1973

The ecological role of fire in the Jackson Hole area, northwestern Wyoming

L.L. Loope

G.E. Gruell

QUATERNARY RESEARCH 3, 425–443 (1973)

The Ecological Role of Fire in the Jackson Hole Area, Northwestern Wyoming

LLOYD L. LOOPE[1] AND GEORGE E. GRUELL[2]

Received March 20, 1973

Fire-history investigations in the Jackson Hole area of northwestern Wyoming reveal that most current stands of aspen and lodgepole pine regenerated following extensive fires between 1840 and 1890 and that widespread fires occurred in the 1600s and 1700s. White man's major effect on the fire incidence has been the successful suppression during the past 30–80 yr. Successional changes in the absence of fire include the deterioration of aspen stands, massive invasions of subalpine fir in lodgepole pine stands, great increase in conifer cover, heavy fuel buildups in lodgepole pine and Douglas fir stands, and increase in sagebrush and other shrubs. Steps are being taken, starting in 1972, to allow fire to play a more natural role in Grand Teton and Yellowstone National Parks. Teton National Forest plans experimental prescribed burning to determine whether fire can stimulate successful aspen regeneration in the presence of large numbers of wintering elk.

T. S. Brandegee surveyed forest conditions on the Teton Forest Reserve for the U.S. Geological Survey in 1897. His report (Brandegee, 1899) stated:

> It is only occasionally that tracts of timber of merchantable size are found, and areas containing notable quantities of merchantable forest are few and limited.
>
> This condition appears to be due simply and solely to fires which have swept over the country so completely and persistently that scarcely any part has been entirely exempt from them, while nearly all portions have been burned again and again within a generation . . . Under present conditions the tree-bearing regions as a whole decrease, while the aspen areas increase at the expense of those now producing conifers.

The area of Teton Forest Reserve which Brandegee surveyed now comprises most of the Teton National Forest and Grand Teton National Park. Ecological conditions have changed over the past 75 yr, mainly due to successful fire suppression. Plant succession in the absence of fire has resulted in an increase in the extent and average age of coniferous forest stands and a deterioration of aspen stands. Shrub cover, especially big sagebrush, has increased markedly. Conifers continue to invade open areas. (See Figs. 1, 2.)

A primary management goal of the National Park Service for Grand Teton National Park is to maintain the park's ecosystems in as natural a state as possible (Houston, 1971). The U.S. Forest Service has similar objectives for the Teton Wilderness Area of the Teton National Forest. The remainder of the Teton Forest is managed for multiple use, which involves commercial logging and management for wildlife habitat, grazing of domestic livestock, watershed quality, and recreation values. It has become obvious to both land-management agencies that an understanding of the nature of pristine ecosystems and the processes that shaped them is necessary for enlightened management.

[1] National Park Service, Moose, Wyoming 83012.
[2] U.S. Forest Service, Jackson, Wyoming 83001.

FIG. 1. Lower Gros Ventre Valley, Teton National Forest (*Above*). 1899. The landscape 20 yr after a major fire. Note the young aspen stands. The vegetation in the foreground is predominantly an herbaceous cover with scattered serviceberry and snowberry shrubs. Courtesy of Wyoming State Archives and Historical Department, Stimson Photo Collection. (*Below*). July 28, 1971. Aspen stands are mature and approaching decadence, 92 yr after fire. Aspen on distant bench has been largely replaced by Douglas fir. The foreground vegetation is now dominated by big sagebrush.

Our studies attempt to document the nature of the pristine vegetation patterns of this area and the influence of fire on these patterns. We try to determine the effects of fire and various stages of plant succession on the outstanding wildlife populations of the Jackson Hole area. Field investigations are mainly within Teton National Forest and Grand Teton National Park, with supplemental observations in Yellowstone National Park and Bridger National Forest.

THE AREA

Northwestern Wyoming has five major mountain ranges—the Teton, Absaroka,

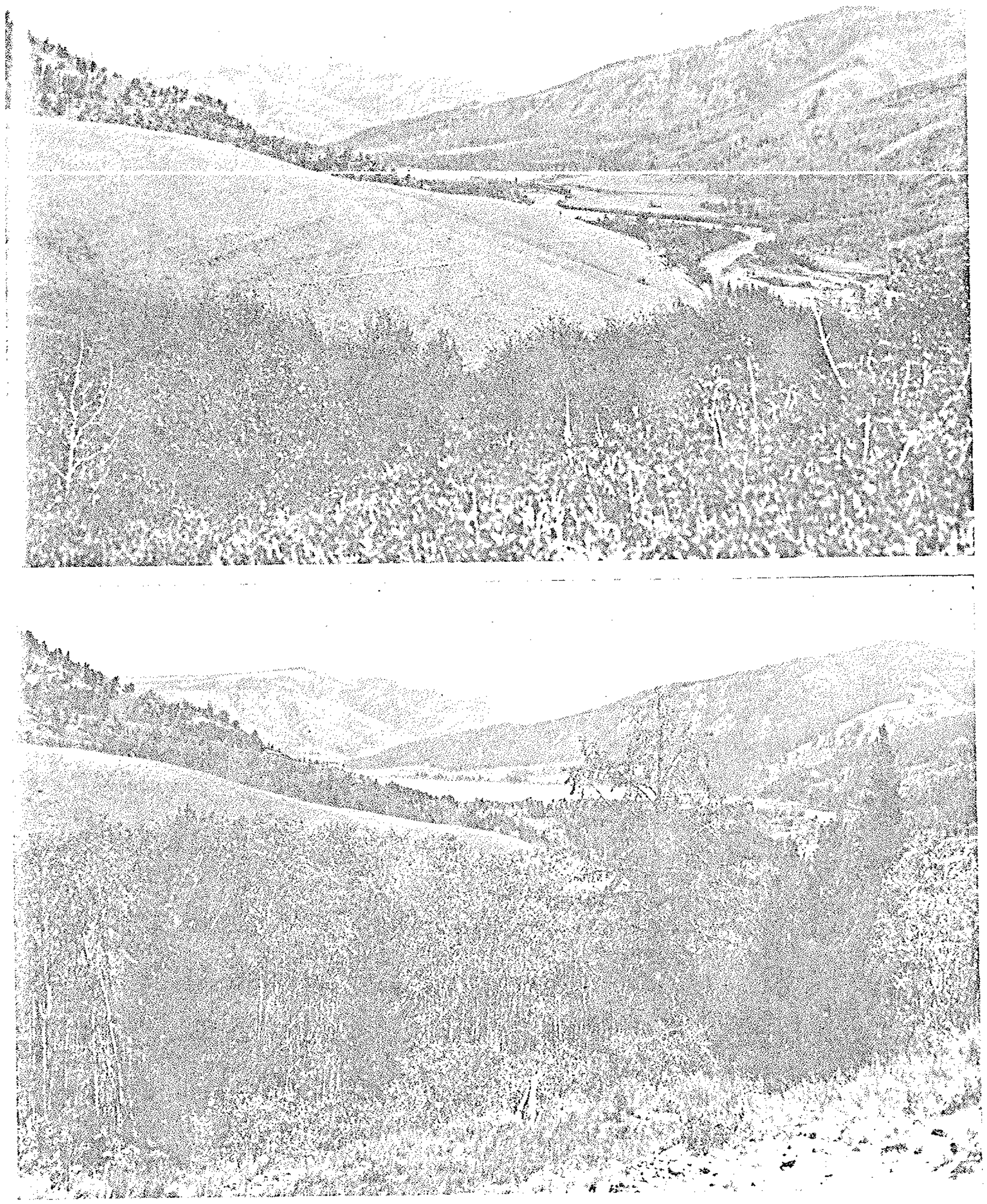

FIG. 2. Lower Gros Ventre Valley (*Above*). 1899. Taken in the opposite direction from Fig. 1. The foreground of this scene shows a vigorous young aspen stand, which sprouted following the 1879 fire. Young conifers are becoming established under fire-killed snags on the distant slopes at right. Courtesy of Wyoming State Archives and Historical Department, Stimson Photo Collection. (*Below*). July 28, 1971. Reproduction is occurring at the margin of the 92-yr-old aspen stand, but not under the canopy. The distant slopes at right are now forested by a dense stand of Douglas fir. The lake formed following a landslide in 1925.

