can be machined easily; power consumption is low and tools dull slowly. However, it is difficult to obtain a clean and smooth surface on aspen unless special care is taken. Aspen's fibers sever less cleanly than most other woods; the tension wood common in aspen tends to leave a fine fuzz on machined surfaces. Also, from a limited number of planing observations, it appears that aspen wetwood seems to fuzz even more than non-wetwood.

Excellent turnings, borings, and planed or sanded surfaces can be obtained if the following conditions are maintained (Davis 1947, 1962; Stewart 1973a, 1973b):

1. Wood moisture content of 6% or less.
2. Knife angle of 25° to 30°.
3. A slow feed rate or lathe speed, maintaining at least 22 cuts per inch (8.7 cuts/cm) while planing.
4. A high cutter head speed, a peripheral speed above 5,000 feet per minute (25 m/s).
5. A shallow final cutting depth of approximately 1/32-inch (0.08 cm).
6. A slow axial feed speed when boring.
7. Avoid sanding with a very fine grit, because it increases fuzz.
8. Use special abrasives, antifuzz sealer, or a wash coat of sizing before final sanding. Fresh, sharp abrasives are required for preparation of good surfaces.

Table 3.—Specific gravity and mechanical properties of quaking aspen (*Populus tremuloides*).

	Kennedy (1965)	USDA Forest Service (1974b)	Kennedy (1965)	USDA Forest Service (1974b)	Haygreen and Wong (1966)	
					Wetwood	Sapwood
Specific gravity (SG)	[1]0.37	[1]0.35	[2]0.41	[2]0.38	[3]0.357	[3]0.393
Moisture content at test (%)	green	green	12	12	green	green
Static bending properties						
Stress at proportional[1] limit (psi)	2,900	--	5,200	--	2,666	3,406
Modulus of rupture (psi)	5,500	5,100	9,800	8,400	4,973	6,059
Modulus of elasticity (psi)	1,310,000	860,000	1,630,000	1,180,000	612,000	1,101,000
Work (inch lb/inch^3)						
To proportional limit	0.37	--	0.99	--	--	--
To maximum load	6.9	6.4	10.3	7.6	--	--
Total	20.2	--	21.0	--	--	--
Compression parallel to grain						
Stress at porportional limit	1,510	--	3,280	--	1,428	1,996
Maximum crushing stress	2,350	2,140	5,270	4,250	1,878	2,348
Modulus of elasticity (psi)	1,250,000	--	1,840,000	--	525,000	1,288,000
Compression perpendicular to grain						
Stress at proportional limit (psi)	200	180	510	370	--	--
Hardness (lbs)						
Side	320	300	480	350	--	--
End	340	--	630	--	--	--
Shear parallel to grain						
Maximum stress (psi)	720	660	980	850	--	--
Cleavage (lb/inch)	180	--	260	--	--	--
Tension perpendicular to grain						
Maximum stress (psi)	440	230	610	260	--	--

[1] *Based on ovendry weight and green volume.*
[2] *Based on ovendry weight and volume at 12% moisture content.*
[3] *Basis not specified; presumably ovendry weight and green volume.*

Drying.—Drying properties of wood are an important consideration in most forms of utilization. Aspen sapwood can be dried easily; but heartwood and wetwood are difficult to dry (Ward 1976). Sapwood usually is dried very rapidly. Kiln temperatures as high as 240°F (115°C), with a drying time of 36 hours, have been used successfully for 1-inch lumber. Because aspen has a high tangential-to-radial shrinkage ratio and an abundance of tension wood, both of which promote warping, proper stacking practices in air or kiln drying are needed to minimize the amount of warp (fig. 1) (Rasmussen 1961).

To reduce the effects of tension wood and casehardening, aspen should be conditioned at the end of drying with 180°F (82°C) dry-bulb temperature and a wet-bulb temperature determined from the wet-bulb depressions shown below. These are similar to those in Rasmussen (1961). Conditioning time for relief of stresses in 1-inch stock, although subject to wide variation, should be 6 to 12 hours.

Desired final moisture content	**Wet-bulb depression**	
(%)	°F	°C
5	14.0	7.8
6	12.0	6.7
7	10.0	5.6
8	8.0	4.4
9	7.0	3.9
10	5.5	3.1
11	4.5	2.5

Collapse is commonly associated with aspen wetwood, even sometimes during air-drying (Clausen and Kaufert 1952, Clausen et al. 1949). Ward (1976) found the kiln drying characteristics of aspen from Rocky Mountain and Wisconsin sources to be similar. Aspen wetwood from both sources invariably developed collapse, honeycomb, and/or ring failure during drying. Wetwood appears to occur mainly in established heartwood aspen in the Rocky Mountains, but also invades the innermost sapwood of Wisconsin trees (Ward 1976). Ward (1976) attributed the slower drying rate of wetwood to its higher moisture content and to the occlusion of vessels by bacterial slime. Normal aspen heartwood dries more slowly than normal sapwood because of tyloses in the vessels. Using a conventional kiln-drying schedule for 1 3/4-inch thick lumber, Ward (1976) found it took 90 hours to dry sapwood, 115 hours to dry heartwood, and 179 hours to dry wetwood.

Figure 1.—Drying of dimension lumber.

Slow drying of wetwood and heartwood is most noticeable in 2-inch and thicker stock. It is much less of a problem for 1-inch stock. Extending the air-drying period reduces kiln time and cost. Intermediate steaming during kiln-drying at high temperatures has been reported to be a suitable means of drying aspen studs (Mackay 1974). Rapid initial drying, followed by a long equalization period, is suitable when energy costs and kiln residence time are not critical. Where possible, aspen with wetwood should be segregated for special drying treatment.

The saw-dry-rip curing process developed by the USDA Forest Service has been used experimentally to dry aspen for studs with promising results (Maeglin 1979). In this process, logs are first sawed into 1 3/4-inch thick flitches; the flitches are kiln dried to 10% moisture content; then they are sawed and planed to produce 1 1/2-inch by 3 1/2-inch studs. This procedure eliminated much of the warping usually associated with aspen studs.

Preservative treatment.—Kaufert (1948) described decay resistance and preservative treatment of aspen. Aspen is very low in natural decay resistance. Untreated aspen posts or lumber in contact with soil may last only 2 years. Because of the low permeability of aspen wetwood and heartwood, it is somewhat difficult to get aspen to accept a uniform preservative treatment (Cooper 1976). Usually, small diameter logs consisting entirely of sapwood treat best.

Gluability.—Laboratory tests and experience have shown that aspen is generally easy to glue. However, because the wood is quite absorptive, rapid assembly may be required to avoid glue-starved joints. Additional water may be required to obtain suitable joints with some water-based adhesives.

Finishing.—Aspen is one of the best hardwoods for holding paint (USDA Forest Service 1974b, Zasada 1947). As with most woods, knots must be carefully primed. Aspen absorbs stains readily; but, uneven absorption can cause a blotchy appearance. A wash coat or application of a sealer before staining will alleviate this problem. As mentioned earlier, aspen also accepts inks very well for direct printing on the wood.

Pulping and fiberizing.—Quaking aspen has been extensively used for wood pulp in the Lake States and Canada (Auchter 1976, Keays et al. 1974). Almost 85% of the pulp mills in the Lake States use some aspen—a region where aspen makes up nearly 50% of total pulpwood production. Aspen is easily pulped using any of the following processes: groundwood, chemimechanical, semichemical, sulfite, and kraft. Aspen yields more pulp than softwood species or other hardwoods in all but the sulfite and kraft processes (Auchter 1976). In those processes, aspen's yield is only slightly less than spruce (*Picea* spp.) and hemlock (*Tsuga* spp.). The fiber characteristics of aspen make it particularly desirable for several types of pulp.

ASPEN PRODUCTS

The characteristics of aspen timber and wood make it quite suitable for some products. As noted previously, because of aspen's unique physical properties, it is a first choice for a few products. For other products, aspen's basic properties are technically acceptable; but, its choice over other woods would depend on availability and economics (see the Utilization Feasibility section in this chapter).

Pulp and Paper

Some of the advantages of aspen as a raw material for paper pulp were discussed previously. For example, groundwood paper of the highest printing quality is produced from aspen. In chemimechanical pulps, used mostly for hardboards and fiberboards, the low wood density of aspen is particularly advantageous in producing low and medium density boards. While aspen is suitable for the semichemical pulps used for both coarse and fine papers, the higher density hardwoods have a cost advantage. Aspen fibers provide special quality characteristics in kraft and sulfite pulps that make them suitable for fine papers. Because of aspen's low density, which makes it less attractive economically for chemical pulping, its future may be limited to groundwood and chemimechanical pulps (Auchter 1976). Blending aspen with a softwood to achieve desired characteristics in kraft pulps is a promising alternative (Hatton 1974).

Other important manufacturing factors are processing water, environmental concerns, technology that favors aspen use, and economic factors associated with harvesting the timber, such as topography, length of harvest season, and roads.

Other Fiber Products

Other fiber products that are technically feasible are panel products and animal feeds and bedding.

Among the panel products, hardboard (including medium density hardboard for house siding) and insulation board are the major consumers of wood fiber. Aspen fiber is well suited for these uses, although a high proportion of wetwood fiber may cause technical problems (Gertjejansen 1969). Markets are growing for a newer product—medium density fiberboard—which is used principally in the manufacture of furniture and cabinets. Aspen's properties make it a preferred raw material for this product, which requires a fine texture throughout to permit shaping and finishing panel edges without costly banding or filling.

The use of both the wood and bark of aspen for animal feeds has received considerable attention in recent years. Successful commercial use has been claimed by some cattle feeders. Aspen wood is about 35% digestible by ruminants and aspen bark, if properly supplemented, appears to be equivalent in nutrition to medium quality hay (Baker 1976) (see the FORAGE chapter). The digestibility of both wood and bark can be improved by physical and chemical treatments. In one feeding trial it was observed that pure aspen bark in pellets was not palatable to cattle.[2] Another study indicated that aspen bark was readily accepted in rations fed to sheep (Fritschel et al. 1976).

Particleboard

Products classified as particleboard have a wide range of properties. Two general types of particleboard are used in nonstructural applications. One type is used for under-flooring and other miscellaneous uses. The other is specifically designed for furniture and cabinet panels; it is usually employed as a solid core in plywoods, but sometimes as a base for grain-printing or opaque finishes.

Particleboards used for under-flooring are cheapest and least demanding of raw materials. Commonly, this inexpensive board is three-layered, with relatively fine particles on the surface and coarser particles in the center. Aspen can be mixed with softwoods and other hardwoods in particleboard (Gertjejansen et al. 1973, Stayton et al. 1971). Including aspen and other low density woods in the particleboard mix results in good bonding of particles at low pressures in the press (Geimer 1976). Therefore, low density (light) boards can be produced that are both strong and durable. Such boards are preferred in most nonstructural applications.

The same principles apply, but with more stringent requirements, for the type of particleboard used in furniture and cabinets. Smoothness, dimensional stability, machinability, and screw holding capability are more critical. Aspen particleboards of sufficient density can be produced to satisfy these requirements.

Aspen is an excellent raw material for both types of particleboard. It has been widely used in the Lake States and Canada for these products, either alone or in mixtures. Residues from sawmills and planing mills have been the preferred and most used raw materials for particleboard.

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[2] Fullinwider, J. A. 1976. Colorado steers and aspen bark. U.S. Department of Agriculture, Forest Service, Rocky Mountain Region, State and Private Forestry. 20 p. [Processed report]

Structural Flakeboard

The newest panel product to achieve international significance is structural flakeboard (Koch and Springate 1983). It is a specialized form of particleboard sometimes called "waferboard" or "oriented strand board." Structural flakeboard can substitute for sheathing-type plywood used in frame construction (fig. 2). Flakeboard differs from conventional particleboard in that the wood elements are thin, parallel-cut flakes of uniform thickness and size, bonded in an alignment analogous to the veneers in plywood.

The particles in waferboard are approximately as wide as they are long, and are bonded parallel to the plane of the panel. The grain direction of individual wafers is random. In oriented strand board, the flakes are longer than they are wide, and alternate layers are perpendicular to each other in a cross-plied arrangement. This is in contrast to the random orientation of the smaller particles in conventional particleboard. With careful alignment of flakes, the strength and dimensional stability of flakeboard is significantly better than particleboard.

Aspen is an excellent raw material for structural flakeboard. While other species have been used, approximately 95% of the structural flakeboard recently produced in Canada and the United States has been made from aspen. Aspen's unique combination of properties including low density, freedom from resinous extractives, and straight grain, make it nearly ideal for this use.

Figure 2.—Structural flakeboard manufactured from aspen.

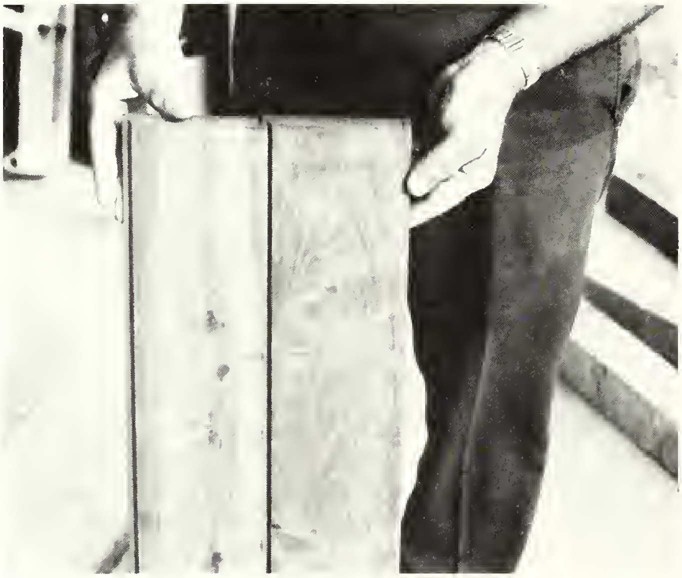

Figure 3.—Stained decorative interior paneling manufactured from dimension lumber.

Sawn Products

Boards, dimension lumber, and timbers all have been produced from aspen in the West. This lumber has been used for a variety of secondary products, ranging from pallets and shipping containers to decorative interior paneling. In the Rocky Mountains, most aspen logs have been processed by sawmills that produce mostly softwood lumber (fig. 3).

In the West, aspen trees that appear to meet sawtimber requirements when standing often prove to be culls when felled. They often have large amounts of heart rot. Lumber grade yield and value of aspen logs processed in New Mexico and Utah were highly variable and could not be accurately predicted by conventional tree or log grading methods (Wengert and Donnelly 1980). Noreen and Hughes (1968) reported recovery of lumber and other products from aspen in Minnesota.

Lumbermaking residues include not only sawdust, planer shavings, slabs, edgings, and trim, but also defective logs or parts of logs, and lumber that does not meet size or grade requirements. Bowyer's (1974) analysis of several forms of integration of aspen production in Minnesota provides a methodology that may be useful to prospective producers in the West.

The small volume of aspen sawed in the interior West has been used in numerous ways. End uses include pallets, paneling, boxes and crates, mine posts, toys, furniture, and construction framing.

UTILIZATION OUTLOOK

Harvesting Opportunities

Pure even-aged stands of mature aspen trees, on flat benches or gentle slopes are the most favorable for harvesting (fig. 4). In these stands, clearcutting is both the best and least costly silvicultural treatment.

Harvesting potential decreases as aspen becomes more intermixed with conifers or grows on steeper slopes. In these instances, aspen harvesting is expensive and may severely damage residual conifers. Many situations exist between these extremes. Uneven-aged stands may have a higher incidence of rot, with consequent lower product yields (Betters and Woods 1981).

Many aspen stands have low volumes of harvestable timber per acre. The high unit cost of harvesting such stands often has prevented their utilization for low-priced products. Combining aspen and contiguous softwood harvesting has been used to reduce costs. Developing efficient harvesting systems, specifically suited to aspen, may be another approach (see the HARVESTING chapter). Size, age, and disease are primary factors in the utilization of aspen. As is true of all timber, it is more economical to process larger trees. Approximately two-thirds of the aspen sawtimber in the Rocky Mountains is 11–15 inches (28–38 cm) in diameter, and 99% is smaller than 23 inches (59 cm). However, when aspen trees reach a diameter of 12 inches (30 cm) or more (typically in 80–100 years), heart rot becomes increasingly prevalent, reducing the net volume of wood in the stand (Davidson et al. 1959, Hinds and Wengert 1977). A sound 20-inch (51 cm) diameter aspen tree is a rarity. Not only does decay cause an appreciable loss of wood, but it also increases harvesting and processing costs per unit of product. To avoid this problem, aspen either must be harvested at a size and age before decay becomes extensive, or utilized for products that are tolerant of unsound wood. One study of logs from a limited area found aspen utilization also was limited by its high yields of low lumber grades, caused primarily by knots and log crookedness (Wengert and Donnelly 1980).

Figure 4.—Aspen logs being skidded with a crawler tractor.

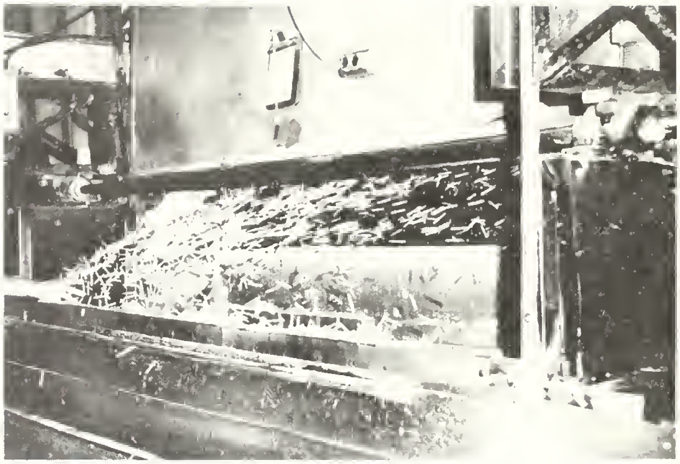

Figure 5.—Manufacture of matchsticks from aspen in the West.

Utilization History

Aspen has a long history of utilization in the West. Baker (1925) reported local use of aspen in Utah for mine props, posts, poles, bridge planking, flooring, and fuelwood. He also reported that early Mormon pioneers made furniture from aspen. Lumber traditionally has been the most common product, usually produced by sawmills that also produce softwood lumber. Other products made from aspen include excelsior, match splints (fig. 5), wall paneling, mine timbers, furniture, roof and siding shakes, pallets, paper pulp, toys, shipping containers, animal (mink) bedding, and beehives.

Site and stand characteristics, and multiple use management decisions have restricted utilization of aspen in the interior West to less than 10 million board feet annually. Typically, most aspen has been harvested in stands mixed with conifers, and has been processed nearby. For sawmills, aspen has been only a small percentage of processors' raw material.

Current and Potential Utilization

Potentially, up to 60 million board feet of aspen per year could be harvested in the interior West on a sustained yield basis (see the WOOD RESOURCE chapter). However, establishment of a major lumber industry based on aspen may not be practical because of aspen's characteristics (small size, high cull, etc.), its inaccessibility, and the high harvesting and transportation costs common throughout the Rocky Mountains.

Despite this, some use of aspen in the Rocky Mountains in the near future probably will continue to be for lumber, lumber products (especially pallets), and excelsior. In addition, use of small amounts for matches and paneling also is likely to continue. If subsurface mining increases in the region, additional markets may develop for aspen mine timbers.

However, aspen in the West currently has greatest potential for particleboards and other fiber products. There has been a rapidly growing interest and market throughout the continent for manufactured composition boards made from aspen flakes. Aspen's suitability for fiberboards and other fiber products makes utilization opportunities promising. Success in these areas would depend largely on the feasibility of concentrating large volumes of aspen roundwood or suitable residues at the processing sites (see the Utilization Feasibility section in this chapter).

Two large plants manufacturing aspen waferboard currently operate in central Colorado. Raw material for these operations is harvested from pure aspen stands. Regardless of the effects of economic cycles on composition board manufacturing, aspen in pure stands is an attractive resource whenever large amounts of aspen fiber must be produced efficiently.

The increased demand for fuelwood has drawn on the aspen supply as well as other species, mostly in the form of dead trees. Harvesting live trees for fuel is becoming more common. If demand continues to increase, future aspen utilization could be largely for fuelwood. Assuming 85 cubic feet of solid wood in a cord of aspen and a moisture content of 20%, the total heating value of the cord would be about 14.7 million BTUs (Milton 1980). At a typical heating efficiency of 55%, the cord of aspen would deliver usable energy of approximately 8.1 million BTU's. This is equivalent roughly to 88 gallons of No. 2 fuel oil at 65% heating efficiency.

One additional use for large amounts of aspen fiber is in paper pulp. While no outlet for aspen pulp is likely soon in the interior West, population expansion in the region could lead to greater production of pulp and paper.

UTILIZATION FEASIBILITY

In addition to technical considerations, several other categories of information need to be examined when considering the possibilities of a business based on the aspen resource. These include information about the aspen forest resource relevant to a particular kind and location of business; information about the product needs and markets that may be served from that location; information about possible production facilities; and analysis of the economic framework that ties together the wood resource, the production facilities, and the product markets.

Elements from each category affect elements elsewhere in an analysis in a highly interactive fashion. Consequently, when performing an analysis based on the ideas following, several iterations are likely.

The Aspen Resource

Some key considerations about the forest resource include: (1) location of aspen stands; (2) species composition of stands classified as aspen; (3) diameter and height distribution, by species, of aspen stands; (4) defect type and proportion (if any) found in the aspen stands; (5) topographical characteristics, including slope and aspect, of aspen stands; (6) soil type; (7) distance from potential manufacturing locations to aspen stands, by road surface type, steepness, and curvature; and (8) administrative requirements of owners or managers of the timberlands.

Anyone considering starting a business based on a particular species of wood, such as aspen, probably has decided on a product idea and has some idea of the scale of enterprise. The next step is to determine how much harvestable aspen is within various distances from the business location, in order to decide whether enough raw material required for the level of production planned exists within a reasonable distance to support the business.

As noted elsewhere in this book, aspen often grows with other species. Up to the point where other species exceed some volume limit, such stands are classed as aspen. However, the timber buyer may have to cut non-aspen species also, to fulfill harvesting or management requirements.

The planned product implies how much attention should be given to diameter and height distributions, by species within aspen stands. Without sufficient inspection, stands may subsequently prove to be too small in acreage, consist of trees poor in quality, or have trees that are too small to be profitably harvested. For a sawn product, diameter and height of trees govern product recovery percentages to a great degree and also may influence quality. For fiber or chip products, such as pulp, flakeboard, or animal bedding, diameter and height are not quite as critical but still determine how many pieces must be handled to get a unit of product. Even for firewood, diameter and height influence the volume of solid wood and the methods that are feasible to handle trees and logs.

The average diameter of quaking aspen logs typically is smaller than most other western sawtimber species. This affects not only the technology used in handling and product manufacturing, but also cost. To some extent, it also limits the timber products that can be made from aspen. For example, in the West, aspen lumber typically is produced in mills that primarily process softwood logs. Because much of the softwood timber processed in the Rocky Mountains is also of relatively small average diameter (fig. 6), sawmills tend to be of the small-log type. Therefore, sawing softwoods and small amounts of aspen in the same mill usually is compatible.

For some products, such as firewood, defects may be tolerable. Conks or tree form, for example, probably make no difference. However, rot, if prevalent in the stand, would diminish firewood recovery. For manufactured products, most kinds of biological (conks, rots, etc.)

or physical (fork, sweep, etc.) defects are undesirable. Whether or not such defects make an enterprise based on aspen uneconomical depends on the extent and severity of defects. Conversely, some specialty products might actually take advantage of defects such as wood grain swirls.

Aspen sometimes grows on slopes too steep or soils too unstable to permit harvesting. Topographical characteristics, along with soil type, determine how easily harvesters can work in the aspen stand and whether the forest environment needs protection with special measures. Slope obviously affects size and type of harvesting equipment. Soil type governs, along with slope, the practicality of the kind of harvesting and when and how soon equipment can be moved onto the site. Aspect, or direction of the slope, is an indicator of duration and intensity of drying sunlight.

The aspen stand location is defined by more information than just overall distance from a manufacturing location. An analysis of harvesting feasibility should look also at the distances to be traveled on various types of road surfaces. Many aspen stands may be inaccessible—too far from existing usable roads to permit economical logging. Further complexities are the distances traveled on roads of varying steepness and curvature. All of these elements significantly affect the cost of raw material transportation from woods to mill.

Finally, various administrative requirements of the owner or manager may be connected with an aspen stand. Such requirements may be based on environmental considerations, on the preferences of the owner, or on existing laws or regulations. For example, benefits from recreation, wildlife, scenic beauty, or watershed protection may be incompatible with harvesting. In total, these items could affect how logs or raw materials are cut, skidded, and transported.

Product Use and Markets

A thorough analysis of how the proposed product will be used, and in what markets the product can compete is important. Rich (1970) provided a detailed examination of forest product markets. In addition, a general text that covers the basics of marketing also can help (e.g., Stanton 1978).

Figure 6.—Aspen sawlogs being loaded onto a log truck.

One of the first major decisions, if aspen is harvested along with other species, is whether to market aspen products alone or to market them together with the same product or a different product from the associated species. For example, if rough, unfinished timber is to be sawn for a local market, perhaps no differentiation of species is needed. However, if quality aspen paneling is to be manufactured, then non-aspen logs must be sold or manufactured into another product.

What product to market depends, in part, on the interests and experience of the entrepreneur. It also depends on whether the product is classed as a commodity or a specialty. Commodities, such as dimension lumber are hard to distinguish (product differentiation); in this case, successful marketing may depend on price and service, rather than on demand for the specific product. For example, one unusual use of aspen, although still as a commodity product, is as a component of animal feeds. In this situation, marketing appears to depend upon the availability of preferred roughages, such as hay. For feeder operations in hay-short areas, but close to aspen sources, aspen may offer a viable alternative. Specialty items, in contrast, may be highly differentiated as products and in specific demand. The nature of the specialty product is such that few other competitive products exist; therefore, price and service are co-equal, or perhaps secondary to the satisfaction of the consumer. Donnelly et al. (1983) discussed how these marketing factors and others interact for forest products in the Rocky Mountain states.

The main point of marketing is to provide customers with a salable combination of product and service. If the product is an undifferentiated commodity, relatively small changes in price likely will cause large changes in demand for the product, as well as demand for the commodity in general. For example if transport costs to a distant market area increase moderately, forcing prices up, customers may stop buying one seller's product in favor of a cheaper, competitor's product. If, in contrast, the product is a differentiated specialty, very much in demand, with few substitutes, then relatively large price changes may have little effect on demand. Some of the factors to be included in a market study are the target consumer profile, location and spatial distribution of target consumers, product line and product mix, pricing policy, channels of distribution, and promotion and selling of the product.

Production Facilities

This chapter cannot examine the specific types of aspen product manufacturing facilities. They range from multimillion dollar, highly engineered facilities, such as particleboard plants, to inexpensive homemade operations, such as tractor powered, belt driven portable sawmills. However, there is common information applicable to all facilities that an operator should consider.

One important basic consideration is the physical flow of material through the manufacturing process. The time-based rate of transformation of raw material affects the cost of the final product. The prospective wood products manufacturer should diagram the flow of the operation in some detail and estimate the rate of flow and the product recovery at each step. The faster the flow and the less waste there is at each step, the greater the likelihood is of a profitable operation.

For every product there probably is a range of fixed and variable costs that are determined by how production facilities are configured. For example, all new, undepreciated equipment has high fixed costs relative to used equipment. Conversely, used equipment may have low fixed costs but also may have high variable costs of repair and maintenance. The choice may depend on ability to maintain equipment and personal expectations about reliability. Production facilities for some products require more capital than for others. Because fixed costs must be spread over more units to lower the unit price, product volume goals depend on the structure of types of costs. Product volume is also highly interrelated with availability of raw material and the marketing facilities available.