Beartooth, Gros Ventre, and Wind River Ranges. Numerous lesser mountain ranges and uplands are present, including, in the vicinity of our study area, the Hoback Range, the Mt. Leidy Highlands, the Pinyon Peak Highlands, and the Yellow-

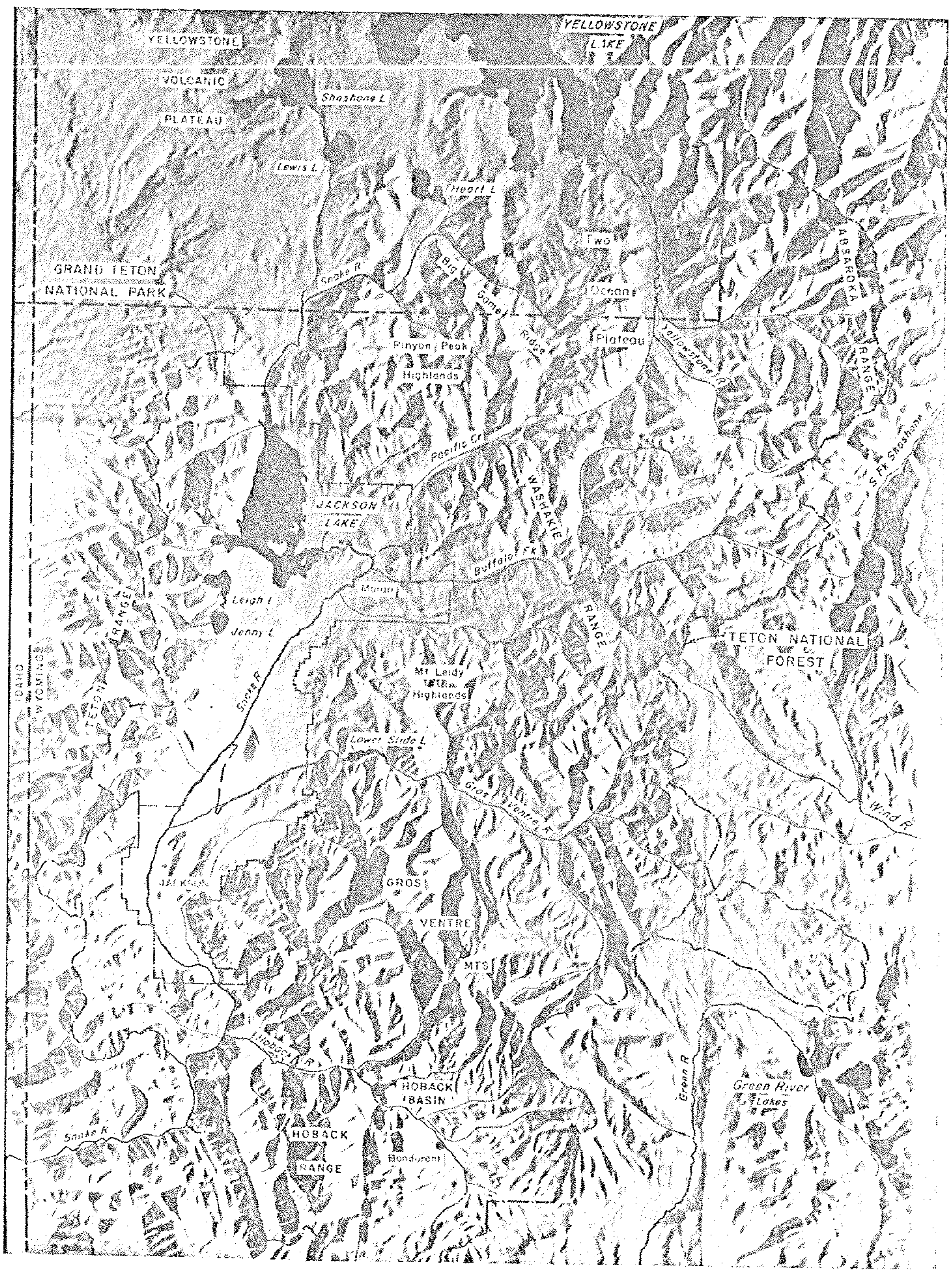

FIG. 3. Map showing location of study area in relation to the major physiographic features of northwestern Wyoming.

stone Plateau. Figure 3 shows the location of the main study area in relation to the major physiographic features of northwestern Wyoming.

The hydrographic divide of the Teton Range comprises the west boundary of Grand Teton National Park. The eastern portion of the park lies entirely within Jackson Hole—a flat-floored valley about 65 km long from north to south and 15–25 km wide, drained by the southward-flowing Snake River. Our major study area within Teton National Forest has been east of southern Jackson Hole in the valley of the Gros Ventre River, which rises in the Gros Ventre Mountains.

The area has a complex geologic history, and a great variety of bedrock types are exposed. The Teton Range is composed primarily of Precambrian granitic rocks. Paleozoic limestone and sandstone predominate in the Gros Ventre Mountains. Mesozoic shale and sandstone outcrop throughout the Gros Ventre Valley. Many of these Mesozoic formations weather into unstable clay soils, which are subject to sliding (Bailey, 1971). The Yellowstone Plateau is composed of Tertiary basalt and rhyolite. Pleistocene glaciation has had profound effects on the terrain. The valley of Jackson Hole is floored with thick, course outwash deposited by glacial rivers. Numerous moraine deposits occur throughout the area.

VEGETATION

The vegetation of the Jackson Hole area consists of a mosaic of nonforested areas and different-aged forest stands, most of which originated following fire. Species composition of parts of the mosaic is determined not only by microclimate and soils, but in large part by the time since the latest fire and by the previous fire history.

The forest portion of the mosaic is composed essentially of eight species of the family Pinaceae and four species of the genus *Populus*. Lodgepole pine (*Pinus contorta*) is often the most abundant tree species at intermediate elevations (1850–2400 m), characteristically occurring in almost pure, nearly even-aged stands of fire origin. Subalpine fir (*Abies lasiocarpa*), the most abundant tree of subalpine forests, is found from 1850 m to timberline at about 3050 m. Throughout the upper part of this zone, fir is mixed with Engelmann spruce (*Picea engelmannii*). Spruce sometimes occurs in almost pure stands in moist, fire-protected areas such as are found in canyons at the east base of the Tetons. Whitebark pine (*Pinus albicaulis*), the other important component of the subalpine forest, is found from about 2400 m to 3050 m, and often grows in nearly pure stands just below timberline.

Douglas fir (*Pseudotsuga menziesii*) is a common species of the lower forest border in this area. Scattered individuals occur up to 2600 m on south-facing slopes of the Teton Range. Douglas fir forms extensive nearly pure stands on calcareous substrates in the Gros Ventre Mountains and elsewhere in northwestern Wyoming. Limber pine (*Pinus flexilis*), less common than other conifers, is found at forest–sagebrush ecotones and on very dry south-facing slopes. Aspen (*Populus tremuloides* is fairly abundant at the lower elevations of the Jackson Hole area, although not nearly so abundant as it is in parts of Utah and Colorado. Aspen often occupies the conifer forest–sagebrush ecotone and stands are frequently mixed with Douglas fir.

Blue spruce (*Picea pungens*), narrowleaf cottonwood (*Populus angustifolia*), balsam popular (*Populus balsamifera*), and black cottonwood (*Populus trichocarpa*) occur on floodplains in Jackson Hole.

Extensive nonforested areas occur in this region. Sagebrush (including *Artemisia tridentata* and *Artemisia arbuscula*), bitterbrush (*Purshia tridentata*), and rabbitbrush (*Chrysothamnus* spp.) are important shrubs, which are associated with numerous species of grasses. Willows (*Salix* spp.) and sedges (*Carex* spp.) dominate swampy sites.

CLIMATE

Climatic conditions vary widely in Jackson Hole because of the great variation in topography. Mean annual precipitation ranges from over 125 cm on the Pitchstone Plateau of southwestern Yellowstone Park to less than 35 cm in the Gros Ventre Valley.

Moran, Wyoming, at an elevation of 2075 m in northern Jackson Hole has a mean January temperature of −12°C (11°F), a mean July temperature of 14°C (58°F), and a mean annual precipitation of 53 cm. At least half the precipitation falls as snow from November to April. The average snow depth at Moran on April 1 is 100 cm. Summers in Jackson Hole are short and cool. Snow cover disappears from valley areas in April and May and from high areas as late as July or August. May and June are typically moderately wet months. July is the driest month, averaging 2.5 cm of precipitation at Moran. Most of the summer rainfall falls in scattered thunderstorms. The prevailing wind direction is from the southwest.

WHITE MAN'S OCCUPATION OF THE AREA

John Colter, who passed through Jackson Hole during the winter of 1807–1808, is generally regarded as the first white man to enter the area. Several parties of fur trappers were in the area between 1811 and 1820, and from 1820 to 1840 there was considerable fur trapping activity in Jackson Hole. This activity ceased abruptly about 1840, however, as a result of the sudden decline in popularity of the beaver hat and the overexploitation of beaver populations. For the 1840–1860 period, there is little or no evidence that white men were present in Jackson Hole (Hayden, 1963; Mattes, 1946, 1948).

Miners, explorers, and hunters were present in Jackson Hole periodically during the 1860s and 1870s. Exploration of the Yellowstone country led to its establishment as a National Park in 1872. The first permanent settlers arrived in 1884 and 1888 (Hayden, 1963).

FIRE CLIMATE AND RECENT FIRE HISTORY

Potential burning conditions vary greatly from summer to summer. The period of highest potential is between July 15 and September 30. August 15–31 is the most likely period for extreme conditions to occur. Periods of high fire potential are usually brief and are terminated by an abrupt change to cooler weather and/or precipitation.

Data from cross sections of fire-scarred trees and weather records since 1916 suggest that conditions conducive to extreme fires have occurred at infrequent intervals. The potential for ignition of extensive fires by lightning storms occurs infrequently, for most lightning storms in the area are accompanied by precipitation. Small lightning-caused fires were apparently frequent in the past. Very large fires were rare, but they did occur periodically when a combination of extremely dry conditions, one or more ignition sources, and high winds coincided. Data from fire-scarred trees show that such conditions occurred in Jackson Hole in the years 1856 and 1879, well before the initiation of fire-suppression efforts. Extensive crown fires swept large areas during these years.

Crown fires occur here only under the most extreme conditions. Even with very dry atmospheric and fuel conditions, fires generally remain in light fuels on the forest floor unless fanned by strong winds. The frequent occurrence of fire-scarred trees in existing forest stands provide evidence of creeping ground fires in the past. Observations made during the 250-hectare Pacific Creek fire of August 22–29, 1971, in Teton National Forest, confirm this hypothesis. This fire burned in a mixed stand of spruce, fir, and lodgepole pine at an elevation of 2450 m under extremely dry conditions but was not pushed by high winds. Its genera behavior was a steady and thorough consumption of the moderately heavy ground fuels, with intermittent spotting and ignition of the crowns. Only in areas of exceptionally heavy fuels, where the heat of the fire generated substantial convection currents, did a crown fire develop. The crown fire died down in lighter ground fuels.

Prior to fire-suppression efforts, it is likely that fires during most years were few and small. Under burning conditions less than extreme, fires would die down and smolder. Periods of warm weather and increased wind would revive the blaze. In dry years, such fires could burn with varying intensity for several months, affecting large acreages.

Organized fire suppression dates back to the establishment of Teton Forest Reserve in 1897. The diary of B. F. Bondurant, a fire guard employed by the U.S. Forest Service, describes how he extinguished a fire, started by a lightning strike, which burned one-half acre in Hoback Basin on August 4, 1904 (Sargent, 1963). The U.S. Army was extinguishing fires in parts of Yellowstone Park in the 1880s, according to Superintendents' Reports (Harris, 1886; Boutelle, 1890). Detection and suppression of fires improved markedly in the 1920s and 1930s with the establishment of fire lookouts throughout most of the forested area of northwest Wyoming. The remarkable success of suppression efforts is reflected in the fact that a total area of about 125 hectares has burned since 1910 in what is now 130,000-hectare Grand Teton National Park. Highly effective suppression of fires in inaccessible parts of Northwestern Wyoming did not begin until about 1940.

Moderate detail is available for fire records since 1931. In the 1931–1940 period, there were seven fires in Teton National Forest larger than 400 hectares each. The total area burned by these fires was over 14,000 hectares. During this same decade, Yellowstone National Park had nine fires over 400 hectares, totaling about 18,000 hectares.

Since 1941, Teton National Forest has had no fires as large as 400 hectares. Yellowstone National Park had two such fires, totaling 1400 hectares. These figures reflect increasing effectiveness in fire detection and early suppression in northwestern Wyoming. Fire suppression has been highly successful during the past 30 yr despite increased fuel buildups. The rarity of extreme burning conditions during this period has probably contributed significantly to this circumstance.

FIRE HISTORY PRIOR TO 1900

Evidence from stand age and from sections of fire-scarred trees has been used to investigate the fire history of Grand Teton National Park and parts of Teton National Forest. Numerous very small fires have occurred in the Teton Range because of frequent lightning strikes, but large fires have been rare because of rugged topography and numerous natural firebreaks—especially bare rock. In contrast, no extensive area in the valley of Jackson Hole has escaped fire for much over 200 yr, and most areas burned in the interval between 1850 and 1885. Fire-scar and standage data suggest that large fires occurred about 1765, in the early 1840s, about 1856, and in the interval of 1878–1885. Most forest stands in the valley originated following the fires of 1856 and 1879. Several square kilometers of lodgepole pine forest burned in the northern Teton Range as recently as 1910.

Sampling from the Gros Ventre Valley in Teton National Forest, contiguous with the eastern edge of Jackson Hole, indicates that fires burned somewhere in the drainage during each decade of the 19th century. However, fires seem to have burned extensive areas only during the 1840s, 1870s, and 1880s. Most forest stands in the Gros Ventre drainage were affected by one or more fires during the 1840–1890 period. Many stands at higher elevations in the Gros Ventre Mountains burned during this period, too, but other stands escaped. Many open lodgepole pine stands contain numerous individuals with two or three fire scars from this period. Some of the largest fires occurred about 1842, 1872, and 1879.

Limited sampling of sections of 300–400-yr-old trees in the Jackson Hole area (mostly Douglas fir) with multiple fire scars suggest that numerous fires occurred in the 1600s and 1700s. Trees of this age may have three or four fire scars, even though a fire generally scars only a small percentage of surviving trees in its path.

The best evidence for comparative fire frequencies in northwestern Wyoming in the 17th, 18th, and 19th centuries comes from Houston (1973). Houston investigated the fire history of the winter range for ungulates of northern Yellowstone Park. Cross sections were obtained from 33 live and 10 dead fire-scarred Douglas firs located at forest–grassland ecotones in the Lamar, Yellowstone, and Gardner River valleys. Vegetation of this area is comparable to Jackson Hole but somewhat drier and warmer. Trees averaged 308 yr old, and eight were over 400 yr old. Individual sampled sections showed an average frequency of scarring of about 50 yr, prior to white man's influence in reducing fire frequency. Comparison of scars from adjacent trees suggests one fire per 20–30 yr. The occurrence of similar fire dates over wide areas suggests the likelihood of eight or ten large fires in the past 300–400 yr. Fire frequencies were very similar during the 17th, 18th, and 19th centuries. The most recent fire scars were generally no later than the 1870s. Only two of the sampled trees on the major study units were scarred in the 1890s, and none of the sampled Douglas firs had been scarred since 1900.