One important aspect of any production facility is the accumulation, storage, and marketing of by-products. Typically, sawmills produce cull logs and log pieces, slabs, edgings, chips, planer shavings, and sawdust. Almost all wood products operations have some type of residue. Two means of reducing residue are to burn it for heat or power, or to sell it to someone else for raw material. For example, the availability of residues from other wood processing industries, such as sawmills, is an important factor affecting pulp production.

Conversely, a planned product may depend on raw material obtained as residue or from harvest. Examples of such products are particleboard, flakeboard, pulp, or fuel. One uncertainty is residue availability. When lumber production from aspen is limited, for example, aspen residues from sawmills and planing mills are not readily available, even in the Lake States. Harvesting aspen specifically for manufacturing particleboard is an alternative; but this may double the cost of raw materials. However, for flakeboard manufacture, roundwood is preferred to sawmill residues; therefore, for this product, aspen is not as economically disadvantageous as it may be for conventional particleboard production.

Economic Analysis

Information about physical product flow and financial cash flow are essential elements that integrate considerations about raw material, marketing, and production. As noted previously, business analysis is likely to be an iterative process with each successive step answering further questions and becoming more complex. At each step, list the major uncertainties associated with the information.

For example, starting with the market, because it is basic to other considerations, first determine how many units of product can be sold at what price. How certain are the figures for each price and volume level? What is the nature of competing products and of competitors? Make a list of all the various possibilities that are likely. Pick two or three that are most likely to use for further consideration.

Given the volume requirements in the market estimates, what kind of production facilities are required to satisfy each of the most likely estimates? Is the range of volume estimates small enough that one plant configuration with slight modification could service the likely range? Or does the volume range imply that radically different plan scales must be considered? These possibilities are examples of uncertainty in the market place feeding back to affect vital decisions in production.

Each marketing scenario, and its corresponding production facility, implies a supply of raw material sufficient to support the operation. What is the range of raw material volume? How likely is it that each level of raw material volume can be obtained? Again list locations and uncertainties.

If, at this point, a decision is made to continue, the next step is to assign costs to all the steps of the preceding iteration. Again, cost estimates are likely to vary and have various levels of certainty. In addition, costs also vary over time, usually increasing; therefore, consider further analysis with higher costs. The result of this analysis should be a range of break-even costs with some idea of the certainty associated with them. How do these cost ranges compare to the price ranges discovered during the marketing research?

At this point, there may be many more questions. In addition to the sources that provided information up to this point, others include USDA Forest Service and state forestry offices, and appropriate publications (e.g., Donnelly and Worth 1981, Kallio and Dickerhoof 1979, Lawson 1972, Markstrom and Worth 1981.

NURSE CROP

Wayne D. Shepperd and John R. Jones

In forestry, a nurse crop generally is a crop of trees or shrubs that fosters the development of another tree species, usually by protecting the second species, during its youth, from frost, insolation, or wind (Ford-Robertson 1971). Aspen may be a nurse crop for shade-tolerant tree species that do not become established in full sunlight (e.g., Engelmann spruce). Through the natural successional process, aspen often serves in this capacity. In the West, aspen also can be considered a nurse crop to the forage-rich mix of shade-tolerant understory species (see the VEGETATION ASSOCIATIONS and FORAGE chapters). Without the aspen overstory, many of these species, particularly the forbs, probably would die.

Aspen is intolerant of shade and able to sprout in full sunlight. Its vegetative habit of regeneration from an existing well-developed root system enables suckers to establish quickly and uniformly over a site, and gives them a spurt of growth during the first 2 years that permits domination over competing vegetation (see the MORPHOLOGY and VEGETATIVE REGENERATION chapters) (fig. 1). Therefore, the best opportunity to utilize aspen as a nurse crop is where it occurs naturally and has a competitive advantage over other species.

Figure 1.—Aspen is one of the first species to reestablish on a site after a fire, giving it a competitive edge over other species.

Incidence of Conifers Under Aspen

Many coniferous species in the West establish more readily under partial shade than in full sunlight (Alexander 1974, Alexander and Engelby 1983, Ronco and Ready 1983, Seidel and Beebe 1983, Williamson and Twombly 1983). Mature aspen stands are ideally suited for providing partial shading because the total leaf area index of aspen stands often is only one-third as much as that of mature spruce-fir stands (Kaufmann et al. 1982) (fig. 2). Much more sunlight reaches the forest floor under aspen than under coniferous stands. However, dense aspen stands do provide considerable shade. For example, light intensities beneath well-stocked stands of aspen in Russia usually were less than 15% of light intensities in the open (Alekseev 1969).

In Arizona and New Mexico, Pearson (1914) noted that, on burned areas above 8,000 feet (2,450 m), Douglas-fir, white fir, and Engelmann spruce thrived in the shade of aspen. In contrast, coniferous reproduction usually was sparse on burned areas occupied by neither aspen nor oak. In the subalpine zone, Engelmann spruce nearly always reproduced well under an aspen over-

Figure 2.—Aspen provides essential shade and favorable climate for the establishment of more shade tolerant conifer species.

story when a seed source was present (Ronco 1975). Stahelin (1943) surveyed many burned areas in Colorado and Wyoming on which the subalpine forest had been killed 50 to 70 years previously. Aspen stands there were far superior to the post-fire meadow for conifer reestablishment. Early studies (Gardner 1905, Pearson 1914, Roeser 1924) showed that an aspen overstory benefited both naturally established and planted coniferous seedlings.

Conifers growing beneath aspen usually are younger than the aspen, because on burns, aspen sprouts promptly from preexisting roots. Shade-tolerant conifers, however, restock from subsequent seed crops, usually a gradual process. Sometimes, conifers may establish rather quickly after a fire; the aspen on these sites may only be 1 or 2 years older than the conifers, especially on coarse-textured granitic soils, where ground vegetation does not seriously inhibit the reestablishment of conifers (Langenheim 1962, Stahelin 1943).

Insolation

Shade is vital for establishment of several conifer species. In the central and southern Rocky Mountains, Douglas-fir seedlings on southerly slopes did not tolerate full exposure to sunlight (Bates 1924, Krauch 1956) and survived better in shade on all exposures (Jones 1974b). Engelmann spruce seedlings are even more sensitive to strong sunlight and drought than are Douglas-fir (Pearson 1914). Engelmann spruce and subalpine fir seeded in full sunlight in Colorado seldom survived beyond the second year (LeBarron and Jemison 1953, Noble and Alexander 1977); and, in Arizona, all corkbark fir seedlings planted on sites without shade soon died (Jones 1974b). On open sites, solarization of Engelmann spruce seedlings (Ronco 1967, 1970a, 1970b, 1975), of Douglas-fir seedlings (Zavitkovski and Woodard 1970), as well as seedlings of other firs perhaps is the major cause of death, although moisture stress and temperature may play roles, too.

Shade also has negative effects, especially after the seedlings are well established. Species differ in their tolerance of shade. Among the important coniferous tree species associated with aspen in the Rocky Mountains, Engelmann spruce, subalpine fir, and corkbark fir are the most shade tolerant. Engelmann spruce has been rated less shade tolerant than the firs (Alexander 1974, Baker 1949, LeBarron and Jemison 1953).

Sampson (1916) wrote that subalpine fir flourished beneath aspen, that white fir was never suppressed by aspen, and that aspen probably was unable to shade out Douglas-fir (fig. 3). Clements (1910) wrote that, unlike Engelmann spruce and subalpine fir, Douglas-fir was not vigorous beneath the heavier aspen canopies, while lodgepole pine seedlings died there (fig. 4). Pearson (1914) wrote that Engelmann spruce grew in the densest aspen thickets, and that Douglas-fir vigor declined with age beneath dense aspen. Harniss and Harper (1982) stated that white fir was able to invade their central Utah study areas more readily than subalpine fir, even though both were considered very tolerant (Baker 1949).

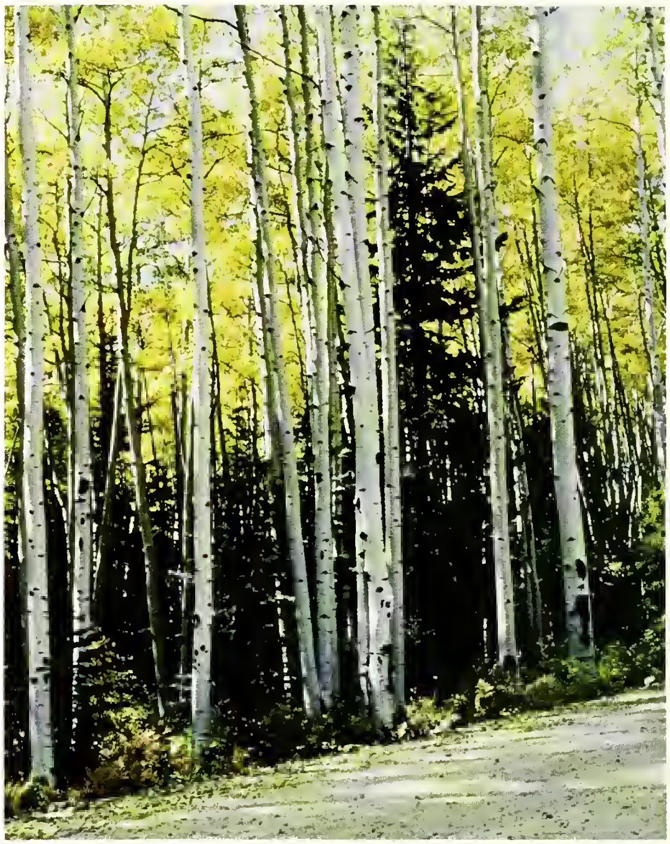

Figure 3.—Shade tolerant species can grow well under an aspen overstory, but may require aspen removal for optimum growth.

Baker (1918b, 1925) reported that survival of underplanted Engelmann spruce, Douglas-fir, and ponderosa pine was best under dense aspen shade; but, he recommended thinning aspen within a few years after underplanting to permit maximum conifer growth.

Shade tolerant conifers in southern Colorado, released by harvesting overstory aspen, subsequently grew faster in both height and diameter (Hittenrauch 1976). In Minnesota, balsam fir saplings and small poles grew fairly well under an aspen canopy but did much better when released (Roe 1952).

Berry (1982), in Ontario, reported substantial release of 22-year-old white pine (*Pinus strobus*), red pine (*Pinus resinosa*), and white spruce (*Picea* glauca) seedlings after the mature aspen overstory was removed. These species were rated intermediate, intolerant, and tolerant, respectively (Baker 1949). Aspen resprouting did not affect the degree of release.

Cayford (1957), in Saskatchewan, found that most of the white spruce beneath aspen overstories up to 100 years old were nearly as old as the aspen that overtopped them. The spruce grew somewhat more slowly beneath aspen than in the adjacent openings. At the age when open-grown spruce were surpassing the aspen in height, those beneath aspen were 10–15 feet (3–4 m) shorter. Spruce leaders, when they began to penetrate the aspen canopy, commonly were damaged by aspen branches moving in the wind. This resulted in forked and crooked tops. In a Manitoba study, Steneker (1963) found that white spruce height growth approximately doubled after release from an aspen overstory.

Temperature

Bare ground or herbaceous cover in the open directly receives maximum radiation during daylight hours; then radiates energy back into space at night. This causes marked daily temperature changes on clear days. In contrast, in the aspen forest, the primary surface receiving and emitting radiation is the deep complex canopy with its high moisture content and very high total surface area. Therefore, the environment beneath an aspen canopy is heated much less by incoming radiation during the day and cooled much less by back radiation at night (see the CLIMATES chapter).

From the subarctic to the tropics, soil surface temperatures in the open reach 120–160°F (49–71°C) on clear summer days. They are higher with decreasing latitude and with increasing elevation (Jen-hu-Chang 1958). Noble and Alexander (1977) recorded soil surface temperatures higher than 140°F (60°C) on mineral soil seedbeds, in a spruce-fir forest clearcut, at 10,600 feet (3,250 m) elevation. In contrast to bare sites, surface temperatures beneath aspen canopies in Russia generally remained below 90°F (32°C) (Alekseev 1969). Besides its direct importance to conifer seedlings, the much lower daytime temperatures beneath aspen, compared to the open, enhance seedling survival by reducing vapor pressure gradients.

Figure 4.—Shade intolerant species—lodgepole pine in this case—are suppressed under aspen.

Nighttime temperatures would be similarly moderated. Miller (1967) wrote that, because of the porous nature of aspen canopies, air cooled by radiation from the upper canopy at night tended to settle through it to the ground. Despite this, he observed that when a summer frost coated the vegetation in a Colorado meadow, there was no frost beneath the aspen.

Wind

Air movement within aspen stands is much less than in the open, especially in summer when the aspen are in full leaf (Marston 1956, Rauner 1958). In well-stocked pole stands in summer, velocities 5 feet (1.5 m) above ground were almost zero when winds above the canopy were greater than 20 miles per hour (32 km/hr). This will reduce moisture stress in coniferous reproduction as well as all understory species.

Water

Over a period of weeks or months, any vegetation fully occupying a site usually will withdraw near equal amounts of water from the surface 2–3 feet (0.5–1 m) of soil. Therefore, by the end of the growing season, water contents of the surface soils under aspen, grassland, shrubs, and conifers usually are quite similar (Brown and Thompson 1965, Houston 1952, Johnston et al 1969). If soil water content was the only consideration, moisture stress for shallow-rooted young seedlings would be similar in all these vegetation types.

In Utah and Colorado studies, interception by aspen crowns reduced summer rainfall received at ground level by about 10% to 15%, compared to that received in the open (Croft and Monninger 1953, Dunford and Niederhof 1944, Johnston 1971).

About 1% to 2% of summer rainfall in Utah aspen stands reaches the ground through stemflow (Johnston 1971), a process that could improve the moisture regime for seedlings developing at the base of aspen trees. Waldron (1961a) found that white spruce seedlings were more frequent on seed spots at the bases of aspen than elsewhere in the stand.

Observation indicates that snow persists later in the spring under aspen than in adjacent openings (see the WATER AND WATERSHED chapter). This prolongs snowmelt later into the growing season, providing developing vegetation beneath the aspen with an abundant supply of water. In Arizona and New Mexico, where May and June are particularly dry, the later snow cover under aspen shortens the period of effective drought that precedes the monsoon rains of July and August.

Moisture stresses in coniferous seedlings are reduced by shade. In some situations, this is essential to conifer seedling survival (Noble and Alexander 1977). On large seedlings, stresses were significantly lower on a shadyside twig than on a sunnyside twig of the same seedling (Jones 1972). The combined protection under an aspen canopy from direct insolation and from drying winds can be quite significant. In eastern Arizona, moisture stresses in coniferous seedlings were highest on a windy day (Jones 1972). Pearson (1914) reported that evaporation in the open on a windy June day was 60% greater when overcast, and 90% greater when sunny, than under aspen. He felt that the better Douglas-fir seedling survival under aspen mainly resulted from lower seedling moisture stresses.

Seedling Burial by Aspen Leaf Fall

Pearson (1914) wrote that one cause of coniferous seedling deaths in Arizona was burial by aspen leaves. "Smothering" by fallen leaves is widely considered to slow conversion to conifers in boreal forests of aspen and birch (Gregory 1966, Hughes 1967, Koroleff 1954, Pratt 1966, Rowe 1955) (fig. 5). In the Sierra Nevada of California, white fir and especially Douglas-fir are particularly susceptible to damping-off fungi when covered during the winter by dead plant material, such as shrub leaves (Tappeiner and Helms 1971). Fallen aspen leaves may have similar effects.

Herbaceous Layer

As noted in the FORAGE chapter, the herbaceous layer under aspen is usually described as heavy, approaching or exceeding that in meadows (Ellison and Houston 1958, Paulsen 1969, Pearson 1914). This herbaceous cover removes water from the soil and also shades conifer seedlings. Like aspen leaves, it buries seedlings temporarily in autumn, when the dead herbs are packed down by snow. Tucker et al (1968) reported burial by dead herbs as a cause of seedling deaths in Canada. This happened even to nursery-grown stock, which were much larger than natural seedlings germinated only a few months earlier in the forest.

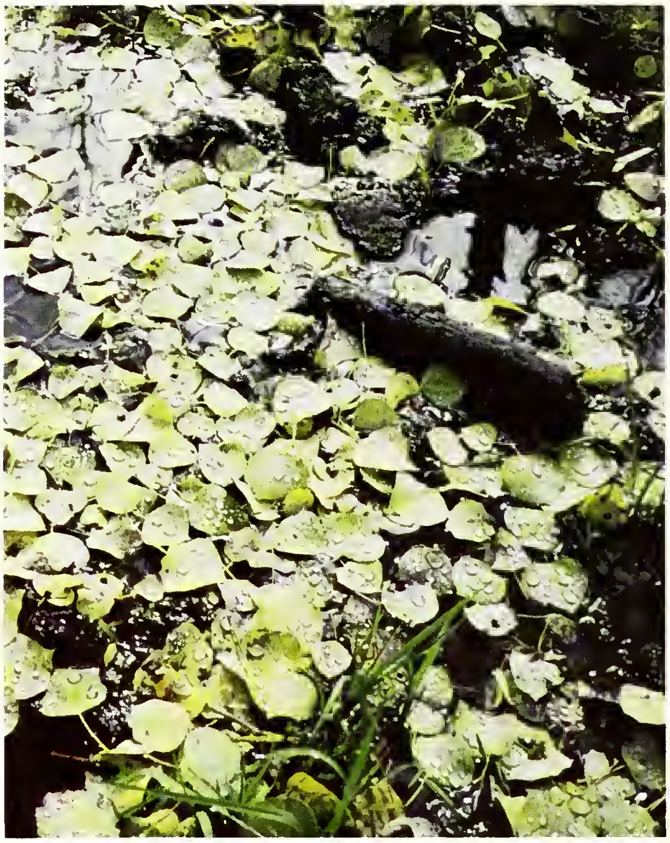

Figure 5.—In some cases, aspen leaf fall may smother newly germinated conifer seedlings.

Sometimes, however, herbaceous cover and shrubs can be somewhat sparse under aspen (Langenheim 1962, Stahelin 1943). Langeheim reported more coniferous invasion where the herbaceous cover was light than where it was heavier.

The degree of understory competition depends on the community type. Some community types may be better suited for use as nurse crop stands than others.

ESTHETICS AND LANDSCAPING

Craig W. Johnson, Thomas C. Brown, and Michael L. Timmons

Aspen is valued for its scenic beauty. One indication of this is the trips to the "high country" that many forest visitors make to view the autumn color changes (fig. 1). Another is the frequency with which aspen is planted in urban and suburban areas. Subjective generalizations about the esthetic uses of aspen, although reasonable, provide only rough guidance for management of scenic quality. They can not be used to compare the relative beauty of different scenes, or to determine how much scenic beauty changes as the physical characteristics of the scene change, either naturally or as the result of management activities. Unfortunately, there has been almost no documented research specifically measuring the relative scenic beauty of different aspen scenes. Therefore, this chapter discusses, in very general terms, the scenic beauty of aspen settings and the use of aspen in landscaping.

Esthetic Attributes in the Natural Landscape

The "Visual Management System" (VMS) (USDA Forest Service 1974a) used by the Forest Service and other land management agencies systematically deals with visual attributes of the natural environment. Landscapes are defined and differentiated based on their unique combinations of visual features (such as land, vegetation, water, and structure) in terms of form, line, color, and texture. Each set of combinations is referred to as a characteristic landscape. Characteristic landscapes are further described as panoramic, feature, enclosed, focal, canopied, detail, or ephemeral. Aspen may play a major role in many of these.

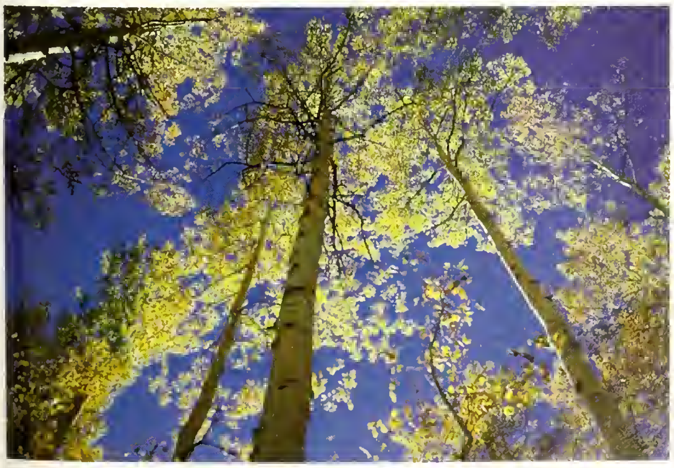

Figure 1.—Autumn gold of aspen leaves against a clear blue western sky. (Photo by Mary E. DeByle)

In the "panoramic landscape" of the high mountain meadow, aspen often forms the dominant or co-dominant vegetative cover. Its soft pale green, autumn gold, or winter gray color gives a distinct appearance to this expansive landscape. A "feature landscape" is dominated by an object or group of feature objects. Although usually more dramatic in nature, this can be created by a cluster of aspen in an otherwise treeless plain, or by a lone patch of brilliant autumn aspen on a hillside of conifers. "Enclosed landscape" is defined by walls of vegetation or earth forms. Although aspen is not as effective at creating enclosure as conifers, it can create significant spatial enclosure in some situations. Space enclosed by any deciduous tree is transient, varying with the seasons. This changing scene gives an added dimension to enclosed landscapes. "Focal landscapes" occur where the observer's eye is led to a point of convergence. A feature terminus, such as aspen contrasted against darker foliage at the convergence point, emphasizes the focal nature of the view. Aspen is somewhat ineffective at creating a "canopied landscape," because of the open nature of most aspen stands, its relatively short stature on most sites, and its deciduous nature.

Three variable factors—season, motion, and light—affect how the "dominance elements" of aspen are perceived. The seasonal variable has been discussed. The trembling motion of aspen leaves, perhaps second only to their autumn color, is probably the trait most commonly positively associated with quaking aspen. Lighting has a special effect on aspen; other trees are subject to two conditions—sunlit or shaded. The translucency of aspen's thin leaf provides an added dimension with back lighting, which creates the illusion of internally illuminated leaves, especially striking during autumn coloration.

The dominance elements and variable factors of aspen appear in varying degrees, depending upon the viewing distance. "Distance zones" or "classes" are divided into foreground, middle ground, background, and very distant (USDA Forest Service 1973, 1974; Buhyoff et al. 1982). The foreground is defined by the VMS as the zone in which details can be perceived. Aspen's line, texture, and color all contribute at this distance, as do the variable factors of season, motion, and light. Middle ground extends approximately 3 to 5 miles (5–8 km) from the viewer. At this distance, aspen primarily contribute color and texture (fig. 2); motion becomes imperceptable. As a background element, where texture is seen as groups or patterns of trees, the color dominance of aspen often is the only variation in an otherwise uniform distant vista. Season becomes an even more important variable, because of its effect on color, where other dominance elements and variables become insignificant.

Aspen may perform an important rehabilitative role on the landscape. Aspen's extremely rapid growth and spread can provide valuable visual rehabilitation of areas denuded by natural or artificial causes. In some situations, buffer plantings of aspen may be appropriate (see the REGENERATION chapter). Once established, a dense aspen stand will screen or soften undesirable visual impact, even in the leafless state.

Because of public interest in the scenic beauty of aspen, aspen management objectives generally have focused on maintaining the more sensitive (e.g., more visible) aspen stands in a healthy condition. Where this objective requires harvesting to regenerate a stand, landscape architects can help to design harvest area contours and can suggest harvesting practices to minimize the visual impact of the harvest (see the HARVESTING chapter).

Assessing Scenic Beauty

There are two landscape management-oriented approaches for assessing scenic quality: (1) expert judgment, and (2) public preference (Daniel and Vining 1983). The expert judgment approach utilizes evaluation by skilled observers with training in either art and design, or ecology and resource management. Usually, decisions about sensitivity, relative visual quality of existing scenes, and relative scenic beauty of management alternatives have been based on expert judgment about esthetic matters and educated assumptions about public preferences. The VMS is an expert judgment method.

The public preference approach relies on the judgment of non-experts about the scenic beauty of whole scenes. Public preference studies have been applied to both urban (Anderson and Schroeder 1983) and rural (Daniel and Boster 1976) scenic beauty. Although no public preference evaluations of scenic beauty have focused on aspen, studies of other forest types provide clues for aspen landscape management.

The public preference evaluations of forest scenic beauty have been restricted largely to either near-view or vista scenes. Near-views contain mostly foreground and some middle ground aspects (Brown and Daniel 1984); vistas contain distant peaks and slopes (Buhyoff et al. 1982). Variables specific to vegetation type have not been included in the preference evaluations of vistas; hence, they have not provided information specifically about aspen scenic beauty.

Figure 2.—Aspen in full autumn coloration highlights the middle ground distance zone of this southern Colorado setting.

Of the near-view studies, only one (Schroeder and Daniel 1981) assessed the relationship of aspen to scenic beauty. Among other parameters, they included the number of aspen present per acre to statistically predict relative scenic beauty in the ponderosa pine type. Most scenes did not contain aspen; those that did represented a range of conditions where aspen was intermixed with other overstory trees. Their regression model showed that aspen made a positive contribution to scenic beauty; as did large ponderosa pine, fir, juniper, Gambel oak, and herbage. Small and medium sized pine and slash decreased scenic beauty. Although they supported the positive effect of aspen on forest scenic beauty, their models were not sufficiently oriented to aspen to facilitate design of patterns of aspen and other vegetation types.

Landscaping

Quaking aspen has increased in popularity as a landscape plant in urban and suburban areas in the Rocky Mountain States. There are several reasons for this. Aspen grows rapidly, which gives a planting composition an acceptable "finished" quality within a few years after establishment (Sutton and Johnson 1974). Group plantings of aspen bring to the suburban home or to the urban setting a wildland character because of its form, bark, trembling leaves, and autumn color. Aspen trees are readily available throughout most of the Rocky Mountain States. With proper care, aspen can be grown and transplanted relatively easily (see the REGENERATION chapter).

The potential uses for fast growing, medium sized trees, such as aspen, in urban and suburban areas are both esthetic and functional. Esthetic landscaping uses include specimen, display, accent, spatial enclosure, and view enframement. Functional landscaping uses include visual screening, noise abatement, erosion control, and microclimate amelioration. Aspen, either planted alone or in combination with other plant material, is potentially suitable for many of these uses. Many planting designers prefer to combine a native tree, such as aspen, with other naturally associated plants (Eaton 1964).

Quaking aspen has unique qualities that affect landscaping schemes. First, the root system sends up sprouts every growing season. These can be a nuisance in lawns and gardens, but can be a positive attribute if an aspen clump or grove is desired. Deep mulching or mulching with plastic may control suckering somewhat. Second, aspen grows fast but doesn't live relatively long (perhaps 40–60 years) in an urban setting. Its life may be shortened further by one or more of the many diseases and insects that attack this species (see the DISEASES and INSECTS AND OTHER INVERTEBRATES chapters). Third, other diseases detract from the tree's appearance. Leaf blights, for example, often turn leaves brown or black in late summer and do not allow development of the expected autumn coloration in planted and irrigated aspen. Failure of expected fall coloration in aspen planted in the urban setting, where the tree's environment is much different than in the nearby mountains, can result from other physiological causes, also. Fourth, although natural aspen in the West grows in genetically identical clones, there is a great genetic and phenotypic variation among clones (see the GENETICS AND VARIATION chapter). This variability can be used to select and develop better aspen planting stock.