A comparison of Houston's data with our data from Jackson Hole suggests that fire occurred less frequently in Jackson Hole than in the grassland areas of northern Yellowstone Park. Few 400-yr-old Douglas firs in our area exhibit more than four fire scars. For most low-elevation sites in Jackson Hole, we estimate the mean natural fire frequency to have been one fire per 50–100 yr. Stands at high elevation or protected by topographic peculiarities are typically influenced by fire less often. Tundra habitats may be virtually free of fire's influence.

SOURCES OF IGNITION

There can be little doubt that forest fires have had a profound influence on the ecosystems of northwestern Wyoming for centuries. Organic material produced by photosynthesis in regions with cool climate accumulates at a much more rapid rate than it decays, creating a fuel source (Beaufait, 1971). During very dry conditions of late summer or early fall, which are attained in occasional years, adequate ignition can produce extensive conflagrations. The fire frequency at a given site partially depends on the frequency of ignition. Two major sources of ignition exist—lightning and man.

Nowhere in the world is lightning such a significant ignition source as in the coniferous forests of western United States (A. Taylor, 1971). About 60% of the modern forest fires in this area are caused by lightning. Data from northwestern Wyoming support this assertion. Lightning ignited 53% of 857 fires from 1931 to 1972 in Teton National Forest. In Yellowstone National Park, 56% of 1228 fires between 1931 and 1967 were ignited by lightning (D. Taylor, 1969). That lightning starts fires now and has caused them in the past is undeniable. We have good data on the relative importance of lightning vs man as a source of ignition at present. How did the past compare with the present in this regard?

It is possible only to speculate on the importance of aboriginal populations in influencing the past fire frequency in the Jackson Hole area. Artifacts from the north end of Jackson Lake suggest seasonal occupancy in this valley over 10,000 y.a. (Frison, 1971). More concrete evidence exists for the periodic occupation of Mummy Cave, a site 105 km northeast of Jackson Lake, for the past 9000 yr (Wedel *et al.*, 1968). Abundant evidence points to the presence of man in Jackson Hole during the past 4500 yr. Shoshone groups are believed to have hunted bison and antelope there (Frison, 197).

The use of fire by aboriginal man in various parts of the world to drive game in hunting is moderately well documented (Stewart, 1956). Stewart considers unextinguished campfires to have been a major ignition source for fires in prehistoric times. No specific information is available for the Jackson Hole area. Early man may have been a significant source of ignition there. The elimination of aboriginal man from the scene in the late 19th century eliminated this potential ignition source.

In many areas of the west, the exploration and settlement by white man clearly increased the fire incidence. Timbering, land clearing, railroads, and campfires were constant sources of ignition, causing some of the largest fires in recorded history (Holbrook, 1943). Militant Indians were blamed for many fires in the Rocky Mountains during the late 19th century (e.g., Hanna, 1934; Town, 1899), though some accounts suggest that their incendiary role has been overestimated by white historians (Brown, 1971).

Most evidence suggests that the white man did not greatly increase the fire frequency in Jackson Hole during the 19th century. An occasional wildfire undoubtedly resulted from a poorly placed or unattended campfire during the 1820–1840 furtrapping period. However, data from fire-scarred trees indicate that fires during this period were less frequent than during most decades of the 1800s. There is little evidence of white man in the Jackson Hole area between 1840 and 1860 (Mattes, 1948). Only a few records exist of his presence there in the 1860s (Raynolds, 1868; De Lacy, 1876).

There is abundant documentation for the presence of white man in the region during the 1870s and early 1880s, with the advent of government surveys, establishment of Yellowstone National Park, prospecting and hunting trips, and initial white settlement of Jackson Hole. Travel and habitation in the area were still infrequent, however (Doane, 1877; Baillie-Grohman, 1884; Buxton, 1893; Fryxell, 1932). The remote setting, harsh environment, and limited mineral wealth of Jackson Hole deterred occupancy. Permanent settlement did not begin until 1884. Native accounts completely lack instances of wildfires caused by white man or Indians during this period.

As previously stated, tree-ring evidence indicates extensive fires during the 1870–1885 period, especially about 1872 and 1879. Historic accounts document fires in 1878, 1879, and 1880. W. W. Jackson passed through Jackson Hole in the late summer of 1878 and photographed the Tetons from Signal Mountain. He was unsatisfied with the quality of his photographs "because of a smoky haziness (caused by forest fires in the vicinity) that filled the air" (Jackson and Driggs, 1929). Thomas Moran visited the west side of the Tetons in August 1879. Conditions for making sketches were far from ideal throughout the trip because smoke from forest fires became "so dense as almost to obscure the peaks of the Tetons" (Fryxell, 1932). W. A. Baillie-Grohman camped at Jenny Lake in August, 1880 but was forced to leave the area when chased by a forest fire several miles to the north of Jenny Lake that was "running before a northwesterly breeze" (Baillie-Grohman, 1884). In these accounts, no mention is made of fires being caused by humans.

Observers of forest conditions in northwestern Wyoming in the 1880s and 1890s felt that white man's carelessness was at least partially responsible for the devastation of forests by fire. Hague (1886) recognized that "evidence of forest fires 150 years ago may still be traced," but felt that "disastrous fires took place, caused by the carelessness of white man" following establishment of Yellowstone Park. He felt that "with the coming of the railroad and the erection of hotels, fires steadily increased," until strict precautions were enforced by the U.S. Army in the late 1880s. Brandegee's (1899) comments for the Teton Forest Reserve are vague as to the cause of the fires. Taylor (1969) points out that the importance of lightning in igniting fires was not appreciated in the 19th century. He determined that Superintendents' Reports for Yellowstone National Park prior to 1899 failed to mention lightning-caused fires. Fires were thus assumed to be man-caused.

One cannot state with certainty that white man did not significantly influence the natural fire frequency in the Jackson Hole area during the period of exploration and settlement. Certain lines of evidence suggest this, however. These include:

1. Fire-scar evidence from 300 to 400-yr-old trees seems to indicate a fire frequency during the 1600s and 1700s roughly similar to that during the 1800s.

2. There is apparently no correlation between frequency of people in the area and frequency of conflagration. (Large areas burned in the 1840s and 1850s, when very few or no white men were in the area. Only small numbers were present during the great fires of the 1870s and early 1880s. After settlement began in the mid-1880s, few extensive fires occurred.)

3. Narrative accounts are almost entirely lacking for accidentally or intentionally set fires. Such documentation is abundant for other areas of the west.

In summary, it appears that the fire regime for the 19th century deduced from fire-history investigations in modern forest stands can be interpreted as fairly typical of pristine conditions. Adequate ignition sources existed before the coming of white man to northwestern Wyoming. Aboriginal man probably started fires, intentionally or inadvertently, but sufficient lightning fires have been ignited by late-summer storms to assure the existence of fire-influenced forests with periodic cyclic disturbances without human ignition. White man's major effect on the fire incidence has been marked reduction of fire frequency during the past 30–70 yr.

ROLE OF FIRE IN MAJOR ECOSYSTEM TYPES

Aspen

The role of fire in aspen ecology is of special concern to land-management agencies of northwestern Wyoming because of the current deteriorated condition of most aspen stands. The failure of aspen reproduction has been a concern in Jackson Hole for over 25 yr. Traditionally, this has been blamed on "overbrowsing" by the Jackson Hole elk herd, which was believed to exceed numbers that existed in primitive times. More recent evaluations of historic elk numbers suggest a decrease in numbers since primitive times (Cole, 1969; Gruell, 1973). Some changes in elk distribution have occurred, particularly adjacent to winter feedgrounds, but in general the forage utilization patterns resemble those of the past. Studies of fire history and fire ecology suggest that the decline of aspen is primarily due to an alteration of the natural fire regime.

In the Rocky Mountains, aspen reproduces almost entirely by sending up vegetative shoots (suckers) from the root system of a clone, and there is apparently very little reproduction by seed. Aspens are readily killed by fire. Large numbers of vegetative sprouts are produced following a fire in an aspen stand; 12,000–20,000 stems per hectare is not unusual. Hague (1886) noted that in northern Yellowstone Park aspen is "the first tree to spring up upon recently burned areas" and that "by so doing it helps to conceal unsightly charred trunks, and adds bright color to the somber hill slopes."

Apparently, fire produces a physiological stimulation of the root system to send up suckers, which is tied to the killing of mature trees of the clone and is thought to be influenced by auxins (Farmer, 1962). Removal of competing vegetation and the cleansing of the stand by disease are other factors involved (Graham *et al.*, 1963). Not only are large numbers of suckers produced following a fire, but these suckers have rapid growth.

Competition among suckers as the stand develops causes rapid reduction in the number of stems per hectare. However, suckering continues for several years after a fire. In the fall of 1971, we made a study of the relationship of tree ages in aspen stands of the Jackson Hole area to the date of the most recent fire influencing each stand, which showed that aspen suckering due to stimulation by fire continues for 10 yr or more after the fire. This may be largely due to the expansion of clones following fire. The age structure of present stands is related to levels of browsing by elk and moose, which are determined by such factors as population densities, forage preferences, topography, and availability of forage species other than aspen. We have found no evidence to suggest drastic increases in elk browsing from natural conditions, except in the vicinity of sites where elk are unnaturally concentrated when supplied supplementary artificial feed in winter. There has been a great increase in moose browsing in the past 50 yr.

In areas where ungulate browsing is naturally heavy at present (and presumably was heavy in the past), all aspen trees that sprouted following the fires of the 1850–1890 period became established within 10–30 yr after the most recent fire. The greatest intensity of reproduction was generally in the 5-yr period immediately following the fire. Virtually no aspens have become established in these stands within the past 70 yr. For example, in a stand near Tent Creek in the Gros Ventre valley, which originated following a fire 120 y.a., all aspens sampled (19) were over 90 yr old. In a stand near the mouth of Goosewing Creek, which originated following a fire 98 y.a., all aspens sampled (9) were at least 89 yr old.

In areas where ungulate browsing is light (now and in the past), aspen reproduction and establishment, though most prolific following the fires of 1850–1890, has continued sporadically until the present. However, in most instances, reproduction during the past 70 yr has been insufficient to replace the deteriorating stands.

Individual aspens 200 yr old rarely occur. Stand deterioration usually sets in after an age of about 80 yr is reached. Various diseases, the most important of which are sooty bark canker and heart rot, are the immediate cause of the death of the trees. Invasion of conifers (limber pine, Douglas fir, lodgepole pine, subalpine fir, and Engelmann spruce) occurs in many initially pure aspen stands and sometimes contributes significantly to the decline of the stands. Mixed stands of aspen and conifer originated following fire on some sites. In most of these stands, the conifers have attained dominance and accelerated the death of aspens through shading and root competition.

Nearly all aspen stands in the Jackson Hole area had their origins following fires between 1850 and 1890. Very little reproduction has occurred since 1900. Most stands are now either in or approaching a critical period. If no fires occur in the next 20–50 yr, many clones will be reduced to a situation in which they no longer contribute significantly to the vegetative cover.

In areas of moderate to light game use, reproduction of aspen on stand margins and under deteriorating stands has been much greater during the past 20 yr than during the previous 50 yr (1900–1950). We attribute this increase in reproductive vigor to the deterioration of parent stands, which accelerated about 20 y.a., when most aspens reached an age of 70–80 yr.

In summary, successful regeneration of aspen stands in the Jackson Hole area was stimulated by fire in the past. Some suckering occurs now without fire, and, in areas with light game use, such suckers can survive to produce mature trees. Even here, however, reproduction is generally not sufficient to maintain the stand. In areas with heavy game use, suckers rarely survive.

Lodgepole Pine

Lodgepole pine is well known as a species that thrives under the influence of fire throughout most of the Rocky Mountains. In many parts of the Rockies, lodgepole has predominantly serotinous cones, which remain closed for many years unless heated above 45°C (113°F) (Fowells, 1965). In northwestern Wyoming, however, serotiny is relatively unimportant. Most cones open without heat, and the seeds are scattered without fire. However, lodgepole pine has abundant seed production and is a successful invader after fire if there is an adequate seed source nearby. The reproductive potential of nonserotinous lodgepole is suggested by the establishment of large numbers of seedlings on mineral soil exposed in roadcuts. The widespread occurrence of living fire-scarred lodgepoles suggested that individual trees often survived past fires and served as a seed source for the new stand. The probability also exists that, when a fire killed an entire stand, enough seeds from unopened mature cones survived the fire to contribute substantially to the seed source for a new stand.

After lodgepole pine stands attain an age of 80–100 yr (and the trees a diameter of 20–25 cm), they become susceptible to attack by mountain pine beetles (*Dendroctonus ponderosae*), which lay eggs in the phloem so that trees are girdled by the feeding larvae. As age and diameter increase further, lodgepoles become increasingly susceptible to attack (Roe and Amman, 1970). Most stands in the area have thus been recently vulnerable to beetle attack, which has killed 10–45% of the trees over 5 in. (13 cm) d.b.h. (diameter at breast height) in much of Grand Teton National Park and Teton National Forest in the past 12 yr (Klein *et al.*, 1972). The mountain pine beetle, a native insect, is a highly significant ecological factor that has influenced lodgepole pine ecosystems for millennia. The high percentage of lodgepole stands in a susceptible stage at present, due to fire suppression, has presumably resulted in high beetle populations over an unprecedented expanse of forest. Photographs taken before 1900 show that some mature stands of lodgepole were decimated by mountain pine beetle before the advent of successful fire suppression, however.

Within 10–20 yr after a fire in a lodgepole stand, a dense level of stocking is usually attained. Typical 90-yr-old stands sampled in Jackson Hole have 1700–2300 trees per hectare larger than 10 cm d.b.h. Many dead stems of suppressed individuals are usually present. The forest floor is highly shaded in such a stand, and there is generally no lodgepole reproduction. Reproductive success of subalpine fir in the understory is variable. At an age of about 120 yr, typical lodgepole stands have 800–1050 stems per hectare. Most stands of this age have been affected considerably by mountain pine beetle attack. With increased sunlight from thinning of the stand and reduced competition, fir reproduction increases.

At an age of about 200 yr, only about 400–650 mature lodgepole pines per hectare remain. The stands have suffered high mortality from mountain pine beetle and become increasingly susceptible to windthrow. Large openings in the canopy occur, and lodgepole reproduction commences. In many 200-yr-old stands, the number of lodgepole seedlings and saplings is greater than those of fir. In the absence of fire, such stands might take several hundred more years for fir to attain dominance. The substantial fuel accumulation in old lodgepole pine stands predisposes such stands to fires, which perpetuate lodgepole dominance.

Subalpine Fir

Subalpine fir might be termed the "climax" conifer species for much of the Jackson Hole country. It has increased greatly in importance due to fire suppression and is the primary species invading lodgepole pine stands and many aspen stands. Its increasing importance and its value as moose browse may have been a contributing factor to the increase in moose population levels in Jackson Hole since 1900.

Fir, like spruce, is easily killed by fire. If an abundant seed source exists near a burn, fir can become established in a mixed stand with lodgepole. A pure, dense lodgepole stand sometimes has little fir reproduction at an age of 120 yr. Generally, by an age of 80–100 yr, substantial fir reproduction has begun in a lodgepole stand. Without fire, shade-tolerant fir would virtually replace lodgepole in most stands within 250–400 yr after a fire. Fir invasion, however, contributes to the fuel buildup. In combination with the fuel from dead lodgepole pines, a fire that will reinitiate the cycle becomes likely.