Esthetic Uses

Specimen plant.—Individual aspen trees, when planted alone, do not develop very effectively into specimen plants, because they usually lack the necessary strong characteristic form (Wyman 1970). However, some aspen trees possess strong characteristic form. This quality could be utilized for landscaping by vegetatively regenerating stock from these selected clones (see the REGENERATION chapter). Specimen aspen trees send up many root suckers, which must be removed if the individual tree character is to be retained.

Accent planting.—The form, texture, color, and density of a plant influence its usefulness for accent purpose. Plants, such as aspen, which have pronounced seasonal changes in leaf color, flower, and fruit frequently are used for accent purposes. The early spring catkins, bright green foliage, trembling leaves, and interesting bark color and texture are all attributes of aspen that make it an excellent plant where accents are desired. Aspen are most striking when seen against a dark background (e.g., dark buildings, coniferous trees, or the dark green foliage of other decidious species). More subtle effects, particularly in winter, can be achieved when aspen are displayed against a light background or are silhouetted against the sky.

Space definition.—For centuries, plant materials have been used to define exterior space—to define ownership boundaries, to create privacy or to create spatial compositions. Trees are capable of displacing and defining exterior space when used alone, or to modify the quality of exterior space defined by landforms or architectural elements, such as buildings, walls, and fences (Robinette 1972). The physical qualities of aspen make it useful in defining exterior space, particularly where light, airy, effects are desired.

Aspen are most useful where a naturalistic plant scheme is being employed. They often are used as a facer planting in conjunction with more dense conifers. However, aspen from most clones are of little value for defining formally structured exterior space where uniform trunk spacing is required, because of their inconsistent form and tendency to sucker. Because aspen self-prune their lower branches, clumps of trees are more effective in defining space than are single rows. Aspen's rapid rate of growth makes it desirable in designs where a quick spatial effect is desired. The seasonal richness of aspen provides quality and variety in plantings for defining both foreground and middleground views. The use of aspen in the urban or suburban setting for defining views of mountainous landscapes is particularly effective because visual associations to the tree in its native habitat.

Sound.—The sound created by breezes passing through aspen leaves is an added amenity. The characteristic whispering sound of quaking aspen leaves is of particular benefit in more intimate spaces and over or adjacent to walkways or other areas where people will be near the trees.

Functional Uses

If urban growth continues in the Rocky Mountain West, the need for plant materials to solve functional problems that accompany this growth will increase. Typical problems include undesirable views, noise, and undesirable microclimatic alterations.

Visual screening.—The attributes of a good deciduous tree for screening purposes include dense foliage; low, dense, and uniform branching; and a long period of leaf retention. Aspen are most effective for screening where adequate space is available for planting clumps or multiple rows, or when combined with other plant material. Single rows of aspen by themselves are too open in character, particularly when fully grown, to make good visual screening trees. However, when they are combined with appropriate shrubs or conifers, excellent screening can result. Aspen's rapid growth provides screening within a few years after planting.

Noise abatement.—The most effective plants for noise abatement are tall, dense, and uniformly branched (Cook and Van Haverbeke 1971). Aspen are effective for noise abatement in urban environments only where ample space is available for massive plantings, or if they are used in conjunction with other species. Because they are deciduous, they lose most of their noise abatement qualities in winter.

Climate control.—The climate of the developed valleys in the Rocky Mountains is characterized by dry summers and snowy winters. The extremes of this climate frequently are exaggerated in urban areas, where buildings and paving create new and often undesirable microclimates.

Tree canopies intercept solar radiation. Shaded spaces may be as much as 10°F (6°C) cooler, and light intensity may be reduced from 60% to 90% (Robinette 1972). During the growing season, aspen has sufficient foliage density to intercept much solar radiation and provide a pleasing, shaded, cool environment. When foliated, aspen also helps reduce glare caused by light reflected from buildings, walks, automobiles, etc. In winter, the open branching pattern of aspen allows sun penetration.

Aspen is not very effective for windbreaks, because it does not branch close to the ground or have dense foliage and branching, and because it is somewhat brittle. However, where adequate space is available for massive plantings of mixed species, aspen can be used effectively in windbreaks and shelterbelts. There, its characteristic suckering may be an advantage for replacing broken or lost overstory plants and for providing a wind-filtering understory.

PART IV. MANAGEMENT

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MANAGEMENT OVERVIEW

John R. Jones, Robert P. Winokur, and Wayne D. Shepperd

The aspen ecosystem may be managed for any one or more of the assets discussed in PART III. RESOURCES AND USES. It is truly a multiple use type, especially in the West, where it has had limited marketability for its fiber (see the WOOD UTILIZATION chapter). Many forest types are managed for their economic value as timber. This value is the source of money for management activities, such as access road construction and maintenance, harvesting costs, regeneration costs, intermediate stand treatments, and other silvicultural treatments.

In the West, however, aspen forests have been used primarily for wildlife habitat, livestock forage, watershed protection, and esthetics and recreation. These uses seldom have generated enough money to actively manage much of the overstory portion of the aspen ecosystem. As a result, adequate measures have not been taken to ensure that this seral species is retained where other resources benefit from its presence. Because of the decrease in severe fires resulting from modern forest fire prevention and suppression practices, natural succession is replacing aspen with conifers or other vegetation types (see the FIRE chapter). Without specific management efforts, some aspen forests in the West eventually may be replaced by coniferous forest or other non-forest vegetation.

On many sites, aspen may not persist unless the stand is periodically destroyed by some event that rejuvenates it by initiating a new stand. Without such an event, aspen can be displaced on many sites by conifers, shrubs, or grass. This successional process is partially offset by aspen dominating areas where fire, insects, or cutting has removed conifer stands. Also, aspen stands sometimes spread into neighboring meadows. (See the VEGETATIVE REGENERATION and FIRE chapters.)

Climax aspen, in the absence of fire or cutting, will become uneven-aged (see the MORPHOLOGY chapter). Uneven-aged aspen stands do not produce optimum yields of wood products. Esthetically, they may be inferior to mosaics of even-aged patches. Compared to forests composed of several age classes in even-aged patches, uneven-aged stands are inferior habitat for some important wildlife species, such as ruffed grouse (see the WILDLIFE chapter).

Many good sites in the West that could produce large yields of aspen fiber are occupied with mostly overmature or uneven-aged aspen stands. They have the potential to be managed as commercial stands if they are regenerated before their eventual replacement by other vegetation. Either suitable markets to utilize these stands need to develop, or the stands must be regenerated at considerable expense to renew their productivity.

Problems in Aspen Management

The volume of aspen harvested annually in the western United States has been relatively small (see the WOOD RESOURCE chapter). Furthermore, annual growth of these predominantly mature and over-mature aspen stands in the West has been much less than their potential under intensive management. As discussed in the WOOD UTILIZATION chapter, the shortage of markets for quaking aspen timber from the West has severely restrained the potential for aspen management.

However, the situation may be changing. Aspen is a rapidly growing source of fiber. As human populations increase and technology advances, this fiber source will become more merchantable, and more likely to be managed as a commercial timber resource (see the WOOD UTILIZATION chapter).

Intensive short-rotation management of aspen is becoming increasingly operational in the Lake States (Bella and Jarvis 1967, Boyle et al. 1973, Einspahr and Benson 1968, Ek and Brodie 1975, Hunt and Keays 1973b, Perala 1973, USDA Forest Service 1976b). Short-rotation management may involve planting selected or genetically improved stock, irrigation and fertilization, and close monitoring and control of damaging agents (see the REGENERATION and INTERMEDIATE TREATMENTS chapters). With this management option, the stand is clearcut at the culmination of either mean annual dry weight growth or net annual growth in cubic volume of stems—usually before age 30 in the Lake States. The entire tree may be chipped on-site, which assures maximum use of most of the fiber produced.

In the West, intensive management of aspen as practiced in the Lake States is unlikely in the near future. Although markets are being developed to utilize small diameters, and sites exist which could support intensive management, the tremendous backlog of older stands with larger trees will have to be utilized before short rotation management becomes economically competitive.

Aspen management is expected to intensify in the West, however. Already, some mature and overmature stands are being harvested. During such harvests, usually the residual, unmerchantable trees are felled to stimulate maximum sucker regeneration and rapid development of a replacement stand. Occasional sucker stands are being thinned. The Southwestern (Crawford 1976), Rocky Mountain, and Intermountain Regions of the Forest Service have transferred part of their commercial aspen land into the regulated component, which requires specific management systems. Wood industries as well as land management agencies in the West are increasing their attention to expanding markets and improving industrial technology for aspen (USDA Forest Service 1976b).

Management Alternatives

Generally, an aspen stand can be successfully managed for several values simultaneously. Frequently, a treatment prescribed primarily to enhance one value enhances others also. Sometimes, however, a prescription that enhances one value substantially impairs others. Managers seldom have had precise means to evaluate immediate or long-term payoffs or trade-offs from alternative management prescriptions. In timber management, for example, past equations and tables for estimating timber yield capacities of sites were marginally satisfactory. More recent research in growth and yield, the development of new volume equations (Edminster et al. 1982), description of stand characteristics (Shepperd 1981), and development of procedures to evaluate trade-offs in local land management planning (Brown 1980) have provided managers with improved methods for better decisionmaking. Similarly, recent methodology to enhance water yields, to improve habitat for selected species of wildlife, and to stratify aspen community types have been made available (see the appropriate chapters in PART II. ECOLOGY and PART III. RESOURCES AND USES, and the MANAGEMENT FOR ESTHETICS AND RECREATION, FORAGE, WATER, AND WILDLIFE chapter).

Other information has been assembled to help managers formulate plans for managing aspen forests. For example, Perala (1977) developed a guide for aspen in the Lake States. Betters prepared a decision-making guideline for aspen management on the Routt National Forest in Colorado.[1] Western habitat and community type descriptions that include quaking aspen have been published (see the VEGETATION ASSOCIATIONS chapter). With these kinds of guidelines, and with the information presented in this book, managers have a better basis for making decisions about aspen management in the West.

Retaining Aspen

Decisions often need to be made about whether to retain aspen on a given site. For example, where aspen occurs in predominantly coniferous forests, management may favor conifers, aspen, or a mixed stand. Pure aspen stands may not be the most desirable vegetation in all cases. Land managers must consider the mix of resources and uses among the alternatives; the social and political constraints; and the costs of retaining, modifying, or converting the aspen.

In seral communities where aspen is to be retained as the permanent, dominant overstory, conifers should be discouraged from invading by cutting existing stock and removing adjoining seed sources. Management required for this option depends on the successional stage of the existing stand (Mueggler 1976b).

Where conifers are preferable, a mixture of aspen can be a form of catastrophe insurance. Fire, extensive blowdown, or severe insect outbreaks may destroy pure stands of conifers; but, if appreciable aspen trees are scattered in the stand, they usually will reforest the site promptly (see the VEGETATIVE REGENERATION and FIRE chapters), thereby protecting the watershed and providing a nurse crop for reestablishment of shade-tolerant conifers (see the WATER AND WATERSHED and NURSE CROP chapters).

Alternating generations of aspen and conifer dominance may be desirable. On some sites, especially those with a high blowdown hazard, management of spruce-fir forests by shelterwood or selection cutting methods that leave residual trees may be risky. Yet, overstory shade is desirable for spruce and fir regeneration (Alexander 1974, 1984; Alexander and Engelby 1983). If aspen is a fairly abundant component of the conifer stand, the stand could be clearcut with the expectation that aspen will promptly reforest the site, thereby forming a nurse crop to shade young conifer seedlings, which should result in higher survival rates or lower seed/seedling ratios. If clearcut openings are small enough to be adequately reseeded by spruce and fir in stands surrounding the openings (Alexander 1974, Jones 1974b), or if most advanced conifer regeneration survives harvesting and slash treatment, a coniferous understory could become established quickly. This understory would dominate the site when the aspen are removed several years later. Aspen suckers would fill the gaps and provide an aspen-conifer mix for the next cycle. A similar approach could be used with a shelterwood system in mixed spruce-fir—aspen stands to allow either heavier shelterwood cutting intensities, fewer entries, or less time between entries. Alternating generations would take advantage of natural processes, providing inexpensive and simple management. If markets for aspen increase, this system may become increasingly attractive.

However, this method may have drawbacks. The environment provided by the aspen nurse crop also is suitable for establishment of herbaceous understory vegetation. Competition from understory species in some plant communities can be severe enough to have a detrimental effect on conifer seedling establishment. Therefore, it is essential to understand the dynamics of plant communities in such areas before using seral aspen stands as nurse crops.

Converting Aspen

Based on the total mix of values, a different vegetation type sometimes may be preferred on a site occupied by aspen. For example, if aspen is abundant in an area, local esthetics may be improved by increasing the acreage of conifers or other vegetation types, thereby increasing the variety of scenery and wildlife habitat (see the MANAGEMENT FOR ESTHETICS AND RECREATION, FORAGE, WATER, AND WILDLIFE

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[1] *Betters, David R. 1976. The aspen: Guidelines for decision making. Report, Routt National Forest, Rocky Mountain Region, USDA Forest Service, 100 p. Steamboat Springs, Colo.*

chapter). If the market value per unit volume of coniferous species remains higher than that of aspen, converting some of these sites to conifers might be justified economically.

Forage in meadows commonly is more suitable for cattle than forage under aspen. Furthermore, open areas usually produce more herbage (see the FORAGE chapter). In areas with extensive stands of aspen growing on poor sites, converting aspen to meadow may be desirable. In areas with extensive forest, the scenic qualities may be improved if sizes, shapes, and locations of these constructed meadows are designed to complement the landscape.

Aspen or other forest types may be converted to herbaceous vegetation to increase water yields from important watersheds (Hibbert 1979). This also may increase livestock forage (see the MANAGEMENT FOR ESTHETICS AND RECREATION, FORAGE, WATER, AND WILDLIFE chapter). However, wildlife habitat, vegetation diversity, timber values, and esthetic quality are likely to diminish, especially if such conversion is widespread.

If long-term management of seral aspen is for conifer conversion, and conifer regeneration is established in the stand already, it may be released by removing the aspen overstory. Success of this option depends on the tolerance of the conifer species released, the stocking density of conifers, the productive capacity of the site, and the resprouting ability of the aspen clones (see the VEGETATIVE REGENERATION chapter). Increase in conifer growth resulting from removal of an aspen overstory has not been documented in the West, but has been reported in Ontario (Berry 1982).

The costs of converting the aspen to another species mix and managing that replacement vegetation is an important factor in decisionmaking. The total of all values and benefits (both tangible and intangible) of the new resource mix should be greater than the total of all values and benefits lost by removal of the aspen. A careful, long-range cost-benefit analysis should be made before beginning any extensive conversion of aspen to other vegetation types.

REGENERATION

George A. Schier, Wayne D. Shepperd, and John R. Jones

There are basically two approaches to regenerating aspen stands—sexual reproduction using seed, or vegetative regeneration by root suckering. In the West, root suckering is the most practical method. The advantage of having an existing, well established root system capable of producing numerous root suckers easily outweighs natural or artificial reforestation in the West. Root suckers do not require good seed years or stringent microclimatic conditions (see the VEGETATIVE REGENERATION chapter), and can be produced in much greater abundance and more economically than nursery grown seedlings or transplants. Although suckering precludes the opportunity for genetic improvement of the new stand, it offers the predictability of knowing the type of stand that probably will develop from the regeneration.

However, occasionally, aspen must be established on new sites, or on sites where clonal root systems have died naturally or have been destroyed. Artificial regeneration, using seedlings, or root and stem cuttings is necessary in such cases. Surface mine reclamation, riparian habitat rehabilitation, and production of landscaping planting stock are examples of situations requiring artificial regeneration, if new aspen stands are to be created.

Figure 1.—Clearcutting stimulates the most suckers.

NATURAL REGENERATION

The easiest way to naturally regenerate an existing aspen stand is to rely on root suckering stimulated by removing the existing overstory in a way that will successfully restock the stand and also meet other resource management objectives. The silvical characteristics of aspen (see the MORPHOLOGY and GROWTH chapters) can complicate the choice of silvicultural technique to be used to naturally regenerate an aspen stand. Aspen is intolerant of shade; it grows best in full sunlight. Individual stems also respond well to release, and grow faster when competing vegetation is removed. However, they also are susceptible to diseases infecting the trees through stem wounds caused by logging. Aspen stands are self-thinning, especially at younger ages (Shepperd and Engelby 1983, Walters et al. 1982). Enough sound, undamaged suckers need to result to provide a stand that is well stocked and free of disease and damage, to meet management objectives.

Clearcutting Versus Partial Cutting

Logging greatly stimulates aspen suckering (Baker 1925; Bartos and Mueggler 1982; Crouch 1981, 1983; Jones 1975; Mueggler and Bartos 1977; Sampson 1919; Smith et al. 1972). The number of suckers that appear is directly proportional to the number of stems removed; the greatest number arise after clearcutting (fig. 1). When only part of a stand is cut, sucker production is stimulated on fewer root systems. If apical dominance is extensively broken or reduced by partial cutting, abundant suckers may arise; but they often develop into inferior stands because of competition and shade from residual trees.

In a Utah aspen clone, Smith et al. (1972) compared regeneration on clearcut plots with regeneration on plots from which 67% of the basal area was removed by cutting the larger diameter trees, leaving 41.2 square feet of basal area per acre (9.4 m² per ha). Four years after treatment, there were only 27% as many suckers on the partially cut plots as on clearcut plots. Twelve years after treatment, partially cut plots had 39% of the regeneration found on clearcut plots, and sucker heights were 13% less on the partially cut plots (Schier and Smith 1979).

In another Utah study, light partial cutting stimulated suckering; but a very high percentage of these suckers died within a few years (Sampson 1919). Partial cutting an Arizona stand, leaving a basal area of 69 square feet per acre (16 m² per ha), did not significantly change the number of suckers surviving 20 years later (Martin 1965).

Partial cutting not only compromises the sustained production of wood products (Walters et al. 1982), but also may severely restrict future silvicultural options in a stand. Once partially cut stands sprout, future entries can not be made without severely damaging the new stand; and any future yields from the residual overstory are forfeited (fig. 2).[1] In addition, growth and vigor of the new stand may be reduced by competition with the residual overstory.

Figure 2.—The 20-year-old saplings in this partially cut stand are being suppressed by the remaining overstory stems; but they would be severely damaged if an overstory removal cut were attempted.

Figure 3.—Heavy partial cutting may adequately regenerate some stands where optimum fiber production is not desired.

In summary, clearcutting is appropriate when the primary management objective is sustained production of forest products—either sawtimber or fiber (Shepperd and Engelby 1983). In such situations, cutting submerchantable stems along with the merchantable ones will maximize sucker production, will minimize the presence of diseased or defective growing stock in the new stand, and will avoid suppression of the new crop by residual overstory stems.

Partial cutting might be feasible in natural, uneven-aged aspen stands that sometimes are found in the central Rockies (Shepperd 1981). If management objectives require vertical canopy diversity or retention of some overstory, partial cutting may result in enough sprouting to adequately regenerate these types of stands (fig. 3). Either individual tree or group selection cutting methods might be applicable (Shepperd and Engelby 1983). Extreme care is necessary to avoid injury to residual stems during logging. Partial cutting is not worthwhile in deteriorating clones where concurrent root system dieback has reduced the clones' ability to sucker (Schier 1975a).

Fire

Burning also can be considered as a natural means of replacing some old stands (fig. 4).

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[1] *Data and/or detailed information on file at the Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo.*

The role of fire in aspen is discussed in the FIRE chapter. Many aspen stands, especially those with only a grass and forb understory, do not readily carry fire (Barrows et al. 1976).[2] Most aspen stands in the West lack the readily flammable fuels needed to produce a fire effective for stimulating regeneration. Even with adequate fuels, the flammability of adjacent grasslands and coniferous forests may make prescribed burning risky. However, where fire can be used with reasonable safety, it is an inexpensive and effective way to naturally regenerate the aspen forest.

A combination of partial cutting and fire is possible. In the Lake States, Perala (1977) reported that a fire in 10 tons per acre (22 t/ha) of dry, evenly distributed, aspen logging slash killed the residual overstory trees and provided favorable conditions for regeneration. Burning should take place as soon after the slash has dried as weather conditions permit. If it is delayed too long, depletion of root carbohydrate reserves by respiration, suckering, and general root deterioration before the burn, will result in poor sucker growth afterwards.

Figure 4.—In some cases, prescribed burning can successfully kill a declining overstory and stimulate the sprouting of a new stand.

To stimulate aspen suckering in mixed stands where a predominantly spruce-fir overstory has been removed, the coniferous slash may be broadcast burned to kill the residual aspen. In this situation, it may be desirable to burn when the duff layer is damp, to avoid killing the many aspen roots commonly growing within the surface organic soil horizon.

Herbicides

Herbicide treatments that kill aspen stems without killing the root system usually result in excellent sucker regeneration (Brinkman and Roe 1975). Aerial spraying with herbicides is an inexpensive substitute for clearcutting, and does not require unusual weather and fuel conditions (DeByle 1976). A single aerial application of a water emulsion of 2-1/2 to 3 pounds (acid equivalent) per acre of a low volatile 2,4-D ester killed nearly all overstory aspen on some study areas in northern Minnesota (Brinkman and Roe 1975). Excellent regeneration resulted.

On a western Wyoming site, 22 years after aspen were killed by spraying with 2,4-D, the sprayed areas had 6,900 more suckers per acre (17,000 per ha) than the unsprayed areas within the same clones. However, there were fewer forbs and shrubs on the sprayed areas (Bartos and Lester 1984).

Aerial application of herbicide, however, subjects the entire forest environment to toxic chemicals, and may have unwanted effects on understory vegetation. Restricted application of herbicide by treatment of individual stems with basal sprays or injection would reduce the environmental impact and, although not yet tested, may result in equally good regeneration.

Girdling

Farmer (1962a) found that severing or girdling roots stimulated suckering distal to that point. The effect of severing was strong; that of bark girdling was weaker and inconsistent. In Utah, plots where all aspen were girdled produced far fewer suckers than plots clearcut or partially cut (Smith et al. 1972, Schier and Smith 1979). Sucker mortality was high on girdled plots; by the 12th year after treatment few suckers were still living. Girdling does not effectively stimulate aspen regeneration for three main reasons.

1. High cytokinin to auxin ratios do not develop in the roots, because, although downward movement of auxin in the phloem is stopped, cytokinins continue to move out of the roots and up the stem through the xylem.

2. Die-back of the root system results, because girdled trees, which can live up to 3 years after treatment, drain the roots of food reserves and other growth factors.

3. Microclimate is unsuitable for sucker development and growth because of shade cast by girdled trees.

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[2] *DeByle, Norbert V. Managing wildlife habitat with fire in the aspen ecosystem. Paper presented at the Fire Effects on Wildlife Habitat Symposium. University of Montana, Missoula, March 1984. Symposium proceedings are in preparation as a USDA Forest Service General Technical Report, to be published by the Intermountain Forest and Range Experiment Station, Ogden, Utah.*

Other Methods

In the Lake States, disking strongly stimulated suckering in understocked aspen stands. However, even with abundant light, sucker survival and subsequent stocking usually were poor because of excessive damage to parent roots. Therefore, disking is no longer recommended (Brinkman and Roe 1975; Perala 1972, 1977).

Less severe wounding or cutting of roots also can stimulate suckering without cutting or killing overstory trees (Barth 1942, Farmer 1962a, Maini and Horton 1966a, Sandberg 1951, Steneker 1974). This technique conceivably could be used to promote suckering under existing overstory stands.

In Michigan, Farmer (1962a) found that severing a surface root at a single point strongly stimulated suckering beyond the cut. Perala (1972, 1977) considered root shearing, despite its expense, to be the most successful mechanical site preparation method in the Lake States. Invariably, it resulted in dense aspen regeneration. The parent root system was least disturbed when roots were sheared with a sharp blade in frozen soils. In Arizona, preliminary work by Trujillo[3] suggested that open overmature stands might be regenerated by severing or shearing many roots, each at a single point only. An aspen stand bulldozed in 1979, on the Routt National Forest, Colorado, had 17,000 sprouts per acre in 1984.[1] Preliminary data from a replicated study in progress in Colorado, comparing bulldozer pushing and chainsaw felling, indicates that suckering can be stimulated greatly by bulldozing (fig. 5).[1]

Figure 5.—Regeneration by bulldozing. Stems must be tipped out of the ground. Cutting through soil with the blade will destroy the lateral root system.

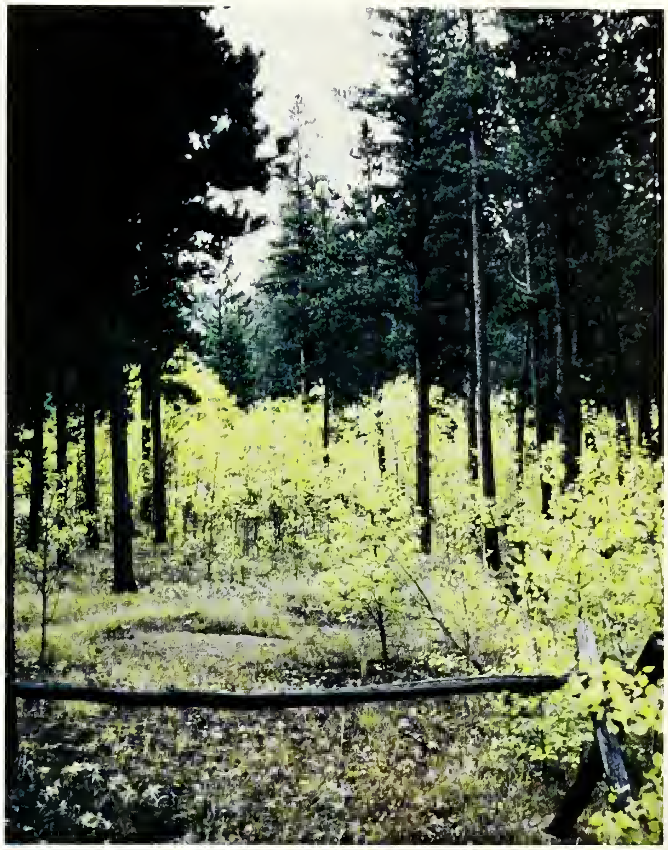

Figure 6.—Removing a conifer overstory can stimulate sprouting from a suppressed aspen root system.

In some circumstances, little or no management action is needed to regenerate aspen stands. For example, in grazed aspen stands with established regeneration, marked reduction or exclusion of livestock for a few years may enable these stands to regenerate. Natural sexual reproduction also is possible, although not common, without deliberate management actions. Williams and Johnston (1984) reported natural aspen seedlings on a phosphate mine dump, in southeastern Idaho. The unusual combination of an adequate seed source, friable mineral soil, limited competition from other vegetation, and a continuous supply of soil water made possible the seedling reproduction.

Natural Regeneration of Mixed Stands

In conifer stands that contain an appreciable mixture of aspen, group selection and shelterwood systems may maintain or even increase the aspen component (fig. 6); but, management by individual tree selection will reduce the amount of aspen over time. After clearcutting or a one-cut overstory removal, aspen regeneration

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[3] *Unpublished findings by David P. Trujillo, Rocky Mountain Forest and Range Experiment Station, Research Work Unit at Flagstaff, Ariz.*

is likely to dominate the new forest (Gottfried and Jones 1975). Cutting the aspen along with the conifers probably will result in more suckering than if the aspen were left standing. However, if aspen are not felled, logging damage to aspen roots and increased insolation resulting from conifer overstory removal also may stimulate aspen suckering (see the VEGETATIVE REGENERATION chapter).

Effects of Logging and Other Activities

Concentrated skidding traffic reduces suckering (Zasada and Tappeiner 1969b). After a fire in a mixed conifer forest in Arizona, the network of skid trails and spur roads from salvage logging were still treeless 23 years later (fig. 7), although the crowns of the bordering young aspen forest, about 30 feet (9 m) tall, were starting to close over them. Suckers also were absent from landings. On the Apache National Forest, many clearcuts in the aspen-conifer mixed stands had only patches of aspen 5 to 10 years after logging, despite a general mixture of aspen in the stands before harvesting. Aspen regeneration appeared to have failed where there was heavy skidding traffic or where slash had been piled.