Engelmann Spruce

Reed (1969) and Oosting and Reed (1952) found spruce-dominated forests at elevations from 2700 m to timberline in the Wind River and Medicine Bow Mountains, respectively. In the Gros Ventre Range, nearly pure spruce stands are largely confined to the higher elevations (2400–3050 m). In the Teton Range, spruce-dominated forests are found primarily in sheltered canyon bottoms and slopes from 2080 m to 2400 m. The spruce stands of the Tetons are characteristically on the west sides of lakes at the base of steep slopes. Fires are therefore much less frequent than in less sheltered areas. Large individuals of spruce, up to 1.2 m in diameter, occur in these forests, which are located mainly at the east base of the Teton Range.

Spruce trees are easily killed by fire, and regeneration is usually slow following fire. The age structure of these stands suggests that even these old-growth spruce forests depend on fire for their establishment, because the stands consist of nearly even-aged spruce, with very little spruce reproduction. The situation resembles that described by Bloomberg (1950) for spruce on the east slope of the Canadian Rockies in Alberta.

Where an adequate seed source and sufficient moisture are present, spruce regenerates following fire and may form mixed stands with lodgepole pine. Douglas fir often establishes individuals in such a postfire stand. Since few lodgepoles survive beyond the age of 200 yr, an almost pure stand of spruce occupies the site from 200 to 500 yr following a fire. During this stage, subalpine fir often comprises less than 10% of the basal area of the stand. But spruce regeneration is minimal after the lodgepole canopy closes. As the age of the stand increases, spruce reproduction approaches zero, except on rotting logs and in openings with exposed bare mineral soil. The accumulation of an organic layer at the soil surface and the low light penetration apparently inhibit spruce seedling establishment. Seedlings of subalpine fir are 10–20 times as abundant as those of spruce in these stands. Oosting and Reed (1952) found a similar ratio of fir seedlings to spruce, but felt that high mortality of young fir resulted in maintenance of a climax spruce community. The nearly even-aged structure of the dominant species here strongly suggests that this community is not "climax."

It appears that fir would eventually replace spruce here in the prolonged absence of fire. The tremendous fuel buildups that accumulate as the spruce canopy breaks up predispose the stands to fire. No present stands exhibit a late stage in the hypothetical succession from spruce to fir.

Spruce is conspicuously uncommon in lodgepole forests of valley areas of Grand Teton National Park. This appears to be partly due to past fire history, which has obliterated a seed source, and partly due to moderately dry late-summer conditions. Fir seeds are larger than spruce seeds and contain much more food for utilization by seedlings (Fowells, 1965; Oosting and Reed, 1952). Seedling fir can develop a root system more rapidly than spruce—an important adaptation where soil moisture is marginal. A few mature spruces occur in these valley lodgepole pine forests, and occasional seedling establishment occurs.

In the Gros Ventre Valley, spruce commonly invades lodgepole pine and aspen stands on north-facing slopes. In this area, a seed source for spruce survived past fires in moist pockets. Moisture from seepage often contributes to spruce establishment.

Whitebark Pine

Above 2600 m, whitebark pine often colonizes areas in spite of its large seeds, which require transport by squirrels, chipmunks, and birds for dispersal. Near Amphitheatre Lake in the Teton Range a nearly pure stand of whitebark pine has become established following a fire about 200 y.a. North of Mt. Berry, in the northern part of the Teton Range, mixed stands of whitebark pine and lodgepole pine occur on an area that burned about 225 y.a. The forest on the summit of Mt. Berry burned about 90 y.a. The reproduction of this burned area is about 75% whitebark pine and 25% lodgepole pine.

Douglas Fir

Extensive stands of Douglas fir occupy the lower slopes of the Gros Ventre Mountains on sedimentary rocks and north-facing slopes at low elevations in eastern Jackson Hole. In much of northern Jackson Hole, Douglas fir is found in special edaphic situations—shallow soils, ridges, and south-facing slopes. On higher-elevation sites, Douglas fir may be seral to subalpine fir, but it maintains itself for several centuries and is perpetuated by periodic disturbance.

Fire in the past played a major role in Douglas fir forests by maintaining an open condition through periodic ground fires. Crown fires undoubtedly occurred in areas of heavy fuel accumulation. The thick bark of Douglas fir allows mature trees to survive most ground fires.

Pure stands of Douglas fir with a mixed age structure on north-facing slopes of Blacktail Butte, a prominence in southeastern Grand Teton National Park, illustrate particularly well the past role of fire and the need for the return of fire to natural ecosystems. Lightning fires swept across the sagebrush flats in the past and ignited these forests every 25 to 100 yr. Large, thick-barked Douglas firs, up to 1.6 m in diameter, have as many as four or five fire scars, some of which date back to the 1600s. The most recent fire, which burned in 1879, affected most of the Butte and left only the larger trees.

From field observations and from reports in the literature for similar ecosystem types (Lyon, 1971), the course of plant succession since the 1879 fire can be postulated. In the summer following the burn, a lush growth of herbaceous species such as fireweed became established, due to an abundant source of nutrients and full sunlight. Scouler's willow and quaking aspen, sprouting from undamaged root systems, attained heights of 1–2 m during the first year and continued rapid growth during the next 2 yr. The invasion of Douglas fir seedlings was slow.

After about 50 yr, such a dense growth of Douglas fir saplings was established that competition became intense. The trees grew in such proximity that branches on the lower half of the trunks died. Aspens and willows died or persisted as relict individuals. The dark forest floor was covered with shade-tolerant pinegrass.

In 1972, 93 yr after the 1879 fire, there is a considerable fuel buildup on Blacktail Butte from dead Douglas fir branches and wood skeletons of aspen and Scouler's willow. If a fire were to reach these stands, most of the young Douglas firs would be killed, but many of the large, thick-barked trees would probably survive.

If fire suppression is continued, it is possible that fire could be prevented from consuming the Blacktail Butte Douglas fir stands for another 50–100 yr, but not indefinitely. In the interim, fuel accumulation would continue to build up to the point where a fire would very likely kill all Douglas firs—even those with the thickest bark. The ecological consequences of such a fire would likely prove highly unfavorable since aspen and willow would have deteriorated beyond the point of potentially successful vegetative reproduction. Also, the seed source for Douglas fir would be drastically diminished.

Sagebrush and Other Shrubs

Fire periodically swept the sagebrush flats of Jackson Hole and the Gros Ventre Valley. Big sagebrush and low sagebrush (*Artemisia tridentata* and *Artemisia arbuscula*) are readily killed by fire. Grasses and other herbaceous plants flourish following the nutrient release and reduction of competition for soil moisture. Sagebrush produces abundant seeds and is capable of rapid reinvasion on sites where competition from grasses is less severe. The grass cover established on productive soils can exclude massive sagebrush seedling establishment for many years. Sagebrush seedlings generally become established on disturbed sites such as pocket gopher mounds or areas trampled by wildlife or domestic livestock.

Near Blacktail Butte, on productive soils where sagebrush is very dense at present, geologist Frank Bradley of the 1872 Hayden survey party reported that "large areas of sage had been burned off, and the grasses had grown up densely, forming fine pasturage and on these we again encountered antelope. . ." (Bradley, 1873). Comparisons of scenes in old photographs with present conditions indicate little change in sagebrush cover on very coarse soils but a considerable increase in cover of sagebrush and other shrubs on finer-textured soils with greater water-holding capacity. We attribute the increase in shrub cover primarily to natural plant succession in the absence of fire. In many localities of the west, and probably in portions of Jackson Hole, heavy range use by cattle or sheep has been a contributing factor in shrub invasion of grasslands. Reduction of fine fuels due to livestock foraging has had a definite influence in reducing fire frequency throughout much of the west (Leopold, 1924; Humphrey, 1958).

Fire greatly influences the shrub composition of various community types. Whereas big sagebrush and low sagebrush are killed even by low-intensity fires, many shrub species are stimulated by fires. Willows (*Salix* spp.), silver sagebrush (*Artemisia cana*), bitterbrush (*Purshia tridentata*), rabbitbrush (*Chrysothamnus nauseosus*), serviceberry (*Amelanchier alnifolia*), chokecherry (*Prunus virginiana* var. *melanocarpa*), snowberry (*Symphoricarpos* spp.), mountain ash (*Sorbus scopulina*), and snowbrush ceanothus (*Ceanothus velutinus*) are some of the shrubs of northwestern Wyoming that may resprout after aerial parts are killed by fire. With many of these species, the stage of growth, the intensity of the fire, and the available soil moisture are critical factors determining whether the plant is killed or stimulated.

ROLE OF FIRE IN MAINTAINING MEADOW AND SAGEBRUSH-DOMINATED HABITATS

Lodgepole pine is invading sagebrush flats on alluvium along the margins of forested moraines in Grand Teton National Park. In the Gros Ventre Valley, a similar invasion is occurring at forest margins. In the Jackson Hole area, recurrent fire seems to have been an important factor in deterring substantial invasion of lodgepole pine into some sagebrush sites. Soil-moisture conditions in sagebrush flats preclude establishment of lodgepole seedlings except in rare favorable years with abundant moisture. Oswald (1966) found that the years 1912, 1925, and 1927 were exceptionally favorable for estabilshment of lodgepole seedlings in the alluvial sagebrush areas along the forest margins in Grand Teton National Park. When a fire kills trees in this situation, it may take years for them to reinvade. In contrast, sagebrush reinvasion can be very rapid.

When a lodgepole pine seed source is deficient, as it may be for high elevation burns, subalpine fir, Engelmann spruce, and whitebark pine become established in burned areas. Many such burns are above the elevational limits of lodgepole or are on unfavorable substrates for its establishment. Reforestation of high-altitude areas takes place very slowly. The importance of fire in maintaining open areas at high elevations in western United States is well documented (Stahelin, 1943; Fonda and Bliss, 1969; Billings, 1969). However, other factors are often involved in the maintenance of subalpine meadows. Despain (1971) has emphasized the importance of edaphic factors in maintaining meadows in the Bighorn Mountains. Most subalpine meadows in the Jackson Hole area appear to be maintained by edaphic conditions, for little conifer invasion is occurring. Massive meadow invasions are occurring in parts of Yellowstone National Park, however.

INFLUENCE OF FIRE ON WILDLIFE HABITAT

The vegetation mosaic produced by a natural fire regime results in a diverse array of wildlife habitats. When fire is excluded from the landscape, plant succession leads to a greater expression of "climatic climax" vegetation than would otherwise be present. Research in other parts of the west has suggested that early successional stages favor most wildlife species.

The infrequency of fire in the Jackson Hole area during the past 75 yr makes a local interpretation of fire's influence on wildlife habitat difficult. There is a critical need for recently burned areas for study purposes. Until we have new burns to study, interpretations can only be made from inference. Only a few tentative generalizations are warranted by the available evidence. However, logic suggests that wildlife populations which evolved under the influence of periodic fire would be best adapted to habitats in early stages of plant succession.

One of the more obvious changes in wildlife habitat due to fire exclusion is the loss of much willow and aspen habitat once used by beaver. Old, barely discernible dams and gnawed stems attest to a more widespread occurrence of these animals in the past. Now that most vegetation is in a late stage of succession, the once abundant food source has greatly declined, and so has the beaver.

On the other extreme, the evidence strongly suggests that mule deer have benefited from fire suppression. From food-habitat studies in the west, it is well established that big sagebrush is very often the staple food item in the winter diet of mule deer. Big sagebrush is highly vulnerable to fire and was generally of a low density and scattered occurrence on winter ranges in former years. With exclusion of fire, the density of sagebrush greatly increased. Some other preferred shrub species also increased in availability. The widespread increase in the critical carrying capacity of winter range appears to be the principal reason for mule deer population increases over pristine levels.

Traditionally, moose have been associated with seral habitats. Interestingly enough, the moose population in northwestern Wyoming was very low during the 19th century, when frequent fires maintained much early successional vegetation. The moose population in Jackson Hole has actually increased with advancing succession. Several contributing factors are undoubtedly involved, but a primary influence appears to be an unprecedented increase in subalpine fir—the staple food item in the diet of a large segment of the moose population. In coniferous forests of Jackson Hole, the present carrying capacity for moose is apparently higher than when much of the forest was in early stages of succession.

Advanced succession has been favorable to cavity-nesting birds such as the tree swallow, mountain bluebird, house wren, mountain and blackcapped chickadees, yellow-bellied sapsucker, woodpeckers, and red-shafted flicker. These species utilize old aspen, which are very often rotten in the center and susceptible to the boring of the sapsucker, woodpecker, or flicker. Opportunities for cavity nesting in young aspen stands are minimal.

MANAGEMENT IMPLICATIONS

Teton National Forest

Fire is a natural phenomenon and has been the agent responsible for periodic removal of the vegetative cover. Strict control of fire during the past three-quarters of a century has largely eliminated its natural role in ecosystems of the Jackson Hole area. Some of the environmental effects and management implications of this long-standing policy are just now surfacing. We are now beginning to understand that changing the effect of one natural force (fire) in the ecosystem has caused the system to respond in certain unanticipated ways. We have found that the energy buildup in the form of accumulated forest litter and some brush species that are favored by lack of fires (big sagebrush) is causing the job of fire control to become more difficult and costly. We also find that the change in natural plant succession due to lack of fire has been detrimental to some wildlife species, whereas others appear to have been favored. It appears that a close reexamination of our fire policies is now in order.

Our investigation suggests that the initiation of a more flexible program—from that of strict fire control to one of fire management—is in order. Appropriate actions that would help bring fire back into the ecosystem appear to include:

1. Delineation of the forest into fire-management zones. In some zones such as valuable timber lands and recreation and developed areas, strict fire control would be practiced. On a large portion of the forest, including wilderness and wildlife habitat, fires would be allowed to burn within predetermined limits.
2. Prescribed burning of certain areas where there is a growing need to return the vegetation to early succession. Candidate types would be livestock and elk ranges where sagebrush has invaded grassland and aspen is deteriorating. If weather conditions permit, a 125-hectare prescribed burn of this type is scheduled for the Gros Ventre winter range in 1973. High priority for prescribed burning should also be made for extensive conifer types where there is a need to break up the fuel and thereby reduce the possibility of large-scale fires.

The foregoing approach to fire management with attendant smoke carries with it the inevitable concern over air pollution. The general public must be made aware that wood smoke composed principally of carbon dioxide and water has been a natural part of the Rocky Mountain ecosystem. In earlier years, a pall of wood smoke hung over the countryside quite frequently during the summer months. Being a natural phenomenon and inevitable, it must be accepted as a natural part of the ecosystem.

Grand Teton National Park

The National Park Service recognizes the need for allowing fire to play a seminatural role in Grand Teton National Park if the management goal of maintaining or restoring ecosystems to as pristine a state as possible is to be realized. During the winter of 1971–1972 a fire–vegetation management plan was formulated for the park and an environmental impact statement was written to cover the effects of its implementation. The plan divides the park into four management zones:

Zone I—All naturally caused fires allowed to burn except under exceptional circumstances (human life endangered, exceptional opportunity for spread to other areas, etc.). Man-caused fires will be extinguished.

Zone II—Naturally caused fires allowed to burn or not allowed to burn according to judgment of a fire-management committee (depending on fire-hazard conditions). Prescribed fires will probably be necessary here.

Zone III—All fires extinguished unless they can be managed as controlled burns. Prescribed fire will be used here to approximate a natural fire frequency.

Zone IV—Developed areas. Manipulation (logging, planting, etc.) used here to approximate effects of fire or managed for aesthetically pleasing appearance.

Additional knowledge of fire behavior in the area will be necessary before full implementation can be attained. Whenever late-summer weather conditions permit, two prescribed burns are planned—one in a Douglas fir stand and one in an aspen–sagebrush area. The primary purpose of these initial prescribed fires will be for research, for obtaining expertise in prescribed burning, and for public education. Also, starting in the summer of 1972, lightning-caused fires will be allowed to burn in the Teton Range (Zone I). In future years, prescribed burning for actual vegetation management is planned.