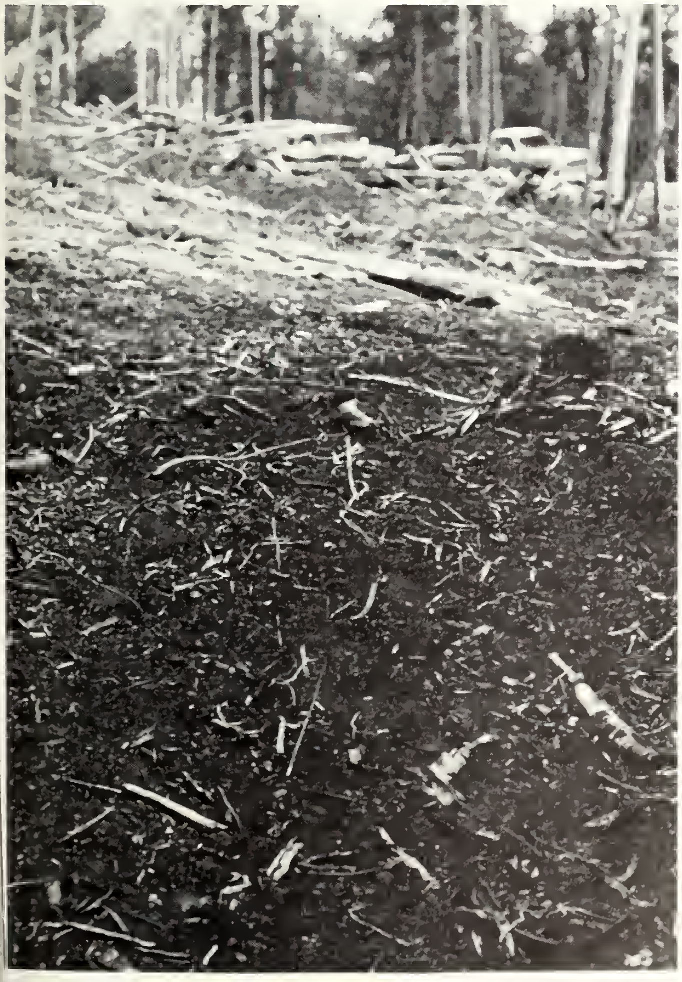

Figure 7.—Concentrated skidding traffic can destroy lateral roots and prevent suckering.

Figure 8.—Heavy concentrations of slash will reduce suckering.

Zasada (1972) found that slash on aspen pulpwood clearcuts in Minnesota did not retard suckering. In the West, however, slash on clearcuts has been somewhat heavier, because usually only sawlogs have been removed, and because of the large volumes of cull material. Suckering can be sparse and sucker growth poor in heavy slash concentrations (Jones 1975, Steneker 1972b). Research in progress has found that heavy slash concentrations (4,000-5,000 cubic feet per acre) can reduce suckering drastically (fig. 8).[1]

Aspen slash usually has been left untreated. It is a negligible fire hazard that decays rapidly and is buried quickly in the dense sucker and understory regrowth. The scattered slash also provides the young sucker stand with some protection from browsing animals.

Grazing, browsing, and trampling by livestock and wildlife can be a serious problem in obtaining aspen regeneration. Limited browsing, however, may result in abnormally dense stocking, partly because of removal of apical shoots and buds (Beetle 1974, Sampson 1919, Smith et al. 1972). Occasional light browsing has little effect on the stem form or height growth of aspen, because a single dominant shoot develops from the uppermost lateral bud below the browsed terminal (Graham et al. 1963, Maini 1966). (See the ANIMAL IMPACTS chapter.)

Time of Treatment

Season of treatment affects number and vigor of aspen suckers. The only time that clearcutting results in substantial suckering during the same growing season as harvest is when aspen is cut in the spring (Baker 1925, Jones 1975, Sampson 1919). Frequently, those suckers that do arise after spring cutting continue growth too long into the fall and then are damaged by frosts. Enough suckers for regeneration generally appear the next year. This reduction in sprouting can be a problem in some vegetation associations where competing understory brush will grow for a full season before aspen suckers arise.

Aspen regeneration in the West generally is adequate wherever aspen is cut during the normal July to November operating season. However, dormant season harvesting could be justified in situations where maximum suckering is critical, such as deteriorating clones, or those subject to extremely heavy browsing or understory competition.

ARTIFICIAL REGENERATION

Aspen planting stock can be propagated from seed or vegetatively. Seed formation creates new genotypes with differing characteristics. Therefore, reproduction from seed results in the full potential for phenotypic variation within the new stand. In contrast, vegetative propagation (e.g., root cuttings) is asexual, and genetic variation during propagation is eliminated. (See the SEXUAL REPRODUCTION, SEEDS, AND SEEDLINGS; VEGETATIVE REGENERATION; and GENETICS AND VARIATION chapters.)

Genotype Selection

Rudolf (1956) suggested criteria for selecting aspen clones for propagation by seed or from cuttings. Where aspen are heavily cankered or attacked by the poplar borer, he suggested selecting clones that show resistance. In old stands, clones that are vigorous and relatively free of heart rot should be chosen. Selected clones should have straight trunks and slender branches (giving less entry to heart rot). Pollen quality should be checked when evaluating male clones for seed production.

Relative time of leafing may be an important consideration in selecting clones in the West. Clones which leaf out earlier than their associates, as well as most high elevation clones, break dormancy at relatively low temperatures. Because physiological threshold temperatures are reached earlier at low elevations, such clones there would break dormancy particularly early. At these lower elevations, clones with low threshold temperatures are likely to be damaged by hard spring freezes after dormancy has broken.

Figure 9.—Clonal differences need to be considered when selecting genotypes for propagation. The branchy growth form of this clone will be passed to its progeny through either vegetative or sexual propagation.

Conversely, late-leafing clones and most clones from low elevations appear to be poor candidates for planting at high elevations, where daytime temperatures are colder. They require relatively high temperatures to break dormancy. At high elevations, these clones may have a very short growing season—too short for adequate growth.

Susceptibility to juvenile diseases should be evaluated among clones. Diseases that are unimportant in a dense, natural sucker stand could be serious in a plantation of, for example, 700 stems per acre (1,730 stems/ha).

Characteristics that are superior in one habitat may be neutral or even unwanted in another. Clonal selection also should be tied to an ecological habitat classification. For example, a natural clone might be described as "84 years old, of good form and superior height on a *Picea engelmanni/Erigeron superbus* habitat, with no indication of decay or insect damage." Planting stock from that clone could be used with considerable confidence on that habitat type, and perhaps on similar types. To use it in an *Abies concolor/Quercus gambelii* habitat might give unsatisfactory results.

An advantage of vegetative regeneration is that the selected clone's performance in a given habitat type can be evaluated in advance (fig. 9). If planting stock is grown from seed, the percentage of the stock that will be well-suited to the intended habitat is unknown. That percentage can be maximized by selecting seed from the best possible female clones that are near good male clones.

There also are advantages to using seedlings. Producing seedlings requires less equipment, labor, time, and space than producing greenwood cuttings (Campbell 1984). A large outplanting of seedling stock will maximize the variation available in the gene pool. This variation benefits reforestation and land reclamation by enhancing the adaptability and survival of the total outplanting. Also, the large amount of planting stock required is more economically grown from seed. Barnes commented that even full-sibling progenies of aspen display considerable genetic diversity.[4]

Once clones have been selected for seed collection, a seed orchard can be established by obtaining sucker cuttings from those clones, planting them in a convenient and suitable location, and treating them for maximum seed production. However, the parent stock should be well evaluated before the seed orchard is established.

Vegetative Propagation

Four methods have been used to vegetatively propagate aspen: root cuttings, stem cuttings, transplanting wildlings, and sucker cuttings.

Root Cuttings

Propagating aspen by planting root cuttings is attractive because of its simplicity. Field plantings, however, have been unsuccessful because of poor sucker production and failure of suckers to initiate new roots. In a Swedish study with *Populus tremula*, planting 5,248 root cuttings produced only 336 rooted plants (Johnsson 1942). An exploratory New Mexico planting was a complete failure. Perala (1978a) was unsuccessful in establishing aspen on old agricultural lands in Minnesota by planting root cuttings, 5 and 40 inches (12 cm and 100 cm) in length, from 10 clones. Initial suckering resulted in one sucker per foot of root length; but mortality was high, and at the end of 6 years only 9% of the suckers survived.

Under greenhouse conditions, Starr (1971) successfully propagated aspen by planting root segments 1/2 to 3/4 inch (1–2 cm) in diameter and 1 inch (2.5 cm) in length. Shoots and roots developed in 6 to 8 weeks; and in 18 months, the suckers grew into small trees. However, this is the only published record found of successful propagating of aspen by planting root cuttings.

Stem Cuttings

Successful reproduction of quaking aspen from dormant stem cuttings has been reported (Barry and Sachs 1968, Schier 1980, Snow 1938); but success is not usual (Barry and Sachs 1968, Barth 1942, Hicks 1971, Maini 1968, Snow 1938).

Using indolebutyric acid (IBA), a rooting hormone, Snow (1938) was able to root a high percentage of cuttings from 1-year-old stump sprouts collected in March, at the first sign of leaf-bud swelling. Results of rooting tests with cuttings taken in January or February usually were negative.

The success reported by Barry and Sachs (1968) was with greenwood stem cuttings from Sierra Nevada clones taken periodically during the growing season. Rooting percentage varied with IBA concentration and stage of shoot growth. They were unsuccessful in rooting dormant stem cuttings except for cuttings taken from a single Mexican clone in April.

Schier (1980) successfully rooted two types of stem cuttings from 2-year-old aspen seedlings—spring shoots and shoots induced to develop by defoliation. A commercial rooting powder significantly increased rooting of both types. Cuttings from spring shoots only rooted when they were treated with the rooting compound. There were significant differences among genotypes in the rooting ability of cuttings from spring shoots.

Stem cuttings, usually taken from the current year's shoot growth, are more difficult to root than sucker cuttings. Hicks (1971) explored anatomical and biochemical differences between sucker cuttings and stem cuttings, but failed to find any reasons conclusive for this. He suspected that differences in rooting ability of the two types of cuttings was a result of different concentrations of root promoting and/or inhibiting substances.

Transplanting Wildlings

The procedure described here is based on observation, common practice, and the experience of John R. Jones at Flagstaff, Ariz. Wildlings should be collected when they are dormant, commonly in the spring. Select healthy looking suckers between 3 and 6 feet (1–2 m) tall. Larger suckers are more likely to die after transplanting. Dig carefully around the base of each selected sucker and locate the parent root. It will probably be within 3 inches (7–8 cm) of the surface. Sever the parent root 6 to 8 inches (15–20 cm) from the sucker on both sides. Remove the sucker and root segment from the ground. If the sucker has developed independent roots at its base, try to keep them intact. Commonly, where the wildling has grown from the root of a living older tree, it will have no roots of its own while it is small. Plant with the root about 6 inches (15 cm) deep. It is advisable to mix sphagnum peat (peat moss) in the soil. Water moderately every 1–2 days the first summer.

The transplanted wildling probably will leaf out later than usual that first spring; but it will almost surely leaf out and will ordinarily persist through the first summer. If it puts out only the small early leaves—those preformed in the buds—plan to get a replacement; it probably won't leaf out again the second year. If it grows some long shoots the first summer, with large leaves, it probably will survive.

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[4] *Personal communication from Burton V. Barnes, University of Michigan, Ann Arbor.*

Choosing a wildling from the edge of a clone adjoining parks may provide a smaller, more independent root system. Top pruning and treatment of the planting hole with a rooting hormone also may increase the probability of survival.

To shortcut the process of obtaining aspen planting stock, many commercial nurseries in the West transplant aspen wildlings; failure is common. Schier (1982) studied 12 clones in northern Utah and found that ramets often lacked sufficient independent roots to survive transplanting. The ramets of a few clones, however, were able to develop independent root systems.

Some commercial landscapers reported good survival after transplanting wildlings as large as 3 to 5 inches (7–13 cm) d.b.h. and 18 to 20 feet (5.5–6.1 m) tall (Campbell 1984). They selected ramets with independent root systems that were firmly rooted in all four directions. A 44-inch tree spade was used to remove the wildlings with minimal disturbance to the root systems. After transplanting, the wildlings were given three foliar applications of a complete fertilizer and one hydraulic injection of fertilizer into the soil. The trees also were sprayed with a systemic fungicide.

Sucker Cuttings

Larsen (1943), working with European aspen (*Populus tremula* L.), found that the difficulty of rooting aspen stem cuttings could be overcome by taking cuttings from succulent, young suckers that arise from excised roots. These cuttings rooted with ease. This has become the standard procedure for vegetatively propagating aspen (fig. 10).

Sucker cuttings have been widely used to produce experimental material, sometimes on a rather large scale, with some modifications in technique practiced by different investigators (Schier 1978b). Certain basic requirements must be met. Don't let the root cuttings dry out or mold. Plant them in a freely drained medium. Maintain moderate temperatures. When the suckers are still small, cut them from the parent root and plant in a freely drained medium. Keep the humidity high and the temperature moderate. When they have rooted, replant them outdoors or individually in containers. At all times, maintain sanitary conditions to keep pathogens under control.

Root collection.—The diameter of collected roots is not very critical. Root segments smaller than 1 inch (2.5 cm) in diameter may produce more suckers per lineal foot (Benson and Schwalbach 1970, Sandberg 1951). However, Starr (1971) found little size-related difference in the sucker production of root cuttings 1/4 to 2 inches (0.6–5.0 cm) in diameter from Wyoming clones. Zufa (1971) recommended diameters of 1 to 2.5 inches (2.5–6.4 cm).

Root cuttings from some clones produce several times more suckers per foot than those of others (Schier 1974, Schier and Campbell 1980). Density of suckers also is a function of collection date (Schier and Campbell 1980, Tew 1970a). The number of rootable suckers produced

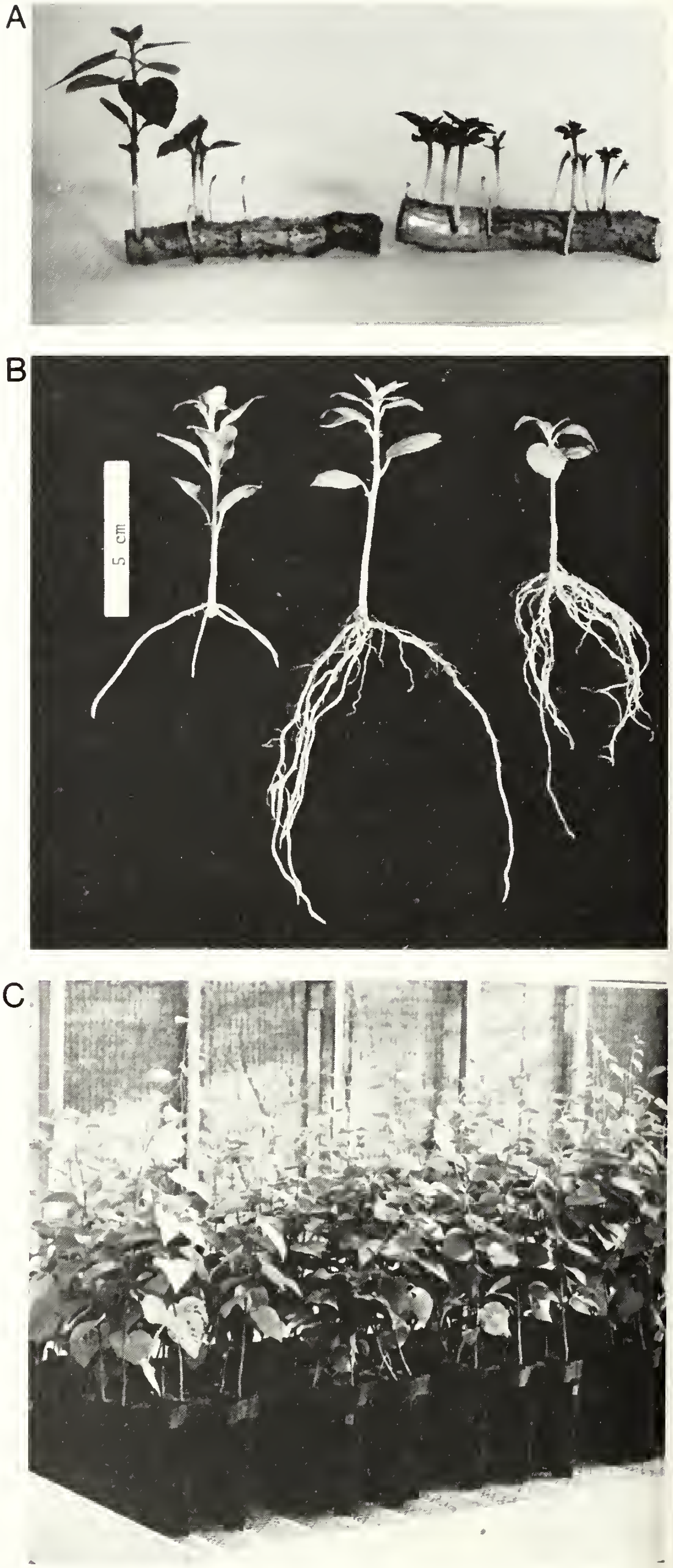

Figure 10.—Three steps toward producing aspen planting stock from sucker cuttings: (A) suckers arise on properly treated root segments, (B) excised suckers develop roots when planted in the proper media and are kept well watered, and (C) container-grown aspen, planted as root cuttings about 3½ months before this photograph was taken.

by cuttings from any clone varies with the date of collection; and the best and poorest dates vary from clone to clone (Schier 1973d, Schier and Campbell 1980, Tew 1970a, Zasada and Schier 1973). Schier (1978b) avoided collecting roots during the spring flush of shoot growth when few suckers are produced. Benson and Schwalbach (1970) recommended autumn as the best time to collect roots.

Root storage.—Many aspen areas in the West are snow covered until May or June, making it difficult to collect roots until late spring. In those locales, roots probably should be collected in October, stored, and then planted in March or April.

In Minnesota, Sandberg (1951) produced and rooted suckers without difficulty from roots collected in November and stored in moist soil at 40°F (4°C) for 75 days. In Wisconsin, Benson and Schwalbach (1970) dug up roots in November and stored them in sand in polyethylene bags, some in refrigeration at 30–40°F (−1°C to 4°C), and some in an unheated building. Taken from storage in April, the roots suckered very well, and the suckers rooted normally. Roots died when overwintered in a deep freeze (Benson and Schwalbach 1970).[5] Schier and Campbell (1978b) made a comprehensive study of the effect of cold storage on suckering. They found that the roots of 10 Utah clones collected in spring, summer, or fall, could be stored safely for prolonged periods. Roots collected in October and stored at 35°F (2°C) for 175 days did not show any significant loss in suckering capacity.

Roots should be treated with a fungicide before either storage or planting to reduce the danger of mold or other disease. If sand or other medium that may be contaminated is used for storing the root segments, the medium should be sterilized with a soil fumigant or should be autoclaved before use. If a commercial medium, such as perlite, is used for storage, sterilization is not needed unless there is reason to believe it has been contaminated. The storage medium should be moist to avoid drying the roots, but not too wet to avoid disease problems.[5]

Root preparation.—To reduce the incidence of disease, the roots should be scrubbed clean with a soft brush, cut into planting pieces not longer than 6 inches (15 cm), and the pieces should be dipped in a fungicide solution (Benson and Schwalbach 1970).[6] Wounds and cuts are then coated with a micro-crystalline wax. Clean tools should be used for cutting. Without careful treatment, insects and decay may destroy entire lots of root segments and suckers (Farmer 1963b, Larsen 1943). Roots from occasional clones decay readily regardless of treatment, and do not produce a satisfactory yield of usable suckers (Schier 1978b).

Root planting.—Planting depths of root segments may vary from 0.6 inch (1.5 cm) in vermiculite (Schier 1978b) or sand (Tew 1970a) to "just covered" (Benson and Schwalbach 1970). They should be covered sufficiently to keep them moist but shallow enough to harvest the suckers conveniently.[5]

Media, in sterilized plastic or wooden flats, successfully used in sucker propagation have ranged from peat (Larsen 1943), to coarse sand (Tew 1970a, Zufa 1971), to fine sand (Maini and Dance 1965, Maini and Horton 1966b), to a coarse sandy loam (Sandberg 1951). Barry and Sachs (1968) and Schier (1978b) used vermiculite with good results. Zasada and Schier (1973) used a 1:1 mixture of vermiculite and perlite. Benson and Schwalbach (1970) recommended a 1:1 mixture (by volume) of vermiculite and sand.

Greenhouse environment.—Maini and Horton (1966b) found constant temperatures from 64° to 87°F (18°C to 31°C) were suitable for suckering root cuttings. Zufa (1971) produced suckers successfully with greenhouse temperatures fluctuating between 60° and 90°F (16°C and 32°C), and relative humidities from 30% to 90%. Zasada and Schier (1973) tested three temperature regimes on cuttings from three Alaskan clones, and had good results at day/night temperatures of 77°/59°F (25°/15°C) and 86°/68°F (30°/20°C). Schier also used the day/night temperature regime of 77°/59°F (25°/15°C) with good results, using roots from Utah and Wyoming clones. Sandberg (1951) found light intensity was unimportant in bringing suckers to readiness for cutting from the root pieces. Benson and Schwalbach (1970) recommended watering the planted root cuttings only enough to keep them from drying out. Overwatering increased the risk of disease.

Severing the suckers.—Suckers begin emerging about the second week after the root pieces are planted (Benson and Schwalbach 1970, Larsen 1943, Sandberg 1951, Zufa 1971). Maximum production occurs in 5 or 6 weeks (Schier 1978b). Suckers may be cut from the root pieces for rooting when they are as short as 0.8 inch and as long as 4 inches (2–10 cm) (Schier 1974, Zufa 1971). Benson and Schwalbach (1970) recommended cutting them off when they are 1 to 2 inches (2.5–5.0 cm) long and have two developing leaves. The cutting tool used should be clean, and sterilized after suckers from each flat have been harvested.[5]

Rooting the cuttings.—Coarse sand (Farmer 1963b), loam (Zufa 1971), shredded sphagnum moss,[4] mixtures of sand and vermiculite (Benson and Schwalbach 1970), and perlite and vermiculite (Barry and Sachs 1968) all have been used for rooting sucker cuttings. The rooting medium is placed in well-drained, sterilized, plastic or wooden containers. Flats or trays that can hold 100 or more cuttings seem to be the most suitable for large-scale production. However, single cuttings in small containers have the advantage of not needing transplanting after the roots develop. They can be left in the containers until the cuttings have a well-developed root system and have substantial top growth. Using this procedure, the roots are not disturbed by transplanting to another container when they are most fragile, and a propagation step is eliminated. Barnes successfully

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[5] *Personal communication from Dean W. Einspahr, Institute of Paper Chemistry, Appleton, Wisc.*

[6] *They used 1 1/2 tablespoons of Captan 50W per gallon of water. Other fungicides probably are also satisfactory.*

propagated single aspen in Jiffy-7 peat pots[7] 1.75 inches (4.5 cm) in diameter by 2.125 inches (5 cm) high.[4] Zufa (1971) rooted cuttings in polystyrene tubes.

Generally, hormone treatments are not necessary for adequate rooting. However, suckers from roots of some clones, collected on some dates, have not rooted well (Farmer 1963b, Schier 1974, Schier and Campbell 1980, Tew 1970a). To overcome this problem, a higher rooting percentage, and more and larger roots per rooted sucker, will result from treating the suckers with indolebutyric acid (IBA) (Farmer 1963b). Cuttings can be treated either by dipping the base in talcum powder containing IBA or by quickly dipping the ends in alcoholic solutions of IBA (Schier 1978b). Commercial powder preparations of IBA are available.

A misting bench, giving an intermittent mist, is most suitable for rooting sucker cuttings (Farmer 1963b, Schier 1978b). Temperatures should be kept between 70° and 80°F (21°C and 27°C), although night temperatures can be slightly lower. If misting facilities are not available, sucker cuttings can be rooted in chambers covered with clear plastic. Periodic watering will maintain a high humidity in the chambers, which will keep the succulent cuttings turgid. The simplest chamber is a rooting tray sealed in a plastic bag (Benson and Schwalbach 1970). Clear plastic boxes 3 × 6 × 12 inches (7.5 × 15 × 30 cm) have been used as rooting chambers.[5] The bottoms have drainage holes, and the lids have air-holes. The boxes are partly filled with a sterilized vermiculite-sand mixture. The 100 suckers in each box are watered as needed, and nutrients are added once only, after they have rooted. Once rooted, the lids are removed to make room for the growing tops. Sucker cuttings from most clones produce well-developed root systems in 2 to 3 weeks (Benson and Schwalbach 1970, Schier 1978b). As might be expected, there is considerable clonal variation in rooting ability (Schier 1974, 1980).

Transplanting.—Unless single cuttings have been rooted individually, sucker cuttings must be transplanted soon after roots form. If the cuttings cannot be transplanted immediately, they are kept from outgrowing their trays by restricting moisture and nutrients (Benson and Schwalbach 1970) and lowering temperatures.[4] After transplanting to nursery beds, the cuttings often reach heights of 3 to 5 feet (1.0–1.5 m) by the end of the summer. They are cut back when lifted. Fertility standards for quaking aspen nursery beds have been given by Williams and Hanks (1976) and Wyckoff and Stewart (1977).

An alternative to nursery beds is transplanting rooted cuttings into individual containers. With increased use of container stock for large-scale reforestation, containers of all sizes and shapes have become available. Schier (1978b) successfully used a tube 2.5 inches in diameter by 10 inches in depth (6.4 × 25.5 cm) filled with a 1:1 vermiculite-peat moss mixture. Planted cuttings were treated with a complete commercial fertilizer. After one growing season, the containers were filled with roots, and the young trees could be outplanted.

Producing Seedlings for Planting

Collecting Seed

First, female clones that bear seed must be selected. They should have desirable characteristics and lack any notable shortcomings. Some female clones are not readily recognized, because they rarely flower in nature (Einspahr 1962). Some that flower bear little good seed, perhaps because the nearest synchronized pollen source is too far away (Baker 1918b, Barth 1942, Reim 1930). At least in Norway, seed production is often severely reduced by insects (Borset 1954).

Pauley (1955) was readily able to obtain good seed from every western state in which aspen grows. During 2 years of collecting, Barnes found many clones bearing good seed throughout the aspen areas of Utah.[4] He also obtained seed from Alberta and Alaska.

Mature capsules that are plump and rounded near the base, and have erect points, commonly contain good seed (Baker 1918b, Barth 1942, Borset 1954). Mature capsules do not contain good seed if they are somewhat flattened and taper rather evenly from base to point. Many seedless capsules have bent or crooked tips.

Baker (1918b) observed that edge trees or isolated trees are more likely to flower than those within dense stands. Therefore, thinning might induce or increase flowering in desirable female clones. Also, some trees that normally do not flower sometimes may be induced to flower by girdling (Einspahr 1962, Jensen 1942). Jensen did this by drawing a wire tightly around the tree. The wire was underlaid by a light metal strip to prevent killing the tree. However, for seed production, simply stripping a ring of bark from a few trees each year will cause little damage to most large aspen clones.

Seed is borne in late spring. Time of flowering is not a useful predictor of collection time. Faust (1936) reported the interval from flowering to seed maturity was 6 to 10 weeks in New York. Time of collection is critical. When the seed has ripened, one windy day can disperse the whole crop (Barth 1942, Borset 1954). Barth (1942) advised collecting catkins when some capsules are beginning to open.