REFERENCES

Bailey, R. G. (1971). Landslide hazards related to land use planning in Teton National Forest, northwestern Wyoming. *U.S. Department of Agriculture, Forest Service, Intermountain Region*, 131 p.

Baillie-Grohman, W. A. (1884). "Camps in the Rockies." Charles Scribner's Sons, New York, 438 p.

Beaufait, W. R. (1971). Fire and smoke in Montana forests. *In* "Forest Land use and the Environment." (R. M. Weddle, Ed.), pp. 1–23. University of Montana, Montana Forest and Conservation Experiment Station, School of Forestry.

Billings, W. D. (1969). Vegetational pattern near alpine timberline as affected by fire-snowdrift interactions. *Vegetatio* 19, 192–207.

Bloomberg, W. G. (1950). Fire and spruce. *Forestry Chronicle* 26, 157–161.

Boutelle, F. A. (1890). "Report of the Superintendent of Yellowstone National Park." U.S. Government Printing Office, 23 p.

Bradley, F. J. (1873). "Report of Frank H. Bradley, Geologist." U.S. Geological Survey of the Territories, U.S. Government Printing Office.

Brandegee, T. S. (1899). Teton forest reserve. *House Document No. 5, 55th Congress, 3d session. Serial 3763.* Washington, D.C.

Brown, D. (1971). "Bury My Heart at Wounded Knee." Holt, Rinehart, & Winston, 487 p.

Buxton, E. N. (1893). "Short Stalks; or Hunting Camps." Edward Stanford, London.

Cole, G. F. (1969). "The Elk of Grant Teton and Southern Yellowstone National Parks." Unpublished manuscript.

De Lacy, W. W. (1876). A trip up the South Snake River in 1863. *Historical Society of Montana Contributions* I, 113–118.

Despain, D. G. (1971). The vegetation of the Bighorn Mountains of Wyoming in relation to substrate and climate. Ph.D. thesis, University of Alberta, 136 p.

Doane, G. C. (1877). "Expedition of Lieutenant G. C. Doane—Fort Ellis, Montana, to Fort Hall, Idaho. Oct. 11, 1876, to Jan. 4, 1877." U.S. Department of the Interior, National Park Service. Photocopy of typed manuscript, 41 p.

Farmer, R. E. (1962). Aspen root sucker formation and apical dominance. *Forest Science* 8, 403–410.

Fonda, R. W., and Bliss, L. C. (1969). Forest vegetation of the montane and subalpine zones, Olympic Mountains, Washington. *Ecological Monographs* 39, 271–301.

Fowells, H. A. (1965). Silvics of forest trees of the United States. *U.S Department of Agriculture, Forest Service, Agricultural Handbook No.* 271, 762 p.

Frison, G. C. (1971). Prehistoric occupation of the Grand Teton National Park. *Naturalist* 2, 35–37.

Fryxell, F. (1932). Thomas Moran's journey to the Tetons in 1879. *Augustana Historical Society Publication No.* 2, 3–12.

Graham, S. A., Harrison, R. P., and Westell, C. E. (1963). "Aspens: Phoenix trees of the Great Lakes region." University of Michigan Press, Ann Arbor.

Gruell, G. E. (1973). An ecological evaluation of Big Game Ridge, Teton Wilderness, Teton National Forest, northwestern Wyoming. *U.S. Department of Agriculture, Forest Service* In press.

Hague, A. (1886). Unpublished manuscript in the National Archives, Washington, D.C.

Hanna, L. A. (1934). The major plant communities of the headwater area of the Little Laramie

River, Wyoming. *University of Wyoming Publications in Science, Botany I* **10**, 243–266.

H[illegible]RRIS, M. (1886). "Report of the Superintendent of Yellowstone National Park." U.S. Government Printing Office, 13 p.

H[illegible]YDEN, ELIZABETH W. (1963). "From Trapper to Tourist in Jackson Hole." 48 p.

H[illegible]LBROOK, S. H. (1943). "Burning an Empire." The Macmillan Company, New York.

H[illegible]USTON, D. B. (1971). Ecosystems of National Parks. *Science* **172**, 648–651.

H[illegible]OUSTON, D. B. (1973). Wildfires in northern Yellowstone National Park. *Ecology*. In press.

H[illegible]UMPHREY, R. R. (1958). "The desert grassland: A history of vegetational change and an analysis of causes." University of Arizona Press, 74 p.

J[illegible]CKSON, W. H., AND DRIGGS, H. R. (1929). "The pioneer photographer: Rocky Mountain adventures with a camera." The World Book Company, Yonkers-on-Hudson, New York.

K[illegible]LEIN, W. H., STIPE, L. E., AND FRANDSEN, L. V. (1972). "How damaging is a mountain pine beetle infestation?" *U.S. Department of Agriculture, Forest Service, Division of Timber Management,* Ogden, Utah.

LEOPOLD, A. (1924). Grass, brush, timber, and fire in southern Arizona. *Journal of Forestry* **22**(6), 1–10.

LYON, J. (1971). Vegetal development following prescribed burning of Douglas fir in southcentral Idaho. *U.S. Department of Agriculture, Forest Service Research Paper* INT-105, 30 p.

MATTES, M. J. (1946). Jackson Hole, crossroads of the western fur trade, 1807–1829. *The Pacific Northwest Quarterly* **37**, 87–108.

MATTES, M. J. (1948). Jackson Hole, crossroads of the western fur trade, 1830–1840. *The Pacific Northwest Quarterly* **39**, 3–32.

OOSTING, H. J., AND REED, J. (1952). Virgin spruce-fir forest in the Medicine Bow Mountains, Wyoming. *Ecological Monographs* **22**, 69–91.

OSWALD, E. T. (1966). "A synecological study of the forested moraines of the valley floor of Grand Teton National Park, Wyoming." Unpublished Ph.D. thesis, Montana State University, 101 p.

RAYNOLDS, W. F. (1868). Report on the exploration of the Yellowstone and Missouri Rivers, in 1859-60. *40th Congress, 2nd session, Senate Executive Document Number 77, Serial Number 1317,* Washington, D.C.

REED, R. M. (1969). "A study of forest vegetation in the Wind River Mountains, Wyoming." Unpublished Ph.D. thesis, Washington State University, 77 p.

ROE, A. L., AND AMMAN, G. D. (1970). The mountain pine beetle in lodgepole pine forests. *U.S. Department of Agriculture, Forest Service Research Paper INT-71,* 31 p.

SARGENT, HELEN C. (1963). Mr. and Mrs. B. F. Bondurant, early pioneers of the Fall River Basin. *In* "Tales of the Seeds-Ke-Dee," p. 229–252. The Sublette County Artists' Guild, Big Mountain Press, Denver.

STAHELIN, R. (1943). Factors influencing the natural restocking of high altitude burns by coniferous trees in the central Rocky Mountains. *Ecology* **24**, 19–30.

STEWART, O. C. (1956). Fire as the first great force employed by man. *In* "Man's role in changing the face of the earth." (W. L. Thomas, Ed.), pp. 115–133. University of Chicago Press, Chicago.

TAYLOR, A. R. (1971). Lightning—agent of change in forest ecosystems. *Journal of Forestry* **68**, 477–480.

TAYLOR, D. L. (1969). "Biotic succession of lodgepole pine forests of fire origin in Yellowstone National Park." Ph.D thesis, University of Wyoming, 320 p.

TOWN, F. E. (1899). Bighorn Forest Reserve (Wyoming). *U.S. Geological Survey 19th Annual Report, 1897–98,* 165–190.

WEDEL, W. R., HUSTED, W. M., AND MOSS, J. H. (1968). Mummy Cave: Prehistoric record from Rocky Mountains of Wyoming. *Science* **160**, 184–186.