Borset (1954) described a straightforward procedure for timing seed collection. When trees approach maturity, collect sample catkins and spread them in a warm dry room. If catkins are collected too early, they will wither. If they are collected nearer to maturity, the capsules will open after a time and the cottony seeds will well out. When that happens, catkins on the trees should be collected for seed extraction.

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[7] *Trade names are used for the benefit of the reader, and do not constitute an official endorsement or approval of any product or service by the U.S. Department of Agriculture to the exclusion of others that may be suitable.*

If relatively few seeds are wanted, branches can be collected and stood in water. The cut ends should be trimmed daily to prevent clogging. If mature, the capsules will open in 2 or 3 days, and the seed can be collected. If insufficiently mature when the branches are cut, some catkins will wither or yield a low percentage of viable seed (Borset 1954, Roe and McCain 1962). High air temperatures (68° to 104°F (20° to 40°C)), gentle ventilation, and low relative humidity hasten the ripening process. The catkins should not be exposed to full sunlight (Food and Agriculture Organization of the United Nations 1979).

Sowing the catkins themselves, or sowing seed with the cotton adhering to them, works with larger-seeded species of *Populus*, but is very unsatisfactory with aspen (Barth 1942). Vacuum cleaners are satisfactory for separating the cottony seed from catkins on cut branches (Roe and McCain 1962) or even from catkins spread on a floor (Borset 1954). In the latter case the vacuum head is held a few inches above the layer of catkins so that the seed and cotton are sucked in, but the catkins remain.

Aspen seed can be separated from the cotton by rubbing it over a fine mesh wire screen (Faust 1936) or by using an air stream and a series of screens (Einspahr and Schlafke 1957, Roe and McCain 1962). Only a small percentage of seed is extractable by rubbing. An air stream and screens is more efficient. From top to bottom, the screens are 20-mesh, 40-mesh, and 60-mesh. A high velocity stream of air tumbles the cottony seed in the upper screen; the seeds are collected on the 40- and 60-mesh screens.

Within at least some species of *Populus*, the larger seeds germinate more and grow faster (Farmer and Bonner 1967, Faust 1936), which should result in better seedling establishment. Therefore, if quaking aspen seed is screened and the smaller are rejected, more desirable results may be obtained.

Drying and Storing Seed

Viability of aspen seed can be maintained for several years by proper drying and cold storage in sealed containers. Faust (1936) found that seed stored better if it had been dried immediately after extraction. Moss (1938) recommended drying for 2 to 3 days at 75°F (24°C). Eight hours of forced air drying is effective; a hair dryer was used in pilot tests (Marjai 1959).

Considerable information has been published on storage conditions (Barth 1942, Benson and Harder 1972, Borset 1954, Busse 1935, Faust 1936, Moss 1938, Wang 1973). Campbell (1984) air dried aspen seed for 2 days and then stored it in a sealed plastic envelope at 36°F (2°C). Germination rate initially was 94%; after 4 years of cold storage, the seeds still had 82% germinability. Temperatures below freezing also are satisfactory for long-term storage. Benson and Harder (1972) reported germination only slightly reduced after 4 years storage at −11°F (−24°C).

Sowing Seed for Bare-root Stock

Barth (1942) described nursery practices for aspen in Norway. Later, the Institute of Paper Chemistry developed an improved nursery system (Benson and Einspahr 1962, Einspahr 1959) and tested it on a commercial scale (Benson and Dubey 1972). An outline of that system as described by Wyckoff and Stewart (1977) follows.

1. Prepare a fine smoothed seedbed. Incorporate a non-burning granular fertilizer into the soil.
2. Fumigate the seedbed with methyl bromide. Aerate for 3 days before seeding.
3. Place a frame around the seedbeds. Sow seed on a still day at a rate of approximately 20 seeds per square foot (215/m^2). After seeding, gently rake seedbed on the contour.
4. To provide shade and protect seedlings from wind and splashing, cover the bed with muslin supported by 1/2-inch (1.3-cm) hardware cloth on a lath frame, all of which is supported by the frame mentioned in step 3.
5. During the first 6 days, water the seedbed several times a day, keeping the surface constantly moist. Afterwards, water beds once a day. If necessary, use acid injection in the irrigation system to maintain the pH between 5.5 and 6.0.
6. Fertilize two more times before lifting. Follow a schedule for applying fungicides and insecticides.
7. Remove muslin after 3 weeks, hardware cloth after 7 or 8 weeks, and framing boards after 10 or 12 weeks.
8. Lift trees in the fall, cut back to about 18 inches (45 cm) in height, prune roots if necessary, and bundle. Bundles are stored over winter in an unheated building where they are heeled-in in sand, watered, and treated with a fungicide.

In the West, where some planting sites are snow-covered well into May or later, an unheated building may not provide suitable storage. In this case, refrigerated storage may be necessary to offset increasing springtime temperatures.

Container-grown Seedlings

An alternative to bare-root planting stock from a nursery are greenhouse-grown container trees. A container seedling is in better physiological condition than a bare-root seedling (Tinus and MacDonald 1979). The container seedling has an undamaged, intact root system, and the original root-to-soil contact is maintained. The container seedling should have a better chance of surviving in the often dry and otherwise harsh environments in the West.

Schier successfully used 2.5- by 10-inch (6.4- × 25.5-cm) tubes and a 1:1 vermiculite-peat moss medium to grow containerized aspen seedlings, the same procedure he used to propagate sucker cuttings (Schier 1978b). The seed was covered with about 1/8-inch

(30 mm) potting soil mix and was lightly watered. Greenhouse temperatures ranged from 60°F (16°C) at night to 77°F (25°C) during the day. After germination, each seedling was fertilized with a dilute solution of a liquid fertilizer to avoid burning the tender plant. Weekly applications of full strength fertilizer solutions were started after 5 to 7 days. Seedlings started in the spring grew from 12 to 18 inches (30 to 45 cm) before bud set in the fall; the containers were full of roots; and the plants had a satisfactory shoot-root ratio.

Site Preparation

Competition from herbaceous plants, particularly sod-forming grasses, in both natural regeneration and plantations of aspen will seriously reduce growth and survival (Aldhous 1969, Bailey and Gupta 1973, Benson 1972). Benson (1972), in Wisconsin, noted that good sod control before planting and for 2 years afterwards resulted in average 2-year heights of 8 feet (2.5 m). Some herbicides may be used; but many harm the aspen. Cultivation works well but is expensive.

Plantation Spacing

Initial spacing may vary from 5 × 5 feet (1.5 × 1.5 m) to as much as 10 × 10 feet (3 × 3 m). However, wide spacing may result in limby trees and reduced quality of the aspen for sawlogs and veneer. Trees with long-lived lower branches are likely to have more degrade from wood stain (Hook and Sucoff 1966). Barth (1942) recommended planting at a spacing of 5 × 5 feet for production of high quality timber (match bolts) in Norway.

Limbiness of the aspen plantation is not detrimental if the purpose is simply to establish aspen on an area for esthetics, to provide wildlife habitat, or to provide a conifer nurse crop. A wide spacing of 9 × 9 feet (2.8 × 2.8 m) requires planting fewer than one-half as many trees as one of 6 × 6 feet (1.8 × 1.8 m)—538 compared to 1,210 per acre (1,330 versus 2,990 per ha).

If the economics of planting at wide spacings are attractive but close spacing is wanted, trees might be planted at 10 × 10 feet (3 × 3 m), for example, then cut back at 5 years (Benson 1972) or at 10 or 12 years (Einspahr and Benson 1968) to provide a much denser sucker stand. This can only be attained at a cost of 5 to 12 years growth.

Planting

There is little published information about planting aspen. In Norway, Barth (1942) recommended planting in dug holes as early as possible in the spring. In Illinois, Gilmore (1976) found that cottonwood seedlings planted in auger holes made better early growth and survived better than those planted with dibbles. In the West, container-grown rooted sucker cuttings were outplanted in the spring of 1976, on north slopes of phosphate mine spoils in southeastern Idaho, on sites that receive about 18 inches (45 cm) annual precipitation. Site preparation included ripping, harrowing, and fertilization. By the fall of 1977, the aspen had grown less than 1 foot (30 cm); but more than 80% survived.[8] Poor height growth probably resulted from grass competition. Survival appeared good in 1983; the aspen were outgrowing the competition with leaders of approximately 1 foot (30 cm) each year.

[8] *From records of the Mine Spoil Reclamation Project, Intermountain Forest and Range Experiment Station, Logan, Utah.*

INTERMEDIATE TREATMENTS

John R. Jones and Wayne D. Shepperd

Intermediate treatments are those applied after a new stand is successfully established and before the final harvest. These include not only intermediate cuttings—primarily thinning—but also fertilization, irrigation, and protection of the stand from damaging agents.

THINNING

By definition, thinning is felling trees in an immature stand primarily to accelerate growth of the remaining trees (Ford-Robertson 1971). The term "thinning" should not be applied to salvage, sanitation, or shelterwood cuttings. Thinning an aspen stand may have any of several objectives (Perala 1978b): (1) to increase yield of large-diameter products, (2) to increase total fiber yield by cutting the trees expected to die because of competition, (3) to bring early financial return from commercial thinnings, (4) to reduce logging costs during the regeneration cut, (5) to improve conditions for regenerating aspen suckers by reducing competition, (6) to favor desirable clones in stands of small adjacent or intermixed clones, (7) to improve access and forage for livestock and wildlife, or possibly (8) to increase visibility for esthetic reasons.

Figure 1.—The annual growth rate of this young aspen stem increased dramatically after thinning.

Small tree diameter has hampered logging, marketing, and utilization of aspen (see the WOOD UTILIZATION chapter). Accelerated decay in stands beyond about age 100 limits the time an aspen stand can be left unharvested to obtain additional growth. Even on good sites, many trees are too slender to log or to mill efficiently for lumber at 100 years of age (Groff 1976, Hittenrauch 1976, Wengert 1976). Recent development of waferboard technology to utilize aspen is changing this.

Most of the available information about thinning aspen comes from the Lake States and Canada, where growing conditions and rotation ages are different than those in the Rocky Mountain West. The degree of applicability of this information to aspen in the West is unknown. Because aspen is self-thinning, decisions about thinning it usually are based on economics, not on any silvicultural necessity.

Kinds of Thinning

Thinnings are classified as commercial or precommercial. In commercial thinning, some or all of the trees cut can be sold to help pay thinning costs. In the West, opportunities for commercial thinning of aspen have been very infrequent.

Thinnings also are classified by the criteria used to determine what trees to cut and what to leave. (1) In thinning from above, mostly the larger trees are cut, and the smaller ones are left. This process, for example, may be applied in early commercial thinnings. (2) Thinning from below removes the smaller trees, leaving the larger trees with greatest vigor and best and earliest potential for high value products. (3) Crop-tree thinning is a refinement of thinning from below, in which the most promising trees are selected for careful tending throughout the life of the stand. Thinning removes only those trees that compete with the best ones. In dense stands with many good trees, there may be little difference between crop-tree thinning and thinning from below. (4) In mechanical thinning, a predetermined spacing is the primary criterion. Most young sucker stands are so dense that mechanical thinning permits leaving the best of several stems at most spacing points. In this case, mechanical thinning becomes essentially a thinning from below.

Growth Effects

Thinning affects diameter growth but not height growth. Height growth, instead, largely depends on site quality. In aspen stands in the West, it appears that thinning will release the diameter growth of aspen of most ages and sizes (fig. 1). Generally, thinning increases diameter growth more on trees that previously had not grown well; but the trees that had grown fastest also respond to thinning, and they maintain their dominant position in the stand (Baker 1925, Bella 1975, Bickerstaff 1946, Sorensen 1968, Steneker 1964, Steneker and Jarvis 1966).

Thinning Very Young Stands

Thinning a new sucker stand does not appear to increase diameter growth. For 3 years after a dense 1-year-old sucker stand in Minnesota was thinned, it was necessary to cut the dense resprouting to retain the thinning (Strothmann and Heinselman 1957). After 15 years, average diameters of the best 400 trees per acre (988 trees per ha) were only slightly larger than those on unthinned plots; and the best 200 trees had virtually the same diameters on thinned and unthinned plots (Sorensen 1968). Schlaegel (1972) reported that, after 20 years, the unthinned plots had the best quality trees. Trees on the most heavily thinned plots were extremely limby and had poor bole form. He concluded that 1-year-old stands were too young to thin.

However, others have had positive results where young stands have been thinned (fig. 2). In central Canada, 2 years after very dense sucker stands 3, 5, and 6 years old were thinned (Bella 1975), there was heavy resprouting; but the new sprouts were overtopped and seemed destined to decline and die. Diameter growth of the best 400 trees per acre (988 trees per ha) in the 5- and 6-year-old stands was substantially better on thinned plots. In northern Minnesota, plots in a 7-year-old sucker stand on an excellent site were thinned from 3,750 stems per acre (9,266 stems per ha) to 695 stems per acre (1,717 stems per ha) (equivalent of an 8- × 8-foot (2.5- × 2.5-m) spacing), when the dominant trees were at least 20 feet (6 m) tall. Twelve years later, the thinned plots had about nine times as much volume in stems larger than 5 inches (13 cm) diameter than did the unthinned plots (Hubbard 1972).

Figure 2.—A thinned 8-year-old sprout stand on the San Juan National Forest, in Colorado.

Figure 3.—Thinning pole-sized aspen stands has produced varied growth results in other areas and may not be justified in longer lived aspen stands in the West (see the ROTATIONS chapter).

Thinning in Older Sapling Stands

Zasada (1952) concluded that the sawtimber rotation had been shortened 10 or 15 years by thinning a Minnesota stand on a good site, at age 20, when the dominants were about 37 feet (11 m) tall. At age 40, the plot with a 15-foot (4.6-m) spacing had 2.5 times as much sawtimber volume as the unthinned plot.

In Manitoba, 14-, 19-, and 23-year-old stands were mechanically thinned to spacings of about 8 × 8, 10 × 10, and 12 × 12 feet (2.5 × 2.5, 3.1 × 3.1, and 3.7 × 3.7 m). Ten years later, most of the thinned plots had substantially more trees in large diameter classes, and it appeared that they would produce a veneer-log harvest about 10 years earlier than the unthinned plots; but no strong recommendations could be made about best spacings (Steneker 1964).

In a detailed analysis of thinning studies in central Canada, Steneker and Jarvis (1966) suggested thinning to 60 square feet basal area per acre (13.8 m² per ha) in sapling stands. However, Perala[1] suggested that the basal area for best growth may change with age.

Thinning in Pole Stands

The results of thinning from below in pole-sized aspen stands are mixed and inconclusive (fig. 3). Thinning an aspen stand in Ontario at age 40 resulted in a marked release. Ten years later, at age 50, even the largest trees on the unthinned plots had not kept pace with those on the thinned plots (Bickerstaff 1946). In contrast, in Minnesota, a 37-year-old stand on a good site was thinned from 113 to 58 square feet basal area per acre (26 m² to 13.3 m² per ha). Ten years later, the 150 largest trees per acre were the same size on the thinned and unthinned plots (Schlaegel and Ringold 1971). When harvested at age 52, however, the thinned plots yielded somewhat more veneer logs than the unthinned plots.[1] Thinning in two other Minnesota stands at ages 31 and 34, on good sites, also resulted in somewhat greater veneer volume 15 years later (Hubbard 1972). Five years after 40- to 70-year-old aspen stands in Utah were thinned, the larger trees showed little or no improvement in diameter growth; but growth had been stimulated in smaller trees (Baker 1925).

On excellent sites in the West (80 feet (25 m) or taller at age 80), some trees may reach merchantable size several years before rotation age, allowing a commercial thinning from above (Curtis 1948). In such an operation in Minnesota, the thinned plots produced no more volume of total products—thinning and final harvest combined—than the unthinned plots (Heinselman 1954). The trees left in the thinning from above did not grow as well as dominants on the unthinned plots, and the best trees, with the greatest potential for high value products, had been harvested for low value products during thinning.

Again, the applicability of these results to aspen in the West is unknown. Martin (1965) described a 70-year-old stand in Arizona that had been thinned from above at age 50. The stand remained healthy; growth on the residual trees had improved, and some were approaching sawtimber size. Shepperd[2] observed several aspen stands in Colorado in which residual stems showed release after a partial cut or commercial clearcut. However, many of these stems were damaged during logging, and were no longer desirable growing stock. Research in progress may help resolve uncertainties about thinning pole-sized aspen in the West.[2]

Other Thinning Effects

Thinning may affect wood quality, incidence of disease and insect attacks, esthetics, use of the stand by livestock and wildlife, regeneration costs, and, in some cases, genetic character.

Wood Quality

Heavy thinning in a 1-year-old sucker stand resulted in excessive limbiness and poor bole form (Schlaegel 1972). Heavy thinnings in a 20-year-old stand and a 13-year-old stand also were followed by poor pruning and reduced log quality (Brinkman and Roe 1975, Zehngraff 1949). Thinning that results in greater persistence of live branches in aspen, will cause larger knots and more product degrade attributable to discoloration, because stain spreads through the wood from the bases of these live branches (Hook and Sucoff 1966). Specific gravity and strength of wood laid down after thinning is likely to be slightly lower; but this usually will not appreciably reduce the value of aspen for lumber or veneer (Kennedy 1968, Paul 1963) (see the WOOD UTILIZATION chapter).

Diseases and Insects

Ewan (1960) suggested that opening a stand by thinnings or partial cuttings may increase attacks by the poplar borer. Such attacks directly affect the tree's health, cause product degrade because of the discoloration that spreads from attack sites and galleries (Graham et al. 1963, Hook and Sucoff 1966), and could introduce disease (Graham and Harrison 1954) (see the INSECTS AND OTHER INVERTEBRATES, and DISEASES chapters). However, careful thinning to not too large a spacing ordinarily does not increase borer attacks much, especially in sapling stands whose canopies tend to close again quickly.

Sunscald can damage pole stands opened too strongly by thinning or other events (Bickerstaff 1946, Hinds 1976, Hubbard 1972). It has not been reported after even heavy thinning in saplings.

Thinning may increase fungal diseases in aspen (Jones 1976) (fig. 4). In the Lake States and Canada, a larger percentage of trees were infected and killed by hypoxylon canker on thinned than on unthinned plots (Anderson 1964, Bickerstaff 1946), even where all visibly infected trees had been removed during thinning (Anderson and Anderson 1968). Preliminary data from a pole stand thinning study in Colorado showed an increase in cankers and subsequent mortality on the treatment with the most trees removed.[2]

In stands with abundant bark wounds (usually caused by logging, sunscald, or vandalism), sooty-bark canker is a major element in a complex of factors that often causes heavy mortality. However, sooty-bark outbreaks have not been found in thinned stands of saplings.

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[1] *Personal communication with Donald A. Perala, North Central Forest Experiment Station, USDA Forest Service, Grand Rapids, Minn.*

[2] *Data and/or detailed information on file at the Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo.*

Careful thinning of saplings causes few bark wounds, and this size of stem may not be susceptible to sooty-bark infection. The risk of sooty-bark infection after thinning or partial cutting in pole-sized stands is greater. Bark wounding of the residual trees is much more likely, especially if the thinned stems are removed from the stand.

Esthetics

The esthetics of a thinned stand involves more than the appearance of the stand itself (see the ESTHETICS AND LANDSCAPING chapter). A person can see farther into, or through, a thinned stand (figs. 5 and 6). Where forest lies between the road and a lake or other vista, thinning may be desirable to provide a better view (Esping 1963). For maximum wood production, thinning probably would be done to a semiregular spacing—a uniform spacing that is limited by the occurrence of satisfactory trees. This would make most efficient use of growing space. But, if visual diversity is desirable, then thinning in a deliberately irregular pattern may be preferable along roads, streams, and other esthetically strategic foreground views. More closely spaced groups may be left and small gaps may be created (see the MANAGEMENT FOR ESTHETICS AND RECREATION, FORAGE, WATER, AND WILDLIFE chapter). Such thinning patterns also can take advantage of the irregular or clumped stem distribution found in some clones.

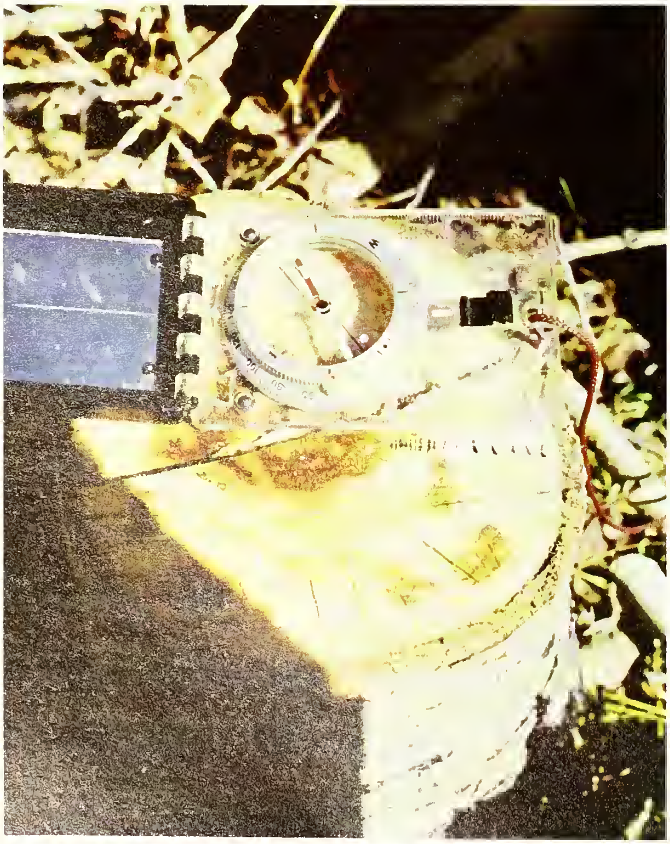

Figure 4.—This stem was damaged during a commercial thinning from above. Although diameter growth increased, the stem subsequently became infected with decay.

Figure 5.—An unthinned, 65-year-old stand.

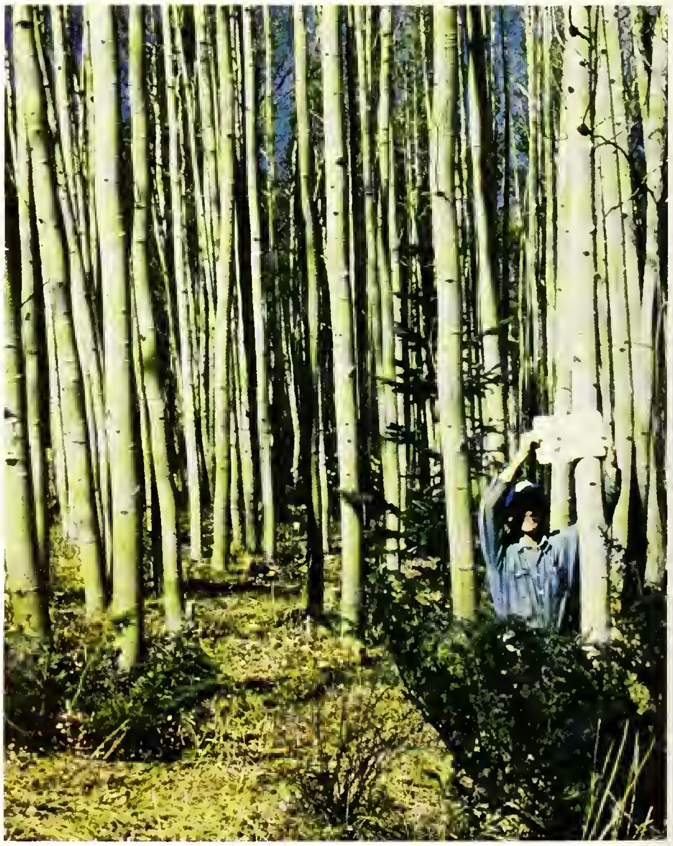

Figure 6.—The same stand after a thinning which removed all dead stems and 25% of the live basal area.

Use by Livestock and Wildlife

Very dense stands of aspen through the sapling stage are used lightly by cattle. Access would be improved by thinning, thereby permitting increased use of understory forage.

The effect of thinning on the quantity or quality of forage is not clear. Harper,[3] and Severson and Kranz (1976) found herbaceous understories were similar beneath open stands of aspen and beneath dense stands. But, these were all unthinned stands on assorted sites, rather than thinned and unthinned plots on the same or similar sites. At least on one Utah site, partial cutting (removal of 50% of the larger trees) increased understory production 36% for 3 years (Smith et al. 1972). The grass-forb ratio is commonly lower in dense young stands than in open stands. If the grass-forb ratio is increased by thinning, and if thinning increases production, then thinning makes the forage more attractive to cattle, and more abundant as well as more available to all ungulates. Also, thinning may cause a brief surge of suckering (Bella 1975), which can provide temporary browse for both livestock and wildlife (see the FORAGE chapter).

Thinning may have adverse impacts on the use of an area by animals. Poles or large saplings that are felled and left create obstacles that inhibit use of the stand by large animals. In Arizona, Reynolds (1969) found thinned stands that were used less than unthinned stands by elk, deer, and livestock. This makes early thinning more attractive for wildlife habitat, because the felled material is small, decays rapidly, and would be a lesser and more temporary hindrance.

Dense aspen stands through the smaller sapling size class provide good habitat for ruffed grouse, snowshoe hares, and several other species of wildlife (see the WILDLIFE chapter). They also provide abundant browse for wild ungulates. Thinning markedly reduces the value of young aspen stands as habitat and as a food source for these species. Thinning sapling aspen stands gives them a structure somewhat similar to a typical pole-sized or mature aspen stand. For wildlife, the value of the dense young stand is lost (fig. 7). In the West, the prevalent naturally thinned stands of pole-sized aspen currently provide adequate wildlife habitat with that structure.

Regeneration Costs

Unthinned stands carried to a sawtimber rotation have many stems too small to use as sawlogs (fig. 8). If these smaller stems are unmerchantable, then cutting or killing them during clearcutting adds to harvesting costs. If they are felled during harvesting, they also contribute to logging slash, and thereby limit animal access and movement, add to fuels, and possibly retard sucker regeneration by excessive shading. Yet, they must be cut or killed to promote a top-quality stand of new suckers. Thinning such stands from below while they are in the sapling stage would remove most of these subdominant trees (Zasada 1952). But, the question remains, would thinning many small saplings at age 15 be less costly than treating the unmerchantable small trees that remain at the harvest cut at age 90? Also, bole sizes that currently are not merchantable may be in demand when the stand is clearcut 75 years later, as technology and the economic situation changes. Therefore, thinning to reduce regeneration costs many years later is a very uncertain practice.

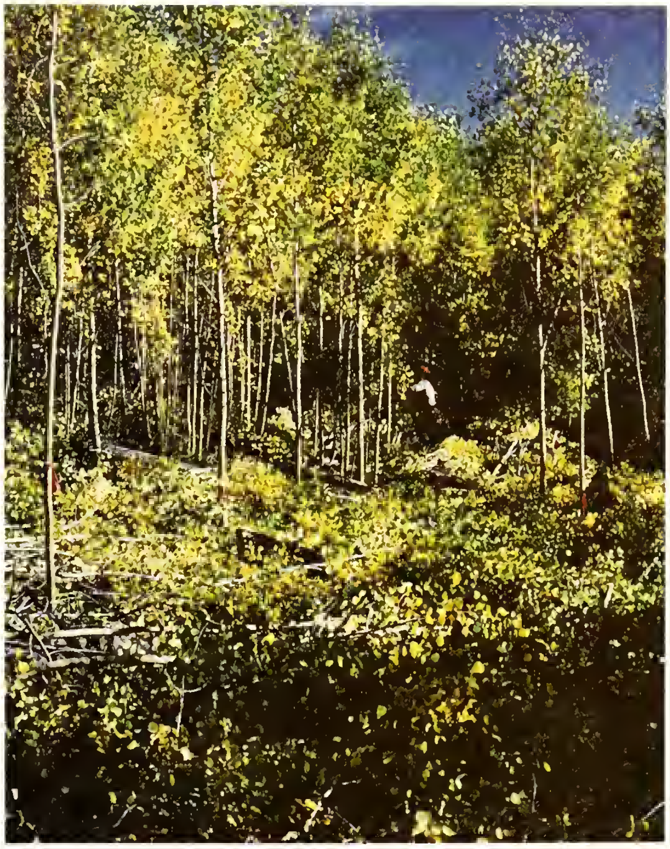

Figure 7.—Hiding cover is lost when young aspen stands are thinned.

Genetic Effects

In the Great Lakes region and central Canada, clones usually are small and often intermingled (Barnes 1966, Kemperman and Barnes 1976, Steneker 1973). Thinning can be used to improve the genetic makeup of such stands by discriminating against inferior clones (Perala 1977, 1978b; Steneker 1974; Wall 1971). Aspen stands in the West commonly consist of large, discrete clones. Genetic improvement of such stands by thinning is possible only along the clonal boundaries; good clones may be expanded and poor ones reduced in area. To do this, poor clones should be removed while keeping a sufficient overstory from good clones and other trees to suppress and ultimately kill regeneration from poor clones.

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[3] *Harper, K. T. 1973. The influence of tree overstory on understory production and composition in aspen forests of central Utah. Society of Range Management [Boise, Idaho, February 1973]. Abstract of paper 26:22.*

Other Effects

In sapling or pole-sized mixed stands of aspen and conifers, thinning the aspen from above will increase conifer growth rates, especially conifer understories (Jarvis et al. 1966) (fig. 9).

Thinning a dense aspen stand by basal spraying or injection of individual trees with herbicides may have unwanted results. Many herbicides can be translocated through the interconnected root system to untreated leave trees, killing much more of the stand than desired (Brinkman and Roe 1975, Hubbard 1972).

Thinning Recommendations

Felling residual trees and thinning new stands may contribute to better growth and stand structure. Ordinarily, only stands on sawtimber sites should be thinned. However, precommercial thinning may be uneconomical, especially if there is a potential market later, at the time of harvesting, for the smaller boles that cannot be used for sawlogs. Clones that are distinctly poor should not be thinned, except to discourage them where they contact better clones.

If a stand will be thinned only once, it seems best to wait until the dominants are about 25 feet (8 m) tall and 2 to 3 inches (5-8 cm) in diameter. On good sites in the West, this is at about age 15. Thin to a spacing of roughly 8 × 8 feet (2.5 × 2.5 m), which leaves about 700 trees per acre (1,730 trees per ha) and usually removes between 3,000 and 15,000 per acre (7,400 to 37,000 per ha). Retain only dominants and very good codominants. With spacing closer than 8 × 8 feet (2.5 × 2.5 m), the trees become crowded again in a few years. Wider spacings, or even 8- × 8-foot (2.5- × 2.5-m) spacing among somewhat smaller trees, may lead to bushy crowns that tend to persist and cause poor quality trees.

Figure 8.—Some mature aspen stands contain many unmerchantable stems.

Figure 9.—Thinning or removing the aspen overstory in this mixed stand would improve conifer growth and allow quick conversion to conifer management.

To thin a stand twice may be more expensive than thinning once; but it may produce better results.[4] The first thinning could be made when dominant trees are about 15 feet (4.6 m) tall (age 5 to 10), to a spacing of roughly 5 × 5 feet (1.5 × 1.5 m), or a density of approximately 1,500 trees per acre (3,700 trees per ha). In a typical aspen stand in the West, this will require cutting 5,000 to 20,000 stems per acre (12,000 to 50,000 stems per ha); but, at this age, most of them will be 1 inch (2.5 cm) or less in diameter—easy and inexpensive to cut. When the dominant and codominant trees that were left have reached about 35 feet (11 m) tall, they will be somewhat crowded again. Many will be about 4 inches (10 cm) d.b.h. Then, the stand should be thinned to an irregular spacing of about 15 × 15 feet (4.6 × 4.6 m), with deviations to keep only the best 200 trees per acre (494 trees per ha). Thinning at this stage of stand development requires cutting about 1,200 trees per acre (3,000 trees per ha). Trees of the sizes considered are easy to control in felling; with proper care during cutting, the remaining trees will not be damaged.

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[4] *Personal observations and conclusions by John R. Jones.*

Among trees 35 feet (11 m) tall, spacing wider than 15 × 15 feet (4.6 × 4.6 m) is undesirable. In Minnesota, thinning aspen to a 20-foot (6-m) spacing, when dominants stood between 35 and 40 feet (11-12 m) tall, resulted in large persistent limbs and impaired quality at final harvest 20 years later. A 15-foot (4.6-m) spacing did not (Zehngraff 1949). A 15- × 15-foot (4.6- × 4.6-m) spacing at this stage will temporarily underutilize the site, but delays later crowding.[1] A 10-foot (3-m) spacing resulted in somewhat poorer growth than a 15-foot (4.6-m) spacing, presumably because the trees became crowded again too soon.

It may be tempting for the manager, to satisfy some markets, to permit commercial thinning from above in previously unthinned stands of pole-sized aspen. Thinning such stands is particularly risky, however. Ordinarily, it will be better to supply the market by clearcutting stands of rotation age or older.

If pole-sized stands are thinned from above, retain at least 60 square feet per acre (13.8 m^2 per ha), and remove no more than 30–40% of the basal area.[1] Otherwise sunscald may result. Extreme care should be used in felling and removing trees in these stands. No logging should be done during the spring and early summer, when the bark is easily peeled from the trees. Trunk wounds then are more easily made, are often much larger, and take longer to heal. Wounding is likely to result in disease, or at least will severely reduce ultimate product value. Wounding of the ultimate crop trees, regardless of how slight, cannot be tolerated in a thinning operation.

Directional felling, and felling and skidding in two or more stages may be necessary to prevent damage to crop trees. Skidding should be done with small machines equipped with winches to reach into tight places. High stumps should be left at key turning points during skidding operations to protect residual trees, and then removed later. Full-tree skidding and tree-length skidding should not be used. Lengths skidded should be short enough to be removed without scraping or wounding the bases of remaining trees.

OTHER INTERMEDIATE TREATMENTS

Irrigation and Fertilization

Aspen will respond to both irrigation and to fertilization on sites where water or nutrients are not in optimum supply. For example, Van Cleve (1973) demonstrated large but irregular growth increases following fertilization of poor quality, 15-year-old aspen growing on an impoverished site in Alaska. Einspahr et al. (1972) found that irrigation alone, on a sandy loam in Wisconsin, increased the 3-year volume growth of a sapling stand 60% over that on untreated plots. The effect was primarily on height growth. Fertilization without watering improved volume growth 16%, mainly by increased diameter growth. On plots which were both watered and fertilized, volume growth was 140% greater than on untreated plots.

Although many of the aspen sites in the West are quite fertile, for maximum growth on high-value sites, the addition of some major nutrient, frequently nitrogen, and sometimes of trace elements such as iron or zinc, may be helpful. During times of high moisture stress, irrigation alone may markedly increase aspen growth and understory forage production.

However, it is impractical to irrigate or fertilize aspen on most sites in the West for the usual objectives of forest or range management. Irrigation and perhaps fertilization may be applied when planting aspen on new sites where it is needed to successfully establish the trees. In unique circumstances, these treatments also may be applied to small key locations to improve esthetics by speeding the growth of planted or natural aspen. If aspen management in the West progresses to the point of using selected hybrids in plantations for rapid production of high-value products, then fertilization or irrigation may become worthwhile.

Protection from Disease

There are no proven forest stand treatments that successfully prevent or control disease in aspen. Maintenance of a well-stocked stand, minimizing wounding of stems and control of damaging agents (e.g., fire, ungulates, and humans), and harvesting at the proper rotation age are the best management recommendations that can be made today. However, there have been some suggestions worth noting.

To limit heartrot by *Phellinus tremulae*, Meinecke (1929) recommended sanitation cutting and removal of culls, blowdowns, and high risk trees. However, control of heartrot is desirable only in lightly infected or uninfected stands which are to be harvested for sawtimber or veneer. In those stands, protection from wounding and proper rotation lengths should provide adequate control. Once stands are heavily infected, clearcutting is the only control.

To control sooty-bark or black canker, Baker (1925) recommended clearcutting infected stands and burning the slash. But, infected leaves are sources of inoculum (Zalasky 1965), and flying insects are both reservoirs and vectors of the disease (Hinds 1972b). It is doubtful, therefore, that Baker's suggestions would provide significant protection to nearby healthy stands.

Protection from Insects

Direct control of insects in the aspen forest usually has not been practical, because the value of aspen has not warranted expensive controls, and because the impact of most insects has not been critical. Also, the environmental side-effects from chemical pesticide spraying usually has not been acceptable in the aspen ecosystem. As with diseases, maintenance of a well-stocked stand and protection from wounding perhaps is the most practical method of coping with insects in the aspen forest. Direct insect control may be appropriate in high-value, special interest stands; where aspen is planted, especially as an ornamental; or during prolonged outbreaks of tent caterpillars.

In British Columbia, an outbreak of the aspen leaf miner was effectively controlled by spraying in the spring with Thiodan and Rogor[5] (Condrashoff 1962). Page and Lyon (1973) reviewed eight chemical insecticides effective on the western tent caterpillar. The western tent caterpillar also has been controlled by spraying with a water suspension of a nuclear polyhedrosis virus mixed with *Bacillus thuringiensis*. This has been very effective in field trials, and has the advantages of being host specific, persistent overwinter in the environment, and contagious within the host species (Clark 1955, 1958; Stelzer 1965, 1967, 1968).

Protection from Mammals

Domestic livestock, wild ungulates, rodents, and hares utilize aspen as food and can have a measurable impact on some stands (see the ANIMAL IMPACTS chapter). Most animal damage can be prevented by careful husbandry of domestic livestock and by population control of wild game species. Because most aspen ranges in the West are grazed by cattle or sheep and have a significant population of wild ungulates, grazing management and game management are important to these forests. Other animals seldom need to be controlled; even when they do, economically practical control measures often are unacceptable.

Deferral of grazing, or fencing clearcuts or burns will control livestock damage during the critical regeneration years. Control of damage by big game during this stage of stand development requires game population control.

Although sapling- and pole-sized aspen stands are susceptible to damage resulting from bark removal by elk, perhaps moose, and porcupines, and from cutting by beaver, control is seldom necessary. However, where elk are concentrated in winter, especially because of artificial feeding, extensive browsing and bark damage may become common, and can contribute to stand deterioration (Hinds and Krebill 1975, Krebill 1972) (fig. 10). Under these circumstances, control is needed to retain the aspen.

Where beavers are considered a serious problem, the only currently acceptable control is removal by trapping. Usually, however, after beavers harvest a particular aspen stand, they exhaust their food supply and are forced to move on. The aspen then sucker in abundance, and a new stand develops.

Miscellaneous Treatments

Some young stands have several older aspen scattered through them. The new stand would benefit from the removal of the older trees; but if cut, their crowns could do considerable damage in falling. It usually is best to girdle the old trees instead of felling them. However, care must be taken to remove a band of bark large enough to prevent regrafting. Stems girdled with a single chainsaw cut have been observed to recover.[6] Girdled, they ordinarily will remain standing until most of their branches have fallen. When a snag goes down, it normally does much less damage than if it had been felled alive. Old, girdled culls may temporarily serve as nesting trees for cavity-nesting birds. It may be desirable to leave culls ungirdled if they already have nesting holes.

Figure 10.—Repeated bark stripping by elk has heavily damaged this stand.

Salvage logging in aspen stands is seldom economical or advisable. An exception would be if the entire stand has been killed by fire, and if it can be logged during the first few months afterwards. Otherwise, to enter an aspen stand to salvage some trees creates too much risk of damage to the remaining stand.

Shearing might be considered an intermediate treatment to regenerate understocked or derelict stands, although it really is a form of non-commercial clearcutting. Perala (1983) successfully used this technique in Wisconsin to bring grossly understocked stands up to potential stocking and growth. He recommended shearing during the dormant season to avoid excessive scarification and disturbance of aspen roots.

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[5] *The use of trade and company names is for the benefit of the reader; such use does not constitute an official endorsement or approval of any service or product by the U.S. Department of Agriculture to the exclusion of others that may be suitable.*

[6] *Personal observations by Wayne D. Shepperd.*

ROTATIONS

John R. Jones and Wayne D. Shepperd

The rotation, in forestry, is the planned number of years between formation of a crop or stand and its final harvest at a specified stage of maturity (Ford-Robertson 1971). The rotation used for many species is the age of culmination of mean usable volume growth [net mean annual increment (MAI)]. At that age, usable volume divided by age reaches its highest level. That volume varies according to standards of usability. For example, if the pulpwood market accepts the entire bole plus branches, then the MAI of aspen grown in the Lake States for pulpwood would culminate between 20 and 30 years (Benson and Einspahr 1972, Einspahr and Benson 1968, Ek and Brodie 1975, Perala 1973).

In the West, however, most markets have been for larger logs (sawlogs and veneer logs), and the situation is complicated by the frequency of two-aged and uneven-aged stands. Also, most aspen in the West lives longer and grows more slowly than aspen in the Lake States (fig. 1). For management purposes, only even-aged stands are considered here; it is the only aspen stand structure suitable to manage for wood products.

Figure 1.—Many existing aspen stands in the West are at or beyond rotation age.

Tables and equations for net MAI of aspen are being developed for application in the West (fig. 2).[1] Gross MAI, in board feet, culminates at about 140 years (Baker 1925); but, gross MAI is not a suitable criterion for setting aspen sawtimber rotations. Decay becomes important from 80 to 90 years of age and older (Baker 1925, Meinecke 1929). They suggested rotations of 70 to 110 years, and usually not more than 80 to 90. At that time, Meinecke (1929) found that stands older than 80 years commonly were fire scarred and had serious decay; fire scars were the infection sites for 68% of all cull resulting from decay. (For a discussion of decay in aspen, see the DISEASES chapter.)

In Colorado, Davidson et al. (1959) studied decay in stands 41 to 170 years old. Decay differed greatly among similar aged stands on the same site class. Some of that variation was a result of decay associated with fire scars, especially in the older stands. Some variation also could be attributed to the absence or rarity in some stands of the principal decay fungus, *Phellinus tremulae*. Shepperd (1981) found rot to be present in about 80% of 140 aspen stands in Colorado and southern Wyoming; but, it affected only 20% of the stems in those infected stands. Incidence of rot was significantly greater in stands older than 100 years.[2]

Meinecke (1929) stated that fire protection would allow longer rotations for aspen. Currently, few stands in the 80- to 90-year age class are fire scarred, and many are just beginning to have appreciable sawlog volume. They will become merchantable in another 20 years, if they remain without serious decay. The best stands of aspen sawtimber in the West are older—many beyond 110 years. These are stands with many trees containing logs of veneer quality. Although some trees are cull because of, or have some volume loss caused by basal rot, overall the stems are sound.

In the past, considerable attention has been given to the volume of waste resulting from aspen decay, with little mention of the volume wasted in trees too small to use at the 80- to 90-year rotation age. If the stand is cut then, all trees must be felled regardless of merchantability, or they become a major deterrent to the development of a new even-aged stand. Those small trees, although sound, effectively are cull, too. They represent an appreciable portion of the biomass in 80- to 90-year-old stands. Many have the potential of becoming merchantable sawlogs in

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[1] *An aspen subroutine for the even-aged stand growth model RMYLD has been completed at the Rocky Mountain Station in Fort Collins, Colo. This subroutine can predict the growth of aspen in the Rocky Mountains under several management strategies and rotation lengths.*

[2] *Data on file at the Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo.*

another 10 to 20 years. Typically, there is a period beyond age 90 when ingrowth into merchantable size classes and into higher value classes is greater than the increase in decay losses. That ingrowth may make the difference in a stand being salable or not salable for sawlogs.

Considering the decay figures of Davidson et al. (1959), and allowing for their inclusion of fire scarred stands, a tentative sawlog rotation of 110 years is suggested for stands with site indexes greater than 75 feet, and 120 years for stands with site indexes between 60 and 75 feet. Stands with site indexes less than 60 feet are unlikely to become merchantable for sawtimber. These rotations should be applied with flexibility and good judgment. External indications of disease might dictate cutting sooner. If diameter growth remains good at rotation age, and conks or serious cankers are minor, the stand may be retained longer, especially if many trees are growing into merchantable or veneer classes.

The merchantability standards and, thus, the rotation ages, change appreciably when other fiber products, such as waferboard, are considered. Stems down to a 3-inch (7.5-cm) top can be debarked, chipped, and effectively used as the raw material for waferboard or similar products (see the WOOD UTILIZATION chapter). Also, the minimum log length is 8 feet (2.5 m), which permits removal of much rot and defect in the harvesting process. Crook, sweep, and other defects common to sawlogs are not a problem, nor are stands containing a wide distribution of stem diameters.

Because stem size does not seriously limit utilization of aspen for waferboard, rotation ages can be shortened to as little as 40 or 50 years, depending upon the site indexes.

However, this type of management is unlikely in most situations. A realistic approach, considering the requirements for other resources as well as the multiple product markets that are expected to develop, would be an intermediate rotation of 80 to 100 years. This would produce both waferboard chips and sawlog volumes in stands still young and healthy enough to avoid large volume losses resulting from decay.

On sites without significant potential for fiber production, volume growth may not be a factor in setting rotation ages. To some extent, this also may be true of some productive sawtimber sites, especially those managed for multiple uses. For example, some stands, or clones within stands, might be burned, sprayed with herbicide, or otherwise killed at rotations of 30 or 40 years to provide maximum forage production for wildlife. Conversely, some stands may be retained until they are seriously deteriorating, at perhaps 130 years, to provide better forest scenery, particularly along roads. Some esthetically pleasing stands that are regenerating successfully without treatment may be continued with no rotation at all. Still others may be managed under an uneven-aged system using a group selection cutting method to provide stands with vertical canopy diversity for wildlife habitat or esthetic purposes.

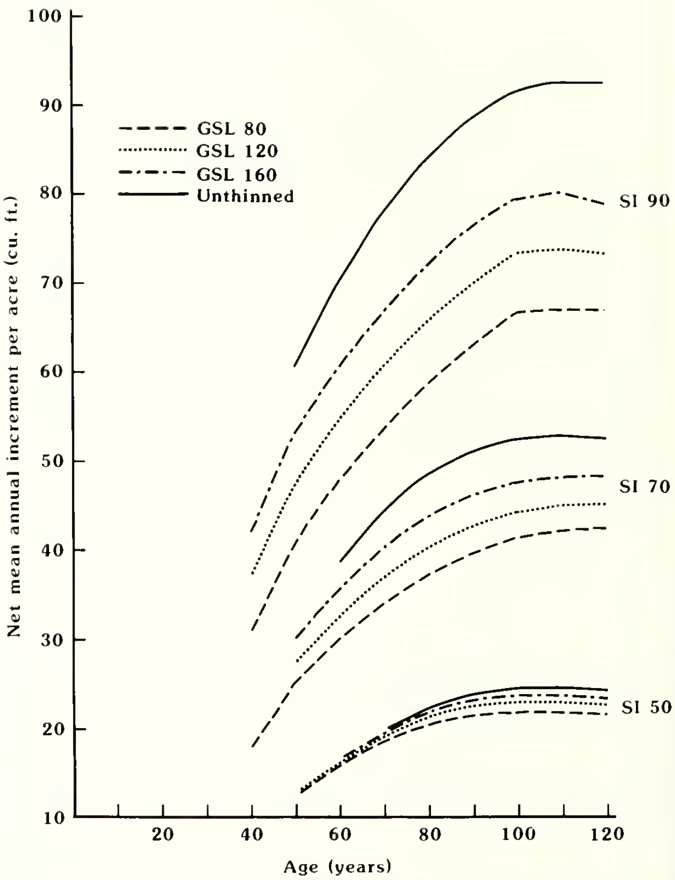

Figure 2.—An RMYLD simulation of net mean annual increment for thinned and unthinned Rocky Mountain aspen stands at three site index classes. Growth of thinned stands was based on a single precommercial thinning at age 20.

HARVESTING

John R. Jones and Wayne D. Shepperd

Harvesting is the removal of produce from the forest for utilization. It includes cutting, any further initial processing, such as topping and trimming, and extraction (Ford-Robertson 1971). Commercial intermediate cutting, such as commercial thinning, as well as regeneration cutting are included. Harvesting and the income that it produces sometimes is regarded as an end in itself. However, it also may be used as a means of renewing or improving a forest. Harvesting is a viable method of retaining aspen forest on many sites where it would otherwise disappear because of natural succession.

In the West, aspen traditionally has been harvested for sawtimber, with excelsior and other markets sometimes taking smaller material. Aspen fuelwood harvests, which utilize considerably smaller and more crooked material, also have become significant near metropolitan areas. However, harvesting aspen for flakeboard may soon account for most of the aspen volume cut in the West.

Logging Considerations

Aspen in the West generally has been logged using systems designed to harvest conifers (fig. 1). This often is inefficient, compared to systems that could be designed specifically for harvesting aspen (Groff 1976). Sawtimber diameters in aspen are small compared to those of most associated conifers (Groff 1976). Unlike forests of coniferous sawtimber, aspen seldom grows in large blocks, but commonly are small and somewhat scattered, on gentle to moderate slopes. Consequently, harvesting equipment should be easy to move from stand to stand and ordinarily does not require a high production capacity. Groff (1976) suggested self-loading trucks and small tractors.

Figure 1.—Until recently, most aspen in the West has been harvested as sawlogs.

Logging these scattered, small stands may require construction of a substantial length of access roads for the relatively small timber volumes to be harvested. If harvesting is desirable for values other than timber products, then other functions might be expected to contribute to the cost of road construction. This seems especially desirable if high road construction standards are required.

If aspen harvest alone is to pay for the cost of building roads to access merchantable aspen stands, a comprehensive harvest schedule and transportation system plan should be developed. This enables a series of timber sales to share road building costs and to utilize a common transportation system. Control and timing of vehicles on such a system will allow roads of minimum design standards and construction costs. (See the WOOD UTILIZATION chapter for a discussion of utilization opportunities and feasibility.)

Time of Logging

Season of logging is influenced by many factors, including mill capacity, markets, inventory, ease of veneer peeling, weather, fire-hazard, and aspen regenerative capacity.

Spring or early summer logging offers the advantage of easy peeling for those milling processes requiring bark removal. Logs are lighter in the summer because of reduced water content (Yerkes 1967). This allows more efficient skidding, loading, and hauling. Sawlog utilization also may be better with logs cut in summer. However, spring logging may affect the quantity and quality of subsequent suckers (see the REGENERATION chapter).

In contrast, soil compaction and erosion hazard are greatest if logging is done with heavy equipment when soils are saturated in the spring. Logging at this time is most damaging to aspen roots, also, which can reduce suckering. Also, because root carbohydrate reserves are lowest in spring (see the VEGETATIVE REGENERATION chapter), harvesting at that time can further reduce sprouting.

Commercial thinning when the cambium is active and the bark is easily peeled from the trees (from budburst in spring until midsummer) can result in more and larger wounds on residual trees, and serious disease problems (fig. 2).

The potentially detrimental effects of spring harvesting may outweigh any logging and processing benefits, making harvesting during the dormant season, when soils are dry, frozen, or snow-covered, most desirable. However, in much of the West, heavy winter snowpacks and late spring melt probably will limit the harvesting season to between mid-summer and late autumn—a realistic compromise.

Cutting

Trees may be felled, and then skidded whole with no further cutting at the felling site. They also may be felled, limbed to the upper limit of merchantability, and topped out for skidding as a full merchantable tree length. Or, they may be felled, limbed, and cut (bucked) into logs prior to skidding.

Lamb (1967) criticized bucking aspen to a single standard length in the Lake States. It was more profitable to maximize grade by bucking into variable lengths while taking into account stem form, defects, and the end product. Whether aspen is bucked at the stump or at a gathering place is likely to be determined in part by skidding considerations.

Figure 2.—Bark can be peeled from aspen easily in the spring, causing extensive damage to residual stems if any form of partial cutting is used.

Figure 3.—Care must be taken in skidding to avoid damaging the clonal root system.

Slash disposal practices used in conifer harvesting are not applicable for aspen in the West. Logging aspen produces less slash than conifers; aspen slash also decomposes rapidly. Slash can be left where it falls. Lopping may be desirable to increase forage use by ungulates. If overbrowsing of the new sucker stand is feared, tops can be left unlopped. If regeneration of even-aged aspen is wanted, any advanced aspen regeneration should be cut at the time of harvest (see the REGENERATION chapter).

Skidding

Choice of skidding methods most often is affected by economics, utilization standards, and available equipment. Multiple-use benefits, such as esthetics and wildlife values, also help determine the method chosen. In Minnesota pulpwood operations, Zasada (1972) stated that skidding of entire trees (full-tree skidding), of full merchantable lengths (tree-length skidding), or of 100-inch (2.5-m) lengths all were equally acceptable for aspen regeneration.

Skidding operations that cause deep cutting or compaction of the soil result in fewer suckers and reduced sucker growth. Therefore, repeat skidding traffic should be kept to main trails as much as feasible (see the REGENERATION chapter) (fig. 3).

Full-tree Skidding

The available information on full-tree skidding of aspen comes from pulpwood operations in northern Minnesota (Zasada 1972; Zasada and Tappeiner 1969a, 1969b). Full-tree skidding does not seem widely suited to sawtimber logging of aspen in the West. Minimum merchantable top diameters for sawlogs are usually 6 inches (15 cm). Thus, a rather large part of each skidder load would be unusable, and daily volume production of merchantable material would be substantially reduced. If, however, the smaller material has utility as chips, it could be feasible to use full-tree skidding to a chipper located adjacent to the landing.

On-site slash is minimized with full-tree skidding (fig. 4). This results in favorable conditions for subsequent use by livestock and big game. Also, the logged site is easier to plant if conversion to light-tolerant conifers is desired. However, at least in the central and southern Rocky Mountains, seedlings of Engelmann spruce, Douglas-fir, and the true firs survive much better in the shade of downed timber or slash (see the NURSE CROP chapter).

With full-tree skidding, one or more limbing-topping sites are needed near the landing. The skidder stops at these sites long enough for limbs and tops to be cut from the trees before proceeding to the landing. This creates concentrations of limbs and tops, which should be piled and burned, or utilized. Otherwise, the piled slash could occupy 5-10% of the total area harvested, based upon aspen stocking and utilization standards in the West and upon Zasada and Tappeiner (1969a).

Figure 4.—Full-tree skidding was used in this clearcut. Soil disturbance and slash are minimized using this technique.

Because of potential damage to residual trees on the site, full-tree skidding is inappropriate for commercial thinning and entirely unacceptable where a coniferous understory is to be spared. Also, long-term site quality may be adversely affected by concentrating the nutrient-rich tops and limbs on a small portion of the area. Full-tree skidding is advantageous where advanced regeneration or understory shrubs are to be destroyed.

Tree-length Skidding

Usually, skidding full merchantable lengths of trees, without branches or tops, is more economical than skidding entire trees. Smaller skidders also may be used.

Premarked, main skid trails leading to the haul road or landings should be used for the bulk of repeat skidding traffic. Felling should begin halfway between these skid trails and proceed toward them. Trees should be felled in the direction away from the trail to which they will be dragged. When cutting has reached a main trail, skidding then begins with the trees closest to the trail. Skidding should be directly to the main trails, and then down them to the road or landing. It should not be cross-country from the felling site to the landing or haul road, except for trees lying close to them.

Skidding Shorter Lengths

The full merchantable tree length may be bucked into logs where it is felled, then skidded as individual logs to the landing. Bucking trees where they fall often is less efficient than bucking at a central point, and considerably more hooking is necessary to skid a given volume in shorter logs.

Skidding short lengths may be desirable if the stand being logged has a coniferous understory that needs protection from logging damage. Also, in commercial thinning operations, skidding should be in short lengths, unless it is done with extreme care. Skidding short lengths will considerably reduce damage to regeneration, or to the butts of aspen left after thinning.

Releasing a Coniferous Understory

Aspen harvesting may be used to immediately convert aspen stands with coniferous understories to conifer dominance (fig. 5). In those cases, great care should be taken to protect the conifers from damage during logging. Special logging methods, such as the use of herringbone skidding, may be appropriate. Other management actions to discourage aspen sprouting also may be necessary (fig. 6).

Herringbone logging is a system that may be used to release conifers. This method was observed in 1955 on a

Figure 5.—Conifer understories can be released by removing an aspen overstory, but extreme care is required.

Figure 6.—Three years after harvest, the conifers in figure 5 are again overtopped by aspen.

large sustained yield unit in the Midwest.[1] It probably is more applicable in the West than dray skidding. A large acreage of undulating terrain had a heavily stocked overstory of mixed jack pine (*Pinus banksiana*) and aspen about 85 feet (25 m) tall. Life-long crowding had resulted in narrow crowns. There was a fully stocked understory of balsam fir (*Abies balsamea*) and black spruce (*Picea mariana*) that were 5 to 15 feet (1.5-5 m) tall. To begin logging, narrow branch trails were cleared at right angles to the main skid trails. Each branch trail was the centerline of a cutting strip about 65 feet (20 m) wide. Cutting began at the end of the strip away from the main skid trail. All trees possible were felled away from the main skid trail at an acute angle to the branch trail. This formed a herringbone pattern, with the branch trail as the backbone and the felled trees as backswept ribs. Trees were bucked where they fell. The logs then were pulled to the branch trail with minimum lateral movement. Tractors stayed on the trails and winched the logs to them. As a result, after the dense overstory of aspen and pine had been removed, the understory of sapling fir and spruce remained essentially undamaged and fully stocked.

Other Harvesting Techniques

Many aspen stands in the West should be well suited to mechanical harvesting using feller-bunchers with accumulating shear heads to prebunch logs for later pickup by grapple skidders, or forwarders. Such equipment works well on moderate terrain and efficiently handles stem sizes commonly found in aspen stands in the West. Because most live branches are near the tops of aspen stems, delimbing attachments would not be needed.

Smaller diameter stands might be harvested effectively using small, radio controlled skidding winches similar to those developed in Europe. These devices allow one person to skid, buck, and deck several cords of wood per day. Damage to the residual stand and understory vegetation can be minimized by using skidding cones and snatch-blocks (attached to residual trees with nylon straps) to direct the movement of logs.

Small skyline logging systems (currently under development) also could be used to log aspen stands. They perform very well on steep ground, but they would not be appropriate in a thinning operation or where residual conifers are to be saved.

Walking harvesters also allow logging of aspen stands on terrain too steep for other equipment. These devices pull themselves across steep slopes on hydraulic legs and are equipped with accumulating shear heads to prebunch stems for later removal by crawler-skidders or cable systems.

Lynch (1983) described these devices in a publication on timber harvesting in the central Rocky Mountains. The increased demand for small and efficient equipment may provide new machines and techniques to harvest not only aspen, but the many acres of other small-diameter species, such as lodgepole pine, that grow in the West.

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[1] *Personal observation by John R. Jones, formerly Principal Plant Ecologist with the Rocky Mountain Forest and Range Experiment Station's Research Work Unit at Flagstaff, Ariz.*

MANAGEMENT FOR ESTHETICS AND RECREATION, FORAGE, WATER, AND WILDLIFE

Norbert V. DeByle

In the West, aspen forests have not been actively managed for wood products largely because of the lack of markets for quaking aspen timber from the Rocky Mountains (see the WOOD UTILIZATION chapter). Despite this, the aspen ecosystem has been used to provide a variety of resources and opportunities (see PART III. RESOURCES AND USES).

Although the aspen ecosystem can be managed for several resources simultaneously, on any given site, aspen usually has been managed primarily for a single resource. In situations emphasizing a single resource, high-quality clones on good sites are best suited for sawtimber, those on medium sites for other wood products, and poor clones and clones on poor sites for wildlife or forage production. Esthetics may be emphasized in key recreation areas. Management for water yield may be the primary consideration on important watersheds.

Even when management focuses on one resource, the others usually are affected and must be considered. For example, abundant forage will be produced even under the most intensive management for timber; aspen ranges will yield good quality water under all but the most abusive livestock or game management practices; and, the aspen-conifer-meadow mix in the montane setting will retain its scenic qualities under even the most intensive management for any other single resource.

Figure 1.—Management of aspen for esthetics is important in the West.

Esthetics and Recreation

Most techniques for managing other forest types for scenic and recreational values, especially hardwoods, can be applied to the aspen type. Small, irregularly shaped clearcuts that blend into the natural landscape are preferable. Permanent scenic vistas are more appealing if they are kept open and intact (fig. 1). Minimizing the visual impacts of management activities, especially if the aspen is within sight of heavily used areas or public roads, helps to preserve the esthetic quality of these forests.

Aspen has qualities that make it relatively easy to manage for both consumptive uses and for esthetics. Even heavily grazed aspen forest retains most of its scenic quality; the trees are visibly unaffected by grazing and removal of the understory. Clearcutting is evident for only a few years, because of rapid regrowth of understory species and abundant aspen suckering (fig. 2) (see the VEGETATIVE REGENERATION chapter). After harvesting, scattered aspen slash may be left in place to decay and practically disappear within a very few years. Burned areas quickly revegetate, also, which lessens the visual impact of fire. In autumn, the leaves on stands of young aspen saplings and poles are just as colorful as the leaves on mature aspen.

Ohmann et al. (1978) and Perala (1977) stated that foreground landscapes in the Lake States could be improved by: (1) providing vistas to expose and frame scenic features; (2) utilizing clearcuts to create variety by opening up dense and continuous stands, and by providing curved lines and irregular openings; (3) leaving attractive or special interest trees; (4) providing diversity in forest types, species mixes, and age/size classes; (5) encouraging transition vegetation along edges; (6) varying the sizes and shapes of cuts; and (7) sometimes converting from aspen to other vegetation types.

At least in the foreground view, the apparent size of even large clearcuts can be reduced by limiting the amount that can be seen from any one point. Islands of trees within the clearcut and feathered edges (by thinning into adjacent timber) also help minimize the visual impact. Also, it is esthetically better not to harvest stands adjacent to clearcuts until an obvious forest stand has reestablished on the clearcuts. A visually pleasing mix of even-aged aspen patches in all size classes can be created if the harvesting plan includes esthetic considerations.

Ensuring that harvesting and intermediate treatment operations appear neat and organized, and, where appropriate, conducting them when public use is minimum will minimize negative visual impact (Perala 1977). Cutting during the dormant season and removing debris minimizes the unsightliness of slash and other material. Skid trails, landings, and logging roads that flow with the landforms and that are progressively treated as the operations are completed cause less visual disturbance. Some landings may have future value as permanent openings (wildlife food patches, parking areas, etc.), and a few logging roads may be kept open to provide public access. Others should be closed or obliterated. (See the INTERMEDIATE TREATMENTS chapter for a discussion of other esthetic considerations.)

Aspen fits well into management for dispersed recreation activities; but, it does not tolerate concentrated use, such as that often found in established campgrounds (Hinds 1976) (fig. 3) (see the DISEASES chapter). Although aspen groves are attractive, encouraging concentrated recreation or developing campgrounds within them can lead to serious damage to the trees, including carving and vandalism, destruction or removal of young suckers, and trampling and disturbance of the soil. However, because of its esthetic qualities, existing aspen might be retained near areas of concentrated use.

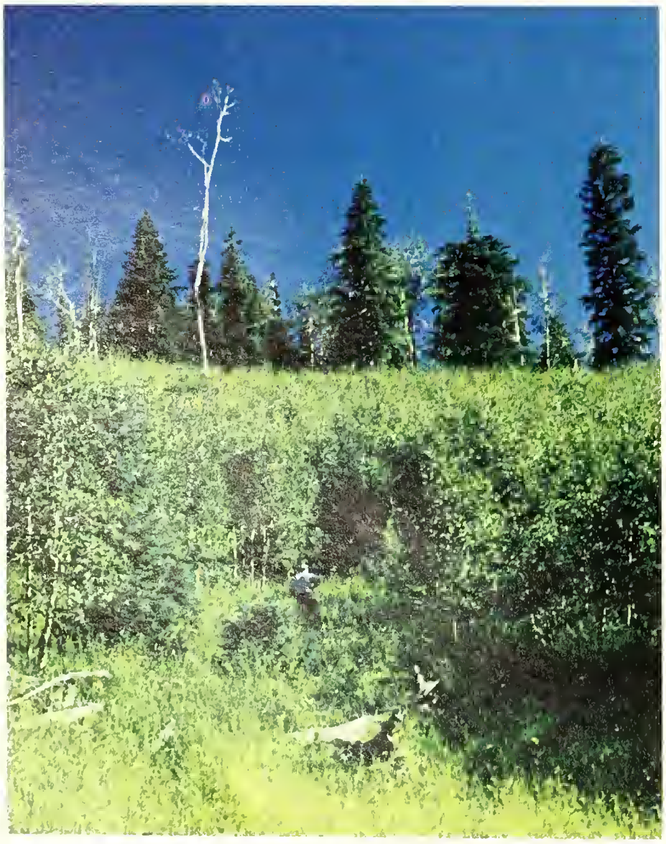

Figure 2.—Aspen clearcuts quickly regain a forested appearance.

Figure 3.—The once healthy aspen stand in this campground is in severe decline.

Concentrated recreational use of snow-covered aspenlands in winter is less damaging than similar use during the growing season. Impacts on the understory, young suckers, and the soil are minimal. Because of uniform snow cover, skiing in open aspen stands is excellent (fig. 4). Developed runs may be cut through existing aspen without exposing soil to erosion; with care, the understory can be kept intact to protect the soil. A mix of aspen and conifer stands adjacent to these runs provides an esthetically pleasing setting.

In foreground landscapes, mixed stands of aspen and conifers probably are the most visually pleasing. However, these usually are temporary conditions. Using practices, such as selective removal of conifers before they dominate the site, may retain such mixes on a given landscape for longer than their usual 20- to 50-year life expectancy. On a long-term basis, landscape management to create a mosaic of discrete stands (conifers, aspen, other) in the middleground would provide pleasing visual diversity.

On many sites, pure aspen stands are essentially climax. They can be retained for their esthetic qualities without any special treatments (see the ROTATIONS chapter). In time, these stands become uneven-aged. Suckers develop in the understory as the overstory breaks up (fig. 5). Often, these climax stands are quite open, especially if insect or disease epidemics kills much of the overstory. Because no expensive stand treatment measures are necessary, these stands are well-suited to management that emphasizes esthetics, recreation, and watershed.

Forage

Successful management of both the aspen trees and the understory forage resource requires careful planning. Grazing practices that maintain or even improve understories may be harmful to the long-term welfare of the aspen. For example, if sheep graze an old aspen stand, heavily enough to remove all aspen suckers each year, the understory forage resource may not be harmed, but the aspen stand eventually will disappear (fig. 6). The aspen overstory is not a static resource. If aspen regeneration is not provided for, the aspen will be lost (see the REGENERATION chapter).

After killing or clearcutting a parent stand, deferment or close control of grazing is necessary to permit development of a new, even-aged stand (fig. 7). Sampson (1919) recommended deferring sheep grazing for 3 or 4 years or until the suckers reach a 45- to 50-inch (1.1- to 1.3-m) height; or, only lightly grazing with cattle for 4 or 5 years or until the sucker crop is 60–70 inches (1.5–1.8 m) tall. During this regeneration phase, it appears that grazing while the herbaceous understory is lush and succulent is less likely to damage aspen than grazing late in the season after the herbaceous plants begin to cure (see the ANIMAL IMPACTS chapter). Succulent aspen suckers often are preferred forage after the herbaceous vegetation cures.

Figure 4.—The uniform snow conditions and lack of branches make aspen particularly enjoyable for ski touring.

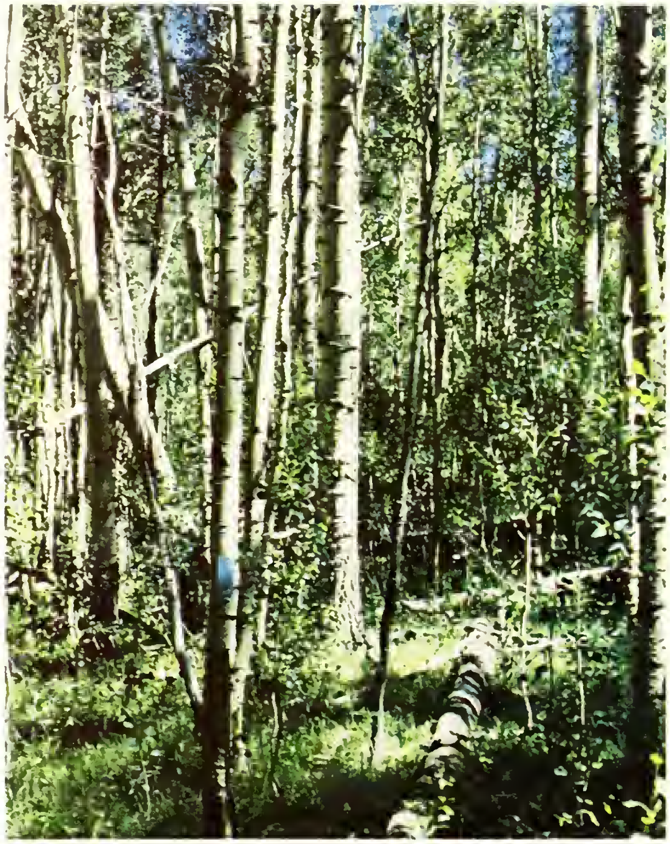

Figure 5.—A typical uneven-aged, multistoried aspen stand.

Aspen stands that are left to regenerate as the overstory dies and breaks up are more difficult to manage for optimum forage utilization. Until further research develops better information, perhaps the best recommendation that can be made is to moderately graze these stands until the aspen overstory begins to decline. Then graze heavily for a couple of years, thereby eliminating or weakening much understory competition. After this, remove virtually all grazing pressure for at least 3 to 5 years (fig. 8). A wave of sucker regeneration should arise and become adequately established under the declining overstory during this time. Then the stand may be moderately grazed. Such a sequence may be applied to climax, uneven-aged stands of aspen every 20 to 30 years.

Some clones and some sites with climax aspen will regenerate adequately with continuously light to moderate grazing, especially by cattle. Others may be difficult to regenerate even with the moderate-heavy-defer sequence recommended. For these, a shift from managing without killing or cutting the overstory to an even-aged management scheme, in which the old aspen stand is killed to provide abundant suckering, may be necessary.

Aspen growing as isolated groves on a shrub-grass range and aspen in riparian zones are most difficult to retain under the usual impacts of livestock grazing. Livestock concentrate in these groves and use them for shade and bedgrounds (fig. 9). If aspen is to be retained under these circumstances, more intensive and expensive measures are required. Fencing out livestock entirely from declining groves for an 8- to 10-year period should permit a crop of sucker regeneration to become established. Clearcutting just before fencing will stimulate many more suckers (see the VEGETATIVE REGENERATION chapter). When clearcutting, high stumps may be left around the perimeter to use as fence posts. However, to expand the grove, place the fence one or two tree heights outside the perimeter. Fire may be used instead of cutting (see the REGENERATION chapter), especially if it is the prescribed treatment for surrounding rangeland. However, because aspen often is difficult to burn (see the FIRE chapter), fire seldom is an effective treatment for only small patches of aspen. After a good stand is reestablished, the fence may be removed, and the grove again may be used by livestock for perhaps 80 to 100 years before retreatment becomes necessary.

Opportunities and methods for improving forage production in aspen communities depend upon forage values, other resource values, and management goals. These vary among regions and over time. For example, management objectives in the Canadian parklands have differed from those in the mountains of the western United States. In the northern parklands, there has been concern about restricting the spread of aspen and converting existing stands into pastures; whereas in the central and southern Rocky Mountains and on the Colorado Plateau, there has been concern about perpetuating aspen communities that are being lost through succession to other vegetation types.

Figure 6.—A declining clone with no regeneration.

Figure 7.—After herbicide spraying in 1965, all ungulates were excluded from the fenced area on the left. Eighteen years later, profuse aspen suckers are present in the protected area; whereas only aspen skeletons, some old aspen trees, and severely browsed aspen suckers are on the outside.

Thousands of acres of aspen parklands in western Canada were cleared of aspen and were seeded solely to improve forage production for cattle (Bowes 1975). The trees were removed by bulldozing, piling, and burning. The cleared areas then were disked and were seeded to desirable forage species such as smooth brome and alfalfa. Herbicides were applied during the two following years to control 95% of the aspen reproduction. Although this intensive treatment resulted in a threefold increase in forage production, it was very expensive and it destroyed the aspen community.

In Alberta, Hilton and Bailey (1974) obtained more than a fourfold increase in herbage production by the second year after applying herbicide to the aspen overstory. Graminoids increased the most without appreciably reducing forbs. Although aspen suckers became dense, cattle still were able to move through the stand and consume 50% of the total herbage. Bailey (1972) suggested that fire, herbicides, and late-season heavy grazing, used singly or in combination, might be an economical means of controlling aspen suckers on such areas. Again, this ultimately destroys the aspen community.

Forage production in aspen stands that are badly depleted by overgrazing can be improved without altering the tree overstory. Desirable forage species can be seeded directly beneath the aspen canopy. Plummer et al. (1955) indicated that no seedbed preparation is necessary; the seed merely should be broadcast between August and early October, before or during leaf fall. The fallen aspen leaves then provide adequate seed covering for successful germination and establishment. They recommended the following seed mixture for aspenlands within the Intermountain Region.

	lbs/acre	kg/ha
smooth brome	7	7.8
mountain brome	3	3.4
orchard grass	2	2.2
tall oatgrass	2	2.2
timothy	1	1.1
meadow foxtail	1	1.1

For openings within the aspen type, Plummer et al. (1955) suggested reducing the first three grasses to 5, 2, and 1 pounds per acre (5.5, 2.2, and 1.1 kg per ha) respectively, and adding 3 pounds per acre (3.3 kg per ha) of intermediate wheatgrass and 2 pounds per acre (2.2 kg per ha) of either chickpea milkvetch or Ladak alfalfa. Thirty years after seeding some 37 species in openings adjacent to aspen at elevations between 7,400 to 9,000 feet (2,250 and 2,750 m) in northern Utah, Hull (1973) found only smooth brome, tall oatgrass, intermediate wheatgrass, and red fescue still had fair to excellent stands. He suggested that forbs such as birdsfoot trefoil, crownvetch, birdvetch, alfalfa, and horsemint might be valuable additions to seeding such rangelands (Hull 1974).

Some of the species suggested for seeding under aspen are not native to these ranges, and may not be desirable if pregrazing conditions are to be reestablished. Smooth brome and intermediate wheatgrass, for example, are highly competitive and persistent enough to slow or prevent reestablishment of native herbaceous species.

Figure 8.—Temporary fencing may be necessary in some situations to protect new regeneration.

Figure 9.—Aspen groves used as shade and bed grounds may be difficult to regenerate without protective measures to reduce concentrated use.

The value of fertilizing aspenlands for improved forage production is questionable. Studies of fertilizer application have yielded variable results, perhaps because of the wide variety of site conditions where aspen grows. Beetle (1974) indicated that application of fertilizers under aspen stands in western Wyoming greatly stimulated the production of native grasses but did not affect aspen growth. In contrast, Hull (1963) fertilized seeded grasses in openings adjacent to aspen communities in southeastern Idaho with no significant response. He attributed this lack of response to leaching and to denitrification in the acidic soil.

Water

Watershed management includes both minimizing soil erosion and preserving or improving the quality or quantity of streamflow (see the WATER AND WATERSHED chapter).

Erosion

Vegetation, litter, and stone control erosion by protecting the soil surface (Meeuwig 1970). Maintenance of at least 65% ground cover with only small bare soil openings helps to prevent undue erosion from intense storms (Marston 1952). This will maintain adequate infiltration. As a result, raindrop splash and overland flow will not move much soil.

Most aspen stands have nearly complete soil cover. Pocket gopher activity and heavy livestock grazing may expose some soil (see the ANIMAL IMPACTS chapter). Sometimes, this may become critical. Generally, however, if the forage resource is not abused, the soil will have sufficient protection.

Fire and harvesting also expose mineral soil. However, the exposure seldom lasts longer than one growing season, if there is adequate soil protection during treatment, especially on erosive sites. Most of the problems from overland flow and erosion come from drastically disturbed soil at roads, landings, skid trails, and fire breaks.

Erosion in the form of mass movement or slumping is common on many geologically unstable sites, which aspen often grows on in the West. Little can be done to control this type of erosion other than to provide careful management and protection of the anchoring vegetation. Structures, roads, and other activities may contribute to instability, and are likely to be damaged by erosion on these unstable areas.

Water Quality and Yield

Studies have shown that clearcutting aspen and keeping the herbaceous understory relatively intact can increase water yields from 4 to 6 area inches (10–15 cm) (Johnston et al. 1969) (fig. 10). In more familiar terms, each acre of aspen clearcut may yield up to an additional one-third to one-half acre foot of water. Verry (1972), in Minnesota, measured an increase of 3.4 inches (8.6 cm) the first year after clearcutting—42% more than pretreatment flows from the cut area. Storm flow volumes and snowmelt peak discharges also increased for 2 years after treatment, then declined to preharvest levels (Verry et al. 1983).

Figure 10.—Clearcutting aspen initially may enhance water yields; but the effect is short-lived because of aspen's rapid regrowth.

At Wagon Wheel Gap, Colorado, Bates and Henry (1928) reported an average increase of nearly 1 inch (2.4 cm) for the 7-year period after clearcutting a mixed aspen-conifer watershed; 83% of this increase occurred during spring snowmelt runoff. Despite the potential, clearcutting only a small portion of a catchment may not result in measurable increases in water yields (Johnston 1984). The increase may be in the stream; but because of natural variability, it may be statistically insignificant. Reduced evapotranspiration on the clearcuts also may be offset by increased evapotranspiration downslope by consumption of increased interflow.

Other methods of destroying the aspen overstory could increase water yields, too. Herbicide spraying, if it has negligible effects on the herbaceous understory or on the sprouting ability of aspen roots, will increase yields about the same as cutting. In central Utah, for example, yields were increased by 4 inches (10 cm) after herbicide spraying killed the aspen overstory.[1] In contrast, if fire is intense enough and uniform enough to kill virtually all aspen trees, it also will consume or kill much of the understory brush and herbaceous plants. Therefore, during the first 2 years after burning, depending upon rates of understory regrowth, water yields from burned watersheds could be about 1.5 inches (4 cm) greater than from clearcut watersheds. However, there are no watershed or plot data available to verify this hypothesis; instead, it is inferred from Croft and Monninger's (1953) and Johnston's (1970) findings that evapotranspiration from bare soil is 1.5 to 2 inches (4–5 cm) less than from the herbaceous cover on plots from which the aspen was removed.

Because aspen forests regrow rapidly, water yield increases may last only 10 years. Soil water savings noticeably declined within 3 years after clearcutting Utah aspen plots (Johnston et al. 1969). Based upon these data, and upon observations of sucker stand development, it is speculated that water yield increases resulting from clearcutting, burning, or herbicide spraying can disappear in as few as 12 to 15 years after treatment.

If entire working circles are managed on 100-year rotations, and water yields are significantly augmented for only 15 years after harvest, then only 15% of any working circle would produce increased yields at any given time. That 15% would yield an average of 1.5 to 2 inches (4 to 5 cm) of increased flow, with the newly cut areas producing 4 to 6 inches (10–15 cm), and those cut 10 or more years earlier yielding only about 0.5 inch (1

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[1] *The Sheep Creek Water Evaluation Project by Max E. Robinson, Fishlake National Forest, Utah. Abridgement by Delpha M. Noble, 1973, USDA Forest Service, Intermountain Region, Ogden, Utah. 24 p., mimeographed.*

or 2 cm) of augmented flows. Average water yields from the entire working circle, therefore, would be increased only about 0.25 inch (0.6 cm). However, if technology changes, and economics permit utilization of small trees; or if the combined values of increased forage, more diversified wildlife habitat, and increased water yields result in rotations of 30 years in the aspen forest; then increased water yields of 1.5 to 2 inches (4–5 cm) over a 15-year period after clearcutting would produce increased yields of nearly 1 inch (2.5 cm) from entire aspen working circles. Hibbert (1979) expanded this line of thought to the entire Colorado River Basin. He calculated that if 20% of the 3.3 million acres (1.34 million ha) of aspen in the entire basin were put on an 80-year clearcut rotation and another 20% on a 25-year clearcut rotation, increased annual yields of 73,000 acre-feet could result.

Transpiration-suppressing chemicals have been tested and generally rejected as a feasible means of increasing streamflow from aspen forests. One foliar application of phenylmercuric acetate, for example, reduced water loss by 43% from potted aspen over a 53-day period, in the controlled environment of a growth chamber and greenhouse.[2] However, when the chemical was applied by helicopter to the forest, water use was delayed several weeks, but the amount of soil water consumption was not significantly affected (Hart et al. 1969).

Water yields may be increased substantially from local areas for a few years after clearcutting, burning, or herbicide killing of the aspen overstory. However, substantially increased water yields from entire river basins can be achieved only by converting aspen to vegetation types that use less water. Grass-herb types use less water per year than does aspen on deep soils. However, before planning vegetation conversion, the costs of conversion, the long range costs of maintaining replacement vegetation, and all negative impacts on other resource values should be considered. These then are compared to the values of predicted water yield increases and to the possible increases in quantity or value of other resources.

It may be possible to increase water yields by converting from conifers to aspen (see the WATER AND WATERSHED chapter). At least net precipitation can be increased substantially (Verry 1976). Models by Gifford et al. (1983, 1984) and Jaynes (1978) indicate that increased water yields are likely. However, because the amount of increase that might be realized by converting conifers to aspen has not been adequately tested, it can not be recommended as a management tool.

Limited studies, cited in the WATER AND WATERSHED chapter, indicated negligible changes in water quality from cutting or grazing aspen catchments. Again, if grazing is moderate, if the riparian zone is given adequate protection, and if logging is done with reasonable care, water quality is not likely to be adversely affected.

Figure 11.—Aspen is important habitat for many wildlife species.

Wildlife

The aspen forest type is important habitat for many species of birds and mammals (fig. 11) (Gullion 1977b), especially in the interior West, where it is the only upland hardwood tree species, and where it frequently is found in groves in the coniferous forests or as isolated stands in mountain grasslands and shrublands (see the WILDLIFE chapter).

Most aspen stands in the West have reached maturity because they have been protected from wildfire and have not been marketable for forest products for most of this century. In Colorado, stands averaged 80 years; those younger than 50 years were difficult to find (Shepperd 1981). During the 70 to 100 years it takes for a dense stand of young suckers to become a mature stand of aspen trees, a progression of different wildlife habitats will have developed.

Animals that depend upon the forage or cover produced in a young aspen community benefit from clearcutting, from prescribed fire (fig. 12), or possibly from top-kill using herbicides. They include many of the major game species—moose, elk, deer, ruffed grouse, and snowshoe hare. Other species do well in old, sometimes derelict, aspen stands—cavity nesting birds, for example. For these, treatment is not necessary for habitat management if the aspen on the site is stable or climax.

[2] *Robert S. Johnston. 1973. Phenylmercuric acetate reduces transpiration of potted aspen. Paper presented at the 46th Annual Meeting of the Northwest Scientific Association at Walla Walla, Washington.*

Other species of wildlife, such as red-backed voles, red squirrels, and pine martens, do best in coniferous forests. Disturbance that retards conifer succession is deleterious for these species.

To provide diversity of habitats and wildlife species, treatments (cutting, fire, or herbicides) usually are needed to maintain a mosaic of plant communities and age classes within these communities. To provide interspersion and edge, the same treatments also can be used to maximize boundary length among the units in this mosaic.

Elk

Elk prefer grassland, shrubland, and recent burns to the mixed forest community (Rounds 1981) (fig. 13). They choose aspen rather than coniferous communities in both summer and winter,[3] although conifers may be used for hiding and thermal cover during times of harassment or during severe weather (Thomas 1979).

To provide optimum habitat for elk, Thomas (1979) recommended managing 60% of the land area to provide forage. Good forage is provided by the herbaceous and shrubby understory in the aspen as well as any aspen suckers less than 6.5 feet (2 m) tall. Peak production of this component of the aspen type is reached within a few years after burning or clearcutting (Bartos et al. 1983) (fig. 14).

During the winter, elk require about 2 units of feed per day for every 100 units of body weight. This feed should have at least 5.5–6.0% crude protein content (Nelson and Leege 1982). Cured or leached grass forage in winter often has less than this minimum. Browse in winter contains more protein but less digestible dry matter than does grass. Elk need winter food with energy levels in excess of 1 kilocalorie per gram (Nelson and Leege 1982). Enhancing high energy foods on the elk winter range will help reduce winter losses and improve calving success. (Forage quality is discussed in the FORAGE and WILDLIFE chapters.)

Figure 13.—Elk foraging in a 3-year-old burn within the the aspen forest community in southern Idaho. (Photo by Kem Canon)

Figure 12.—Prescribed fire being applied with a helitorch to kill the declining aspen overstory, to stimulate suckering, and to provide increased forage for livestock, and food and cover for wildlife.

In late spring, with emergence of green and succulent forage, the typical elk diet rapidly shifts from a winter regimen that is high in fiber and low in protein to one that is high in protein and low in fiber. High quality summer range is important, because that is when the elk raise calves and rebuild body condition for breeding and for winter survival.

A mix of cover can be provided on the remaining 40% of the elk range not devoted to forage production. Patches of at least 25 acres (10 ha), and preferably up to 65 acres (26 ha), provide best hiding or security cover for elk. Thermal cover is provided, also, if trees in these patches are more than 40 feet (12 m) tall and have a crown cover of at least 70% (Thomas 1979). Pole-sized aspen provide thermal cover in summer, as well as security cover and quality forage. After leaves drop in autumn, the thermal cover and much of the security cover is lost in aspen stands; conifer patches then provide the best security and thermal cover.

Elk commonly forage within 100 yards (90 m) of cover. They prefer to bed near where they finish feeding, in or near cover (Collins 1979). During summer, elk usually are found within a 0.5 mile (1 km) of drinking water. The prevalence of biting insects, especially horseflies, in the aspen type affects elk behavior (Collins and Urness 1982), and may force them away from otherwise optimal habitat.

Concentrated populations of elk may adversely impact the aspen ecosystem, especially aspen regeneration (see ANIMAL IMPACTS chapter). Under these conditions, long-term management of both the elk herd and the aspen is difficult. Elk are very difficult to control with fences; a more practical control is population manipulation. DeByle (1979) proposed cycling individual elk herds through high and low population densities. During the low population phase, treatments such as fire or cutting could be applied to any declining or overmature aspen stands to stimulate regeneration. That way, regeneration would be sapling-sized and out of reach of the elk before the herd rebuilds. Carrying

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[3] *Ackerman, Bruce, Lonn Kuck, Evelyn Merrill, and Thomas Hemker. 1983. Ecological relationships of mule deer, elk, and moose in southeastern Idaho. Idaho Department of Fish and Game, Project No. W-160-R, completion report. 123 p. Boise, Idaho.*

capacity thereby becomes a dynamic concept, low during the regeneration phase, but quite high when aspen and shrub regeneration is not seriously threatened.

Moose

Moose primarily browse willow and aspen (see the WILDLIFE chapter). Small aspen suckers and the typical understory forbs and shrubs in the aspen type are favorite moose forage.

The best upland moose habitat in the West probably has a good distribution of aspen and associated trees and shrubs in a mosaic of age classes (Gordon 1976). Conifer patches for hiding cover are also desirable, perhaps essential. Thermal cover in winter appears to be unnecessary for moose; in summer it is abundant in either the aspen or coniferous forest.

Extensive regeneration of young vigorous stands of aspen, willow, and associated shrubs, often after fires, improves moose habitat and may result in a temporary moose population increase until the browse grows out of reach (see the WILDLIFE chapter).

Management of aspen to provide a variety of size classes on the landscape appears to provide the best moose habitat. The size of the treated areas is not as critical as it is for species with small home ranges (which must have all required habitat components relatively close), or for deer and elk (which may concentrate on small treated areas and destroy regenerating aspen). Clearcuts or burns of 40 to 240 acres (15–100 ha) may be satisfactory. Retention of conifer patches are likely to benefit moose. Encouragement of subalpine fir as an understory in the aspen will provide moose with a choice browse. However, the conifers may replace the aspen, if the stands are not treated later.

Deer

In the West, deer use aspen forests mostly in summer and fall. During these seasons, thermal and hiding cover as well as nutritious forage are abundant in the aspen type.

Figure 14.—A dense stand of aspen suckers exists amidst a profusion of other forage species 3 years after prescribed fire was applied to this aspen stand in southern Idaho.

The impact of deer on aspen regeneration can be greatest in late summer and autumn (see the ANIMAL IMPACTS chapter). They readily eat young, succulent aspen sprouts on recent burns and clearcuts. They also browse on aspen up to a 5-foot (1.5-m) height, and, therefore, can have a significant impact on aspen suckers younger than 4 or 5 years or on those suppressed by browsing to heights of less than 5 feet (1.5 m) (Mueggler and Bartos 1977).

On their summer range, deer benefit from having plenty of aspen habitat available, especially if it contains an abundance of understory forbs and shrubs. Because both aspen suckers and the aspen understory are in greatest abundance within a few years after burning (Bartos et al. 1983) or clearcutting (Bartos and Mueggler 1982), management to provide an array of aspen age classes on the range would seem to provide the best overall deer habitat. However, if units are too small, deer may overbrowse the aspen regeneration. Perhaps 10 to 40 acres (4–16 ha) per unit, managed with aspen rotations of 40 to 80 years, would provide optimum deer habitat.

Snowshoe Hares

In the Rocky Mountains, most pure aspen stands provide poor snowshoe hare winter habitat because of deep snowpacks (see the WILDLIFE chapter). Aspen with a very dense understory of tall shrubs may provide marginal winter cover; but usually only conifers will suffice (Wolfe et al. 1982). During summer, when snowshoe hares disperse somewhat from coniferous cover and shift to a diet of succulent plant material (Wolff 1980), the aspen type provides adequate cover and excellent forage.

Even the peak density of aspen suckers and shrubs on most aspen burns or clearcuts in the West probably do not provide adequate snowshoe hare habitat in winter. Working in Michigan, Conroy et al. (1979) recommended small clearcuttings that were shaped so that adequate canopy cover remained within 200 to 400 yards (200–400 m) of all parts of the opening. In the western United States and adjacent Canada, perhaps small, irregularly shaped clearcuts and encouragement of small but dense conifer patches throughout the aspen forest would provide maximum snowshoe hare habitat in the aspen type.

Beaver

As stated in the WILDLIFE chapter, potential beaver habitat is a strip 200–300 yards (200–300 m) wide along any relatively placid perennial stream flowing through the aspen type. By flooding, the beaver may be able to considerably widen that strip of habitat. If the aspen in this zone are managed for beaver, encouraging dense stands of 2- to 6-inch (5- to 15 cm) diameter trees is likely to result in greatest utilization by beaver.

Beavers often temporarily destroy their habitat in the aspen type. After removal of all trees within reach, they move on. The aspen then will resprout if they weren't flooded, killing the roots. After a new stand develops, and trees large enough for dam construction are present, the beavers may return and begin the cycle over again.

If aspen are to be managed in the riparian zone for products other than beaver dams and food, then beaver populations may have to be rigidly controlled.

Bear

The aspen forest appears to be better feeding habitat for black bears than the associated conifers, largely because of an abundant and varied aspen understory (see the WILDLIFE chapter). Biologists in Colorado have developed preliminary guidelines for aspen management to accommodate bears.[4] Where a mosaic of conifers and aspen occur, retaining the aspen will provide better bear feeding areas. Controlling livestock grazing will permit adequate development of understory forbs and berries, which are important bear food. Bears feed on aspen buds in the spring. It appears that they select and favor individual clones. If these clones are critical to the bear's food supply, management to retain mature trees of these clones at all times may be appropriate.

Ruffed Grouse

The aspen type is heavily utilized as food and as cover by the ruffed grouse (see the WILDLIFE chapter). The tree and associated vegetation provide a highly nutritious food source (Gullion and Svoboda 1972), protection from the weather (Bump et al. 1947), and escape from predation (Gullion et al. 1962).

Management for optimum ruffed grouse habitat centers on the aspen ecosystem and nearby dense, brushy vegetation. For Idaho and Utah conditions, Stauffer and Peterson[5] recommended a diversity of habitat structure within 40- to 50-acre (16- to 20-ha) units. Optimum drumming (breeding) sites have 200 to 450 trees per acre (about 450–1,100 trees per ha) that provide 80% to 95% tree cover and at least 2,500 small stems (shrubs and aspen sprouts) per acre (about 6,000 stems per ha). Hens with broods prefer 50% to 75% tree cover, about 600 to 2,800 small stems per acre (1,500–7,000 stems per ha), and openings with abundant herbaceous cover more than 20 inches (50 cm) tall. In winter, large, mature aspen provide food and some conifers add cover. In Minnesota, Gullion (1977a) recommended practices that maintain heavily stocked, fast-growing aspen stands in a variety of age (size) classes within the daily range of grouse. He questioned the value of conifers, because they harbor avian predators. Stauffer and Peterson[5] and Landry (1982) emphasized the importance of a dense shrub layer in aspen or mixed aspen stands for ruffed grouse habitat in the West.

Even-aged management of 10-acre (4-ha) units on rotations of about 60 years may produce the best ruffed grouse habitat in the interior West. Treating one unit (burning or clearcutting) every 15 years within each 40-to 50-acre (16- to 20-ha) block, should produce the diversity of habitat needed within the range of individual grouse. Clearcutting units as small as 10 acres (4 ha) usually is the most viable treatment. Larger areas that are being taken over by conifers may be burned to set back succession, then later put into the rotation system of small 10-acre (4-ha) units.[5]

Sharp-tailed Grouse

Aspen is useful as small thickets of young growth 3 to 6 feet (1–2 m) tall and as larger patches of taller trees for winter food and cover (Evans 1968, Hamerstrom 1963) (see the WILDLIFE chapter). However, significant invasion of grassland by aspen reduces sharp-tailed grouse habitat (Moyles 1981).

Fire in relatively short intervals (e.g., 20 years) could be used for management of sharp-tailed grouse habitat. Large units of several hundred acres could be burned, if patches of large aspen trees are protected.

Cavity Nesting Birds

About 34 bird species, most of which are insectivorous, are cavity nesters in the aspen type in the West (Scott et al. 1980) (see the WILDLIFE chapter). Guidelines have been published for snag management in some of the conifer types to retain cavity nesting habitat. As a general rule, snag management in the aspen type in the West may be fairly simple. Except to prevent indiscriminate removal of standing aspen snags by firewood cutters, very little modification of current management practices is needed to maximize this habitat. Currently, little or no cutting is done in the aspen forest until it is mature to overmature, and then most harvesting is in the form of small (2.5- to 12-acre (1- to 5-ha) clearcuts. This preserves natural cavity nesting habitat until the stand is overmature.

If scattered aspen are to be left for perching sites or for cavity nesters in clearcuts, the chosen trees should be dead or should be killed so they do not have adverse effects on the developing aspen suckers (see the REGENERATION and HARVESTING chapters). Small, irregularly shaped clearcuts, or clearcuts with islands of mature or overmature leave trees, may retain the best overall bird habitat in managed aspen forests.

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[4] *Personal communication from Tom Beck to Mike Ward, Paonia Ranger District, and included in the Aspen Management Guidelines for the Grand Mesa, Uncompahgre, and Gunnison National Forests, Colorado on August 16, 1983.*

[5] *Stauffer, Dean F., and Steven R. Peterson. 1982. Seasonal habitat relationships of ruffed and blue grouse in southeastern Idaho. University of Idaho; College of Forestry, Wildlife and Range Sciences; Forest, Wildlife and Range Experiment Station, Moscow. 138 p.*

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APPENDIX

Scientific and Common Names of Vascular Plants Cited in the Text[1]

Scientific Name	Common Name
Abies spp.	fir
Abies balsamea	balsam fir
Abies concolor	white fir
Abies lasiocarpa	subalpine fir
Abies lasiocarpa var *arizonica*	corkbark fir
Abies magnifica	California red fir
Acer spp.	maple
Acer glabrum	Rocky Mountain maple
Achillea spp.	yarrow
Achillea millefolium	western yarrow
Agastache spp.	horsemint; giant hyssop
Agastache urticifolia	nettleleaf horsemint
Agoseris spp.	agoseris
Agropyron spp.	wheatgrass
Agropyron caninum	bearded wheatgrass
Agropyron intermedium	intermediate wheatgrass
Agropyron richardsonii	bearded wheatgrass
Agropyron riparium	streambank wheatgrass
Agropyron subsecundum	bearded wheatgrass
Agropyron tenerum	bearded wheatgrass
Agropyron trachycaulum	slender wheatgrass
Agrostis spp.	bentgrass
Alnus spp.	alder
Alnus tenuifolia	mountain or thinleaf alder
Alopecurus pratensis	meadow foxtail
Amelanchier spp.	serviceberry
Amelanchier alnifolia	Saskatoon serviceberry
Androsace septentrionalis	pygmy rockjasmine
Angelica spp.	angelica
Aquilegia caerulea	Colorado columbine
Aralia nudicaulis	wild sarsaparilla
Arctostaphylos	manzanita
Arnica spp.	arnica
Arnica cordifolia	heartleaf arnica
Arrhenatherum elatius	tall oatgrass
Artemisia spp.	sagebrush
Artemisia ludoviciana	Louisiana sagewort
Artemisia tridentata	big sagebrush
Aster spp.	aster
Aster conspicuus	showy aster
Aster engelmannii	Engelmann aster
Aster foliaceus	alpine leafybract aster
Aster laevis	smooth aster
Aster lindleyanus	Lindley aster
Aster perelegans	Nuttall aster
Astragalus spp.	milkvetch
Astragalus bourgovii	Bourgeauv milkvetch
Astragalus cicer	chickpea milkvetch
Astragalus miser	weedy milkvetch

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[1] *Scientific and common name list compiled from Beetle (1970), Garrison et al. (1976), Hitchcock et al. (1969), Hitchcock and Cronquist (1981), Little (1979), and Plummer et al. (1977).*

Scientific Name	**Common Name**
Berberis spp.	barberry; Oregon grape
Berberis repens	creeping hollygrape; Oregon grape
Betula spp.	birch
Betula papyrifera	paper birch
Bromus spp.	brome
Bromus anomalus	nodding brome
Bromus carinatus	mountain brome
Bromus ciliatus	fringed brome
Bromus inermis	smooth brome
Bromus marginatus	mountain brome
Bromus polyanthus	foothill brome
Calamagrostis canadensis	bluegjoint reedgrass
Calamagrostis rubescens	pinegrass
Carex spp.	sedge
Carex festivella	ovalhead sedge
Carex geyeri	elk sedge
Carex hoodii	Hood sedge
Carex rossii	Ross sedge
Castilleja linariaefolia	Wyoming Indian paintbrush
Castilleja miniata	scarlet Indian paintbrush
Ceanothus spp.	ceanothus
Ceanothus velutinus	snowbrush
Cerastium spp.	chickweed
Chenopodium fremontii	Fremont goosefoot
Cirsium spp.	thistle
Cirsium undulatum	wavyleaf thistle
Collinsia parviflora	little flower collinsia
Collomia linearis	slenderleaf collomia
Cornus canadensis	bunchberry dogwood
Coronilla varia	crownvetch
Corylus spp.	hazel; filbert
Corylus cornuta	beaked hazelnut
Corylus rostrata	beaked hazelnut
Cynoglossum officinale	common hounds tongue
Dactylis glomerata	orchard grass
Danthonia californica	California danthonia
Delphinium spp.	larkspur
Delphinium barbeyi	Barbey larkspur
Delphinium occidentale	duncecap larkspur
Deschampsia caespitosa	tufted hairgrass
Descurainia californica	California tansy mustard
Elymus spp.	wildrye
Elymus glaucus	blue wildrye
Epilobium spp.	willowherb
Epilobium angustifolium	fireweed
Equisetum arvense	field horsetail
Erigeron spp.	fleabane; daisy
Erigeron elatior	tall fleabane
Erigeron macranthus	aspen fleabane
Erigeron peregrinus	peregrin fleabane
Erigeron speciosus	Oregon fleabane
Erigeron superbus	----
Eriogonum spp.	wild buckwheat
Fagus spp.	beech
Festuca arizonica	Arizona fescue
Festuca idahoensis	Idaho fescue
Festuca rubra	red fescue
Festuca scabrella	rough fescue
Festuca thurberi	Thurber fescue
Fragaria	strawberry

Scientific Name	**Common Name**
Fragaria bracteata	bracted strawberry
Fragaria glauca	blueleaf strawberry
Fragaria vesca americana	American strawberry
Fragaria virginiana	Virginia strawberry
Frasera speciosa	Showy frasera; elkweed
Fraxinus americana	White ash
Galium spp.	bedstraw
Galium bifolium	twinleaf bedstraw
Galium boreale	northern bedstraw
Galium triflorum	sweetscented bedstraw
Gayophytum ramossissimum	branchy groundsmoke
Gentiana amarella heterosepala	annual gentian
Geranium spp.	geranium
Geranium fremontii	Fremont geranium
Geranium richardsonii	Richardson geranium
Geranium viscosissimum	sticky geranium
Geum spp.	avens
Glyceria spp.	mannagrass
Glycine max	soybean
Hackelia spp.	tickweed; stickseed; stickweed
Hackelia floribunda	showy stickweed
Hackelia mierantha	----
Helenium hoopesii	orange sneezeweed
Helianthella quinquenervis	five nerve helianthella
Helianthella uniflora	one flower helianthella
Heracleum spp.	cow parsnip
Heracleum lanatum	common cow parsnip
Heracleum sphondylium	hogweed cow parsnip
Hydrophyllum capitatum	ballhead waterleaf
Iris spp.	iris
Juniperus spp.	juniper
Juniperus communis	common juniper
Larix spp.	larch; tamarack
Lathyrus spp.	peavine
Lathyrus lanszwertii	thickleaf peavine
Lathyrus leucanthus	aspen peavine
Lathyrus ochroleucus	cream peavine
Lathyrus pauciflorus	few flower peavine
Ligusticum spp.	lovage
Ligusticum filicinum	fernleaf lovage
Ligusticum porteri	Porter lovage
Lonicera spp.	honeysuckle
Lotus corniculatus	birdsfoot trefoil
Lupinus spp.	lupine
Lupinus alpestris	mountain lupine
Lupinus argenteus	silvery lupine
Lupinus leucophyllus	velvet lupine
Lupinus parviflorus	lodgepole lupine
Madia glomerata	cluster tarweed
Mahonia spp. (*Berberis* spp.)	barberry; Oregon grape
Medicago sativa	alfalfa
Melica spp.	melic, oniongrass
Melica bulbosa	oniongrass
Mertensia spp.	bluebells
Mertensia arizonica	tall bluebells
Mertensia pilosa	----
Monarda fistulosa	wild bergamot beebalm
Monardella odoratissima	Pacific monardella
Nemophila breviflora	Great Basin nemophila
Oryzopsis asperifolia	roughleaf ricegrass

Scientific Name	Common Name
Osmorhiza spp.	sweetroot; sweet cicely
Osmorhiza chilensis	spreading sweetroot
Osmorhiza depauperata	bluntseed sweetroot
Osmorhiza obtusa	bluntseed sweetroot
Osmorhiza occidentalis	sweetanise
Ostrya virginiana	American hophornbeam
Pachistima spp.	pachistima
Pachistima myrsinites	myrtle pachistima
Pedicularis spp.	lousewort
Pedicularis racemosa	sickletop pedicularis
Penstemon spp.	beardtongue, penstemon
Phleum pratense	timothy
Phlox spp.	phlox
Physocarpus spp.	ninebark
Physocarpus monogynus	mountain ninebark
Picea spp.	spruce
Picea engelmannii	Engelmann spruce
Picea glauca	white spruce
Picea mariana	black spruce
Picea pungens	blue spruce
Pinus spp.	pine
Pinus banksiana	jack pine
Pinus contorta	lodgepole pine
Pinus ponderosa	ponderosa pine
Pinus resinosa	red pine
Pinus strobus	eastern white pine
Poa spp.	bluegrass
Poa fendleriana	mutton bluegrass
Poa nervosa	Wheeler bluegrass
Poa pratensis	Kentucky bluegrass
Poa reflexa	nodding bluegrass
Polemonium spp.	polemonium
Polemonium foliosissimum	leafy polemonium
Polygonum spp.	knotweed; smartweed
Polygonum douglasii	Douglas knotweed
Populus spp.	poplar; aspen; cottonwood
Populus alba	white poplar
Populus angustifolia	narrowleaf cottonwood
Populus balsamifera	balsam poplar
Populus bonati	(an Asian aspen species)
Populus canescens	gray poplar; Carolina poplar
Populus grandidentata	bigtooth aspen
Populus monticola	----
Populus nigra	black poplar
Populus nigra var *italica*	Lombardy poplar
Populus rotundifolia	(an Asian aspen species)
Populus tacamahaca	balsam poplar
Populus tremula	Eurasian aspen; European aspen
Populus tremuloides	aspen; quaking or trembling aspen
Populus trichocarpa	black cottonwood
Potentilla spp.	cinquefoil
Potentilla fruticosa	shrubby cinquefoil
Potentilla glandulosa	gland cinquefoil
Potentilla pulcherrima	showy cinquefoil
Prunus spp.	cherry; plum
Prunus virginiana	chokecherry
Pseudotsuga menziesii	Douglas-fir
Pteridium aquilinum	bracken fern
Quercus spp.	oak

Scientific Name	**Common Name**
Quercus gambelii	Gambel oak
Ranunculus alismaefolius	plantainleaf buttercup
Rhus spp.	sumac
Ribes spp.	currant; gooseberry
Ribes cereum	wax currant
Ribes lacustre	prickly currant
Ribes missouriense	Missouri gooseberry
Ribes montigenum	mountain gooseberry
Ribes setosum	Missouri gooseberry
Rosa spp.	rose
Rosa acicularis	prickly rose
Rosa nutkana	bristly nootka rose
Rosa woodsii	woods rose
Rubus spp.	raspberry; blackberry
Rubus parviflorus	western thimbleberry
Rubus triflorus (pubescens)	dwarf red blackberry
Rudbeckia spp.	coneflower
Rudbeckia occidentalis	western coneflower
Salicaceae (family)	willow family
Salix spp.	willow
Salix scouleriana	Scouler willow
Sambucus spp.	elderberry; elder
Senecio spp.	groundsel; ragwort
Senecio serra	butterweed groundsel
Sequoia spp.	sequoia; redwood
Shepherdia spp.	buffaloberry
Shepherdia argentea	silver buffaloberry
Shepherdia canadensis	russet buffaloberry
Smilacina stellata	starry false solomonseal
Solidago decumbens	decumbent goldenrod
Spiraea spp.	spiraea
Spiraea betulifolia	birchleaf spiraea
Spiraea lucida	shinyleaf spiraea
Stellaria jamesiana	tuber starwort
Stipa columbiana	subalpine needlegrass
Stipa lettermani	Letterman needlegrass
Swertia radiata (Frasera speciosa)	showy frasera; elkweed
Symphoricarpos spp.	snowberry
Symphoricarpos albus	common snowberry
Symphoricarpos occidentalis	western snowberry
Symphoricarpos oreophilus	mountain snowberry
Symphoricarpos palmeri	----
Symphoricarpos pauciflorus	----
Symphoricarpos utahensis	Utah snowberry
Symphoricarpos vaccinioides	whortleleaf snowberry
Taraxacum spp.	dandelion
Taraxacum officinale	common dandelion
Thalictrum spp.	meadowrue
Thalictrum dasycarpum	purple meadowrue
Thalictrum fendleri	Fendler meadowrue
Thalictrum occidentale	western meadowrue
Thalictrum venulosum	veiny meadowrue
Tilia spp.	basswood; linden
Trifolium spp.	clover
Trifolium repens	white clover
Trisetum spicatum	spike trisetum
Tsuga spp.	hemlock
Typha spp.	cattail
Vaccinium spp.	blueberry, huckleberry

Scientific Name	Common Name
Valeriana spp.	valerian
Valeriana edulis	edible valerian
Valeriana occidentalis	western valerian
Valeriana sitchensis	sitka valerian
Veratrum californicum	California false hellebore
Veratrum tenuipetalum	false hellebore; skunk cabbage
Veronica biloba	speedwell
Viburnum pauciflorum	mooseberry viburnum
Vicia spp.	vetch
Vicia americana	american vetch
Vicia cracca	birdvetch
Viola adunca	hook violet
Viola canadensis	Canada violet
Viola nuttallii	yellow prairie violet
Wyethia spp.	wyethia
Wyethia amplexicaulis	mulesears wyethia
Zea mays	corn

Subject Matter Index

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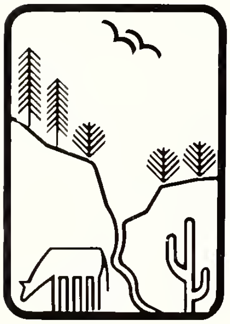
Information about the biology, ecology, and management of quaking aspen on the mountains and plateaus of the interior western United States, and to a lesser extent, Canada, is summarized and discussed. The biology of aspen as a tree species, community relationships in the aspen ecosystem, environments, and factors affecting aspen forests are reviewed. The resources available within and from the aspen forest type, and their past and potential uses are examined. Silvicultural methods and other approaches to managing aspen for various resources and uses are presented.

Keywords: *Populus tremuloides*, ecology, forest management, silvics, silviculture, wildlife habitat, diseases, insects, fire, watershed management, forest products.

Rocky
Mountains



Southwest

Great
Plains

U.S. Department of Agriculture
Forest Service

Rocky Mountain Forest and Range Experiment Station

The Rocky Mountain Station is one of eight regional experiment stations, plus the Forest Products Laboratory and the Washington Office Staff, that make up the Forest Service research organization.

RESEARCH FOCUS

Research programs at the Rocky Mountain Station are coordinated with area universities and with other institutions. Many studies are conducted on a cooperative basis to accelerate solutions to problems involving range, water, wildlife and fish habitat, human and community development, timber, recreation, protection, and multiresource evaluation.

RESEARCH LOCATIONS

Research Work Units of the Rocky Mountain Station are operated in cooperation with universities in the following cities:

Albuquerque, New Mexico
Flagstaff, Arizona
Fort Collins, Colorado*
Laramie, Wyoming
Lincoln, Nebraska
Rapid City, South Dakota
Tempe, Arizona

*Station Headquarters: 240 W. Prospect St., Fort Collins, CO 80526