1974

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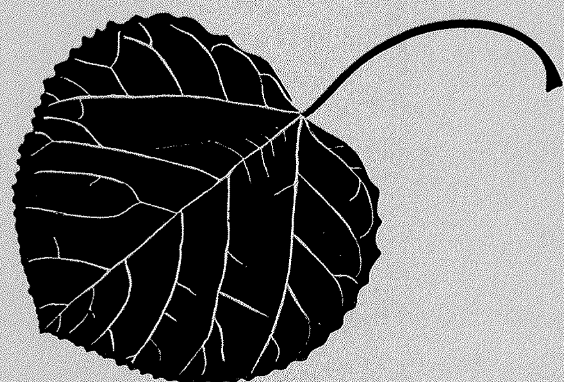

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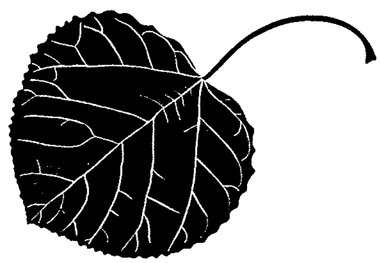

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Contents

Abstract

Evidence from stand age of lodgepole pine and ring counts of fire scarred conifers suggests that the majority of aspen communities in Jackson Hole burned between 1840 and 1890. Determination of aspen age structure within selected stands on elk winter range showed that establishment occurred in this period. Stand age varied between 9 and 31 years. Historical narratives suggest that elk were a major biotic influence on aspen during early successional stages. Little successful establishment of aspen has taken place on elk winter ranges since 1900.

Aspen regenerates successfully without fire within exclosures. It also regenerates successfully without fire within deteriorating stands and on the margin of some stands that are not on elk winter range, but stocking levels are believed to be generally below those which created parent stands.

Aspen has regenerated successfully in the few burns which have occurred in aspen communities since 1930. Fire suppression during the past 50-70 years is considered a major factor contributing to the current decline of aspen in Jackson Hole. Our study suggests that without fire, particularly on elk winter range, aspen stands will continue to deteriorate. Whether current browsing by elk and moose is capable of suppressing aspen regeneration following burning can only be answered through large-scale return of fire to aspen communities.

Introduction

The decline of aspen (*Populus tremuloides* Michx.) and the sparsity of successful regeneration (Figs. 1, 2) have been a source of concern in the Jackson Hole area of northwestern Wyoming for over 30 years. Traditionally, this decline has been attributed to overbrowsing by elk. Our preliminary observations suggested that proponents of this interpretation had not considered other biotic and abiotic influences on aspen. It was particularly apparent that studies of aspen in this area had neglected the role of fire. Since there is abundant evidence of past fires in forests of the Jackson Hole area, we suspected that this factor should be investigated in some depth. From a literature search, it was also evident that past historical interpretations of the Jackson Hole elk herd were made without benefit of important narratives. These narratives indicate that wintering elk were numerous in Jackson Hole when current aspen stands were in early successional stages.

The study area is located just south of Yellowstone National Park, in northwestern Wyoming (Fig. 3). Aspen stands in this region occur largely on public land managed by the Forest Service (Teton Division of Bridger-Teton National Forest) and the National Park Service (Grand Teton National Park). Our study was initiated to contribute to a better understanding of the ecology of aspen communities and to aid these agencies in meeting land management objectives.

Fig. 1. Ninety-year old aspen stand in an advanced stage of deterioration. Suckers are kept at heights less than 1 m by elk and moose browsing. Lower Spread Creek, Bridger-Teton National Forest.

Fig. 2. Deteriorating aspen stand. Pacific Creek Road, Grand Teton National Park.

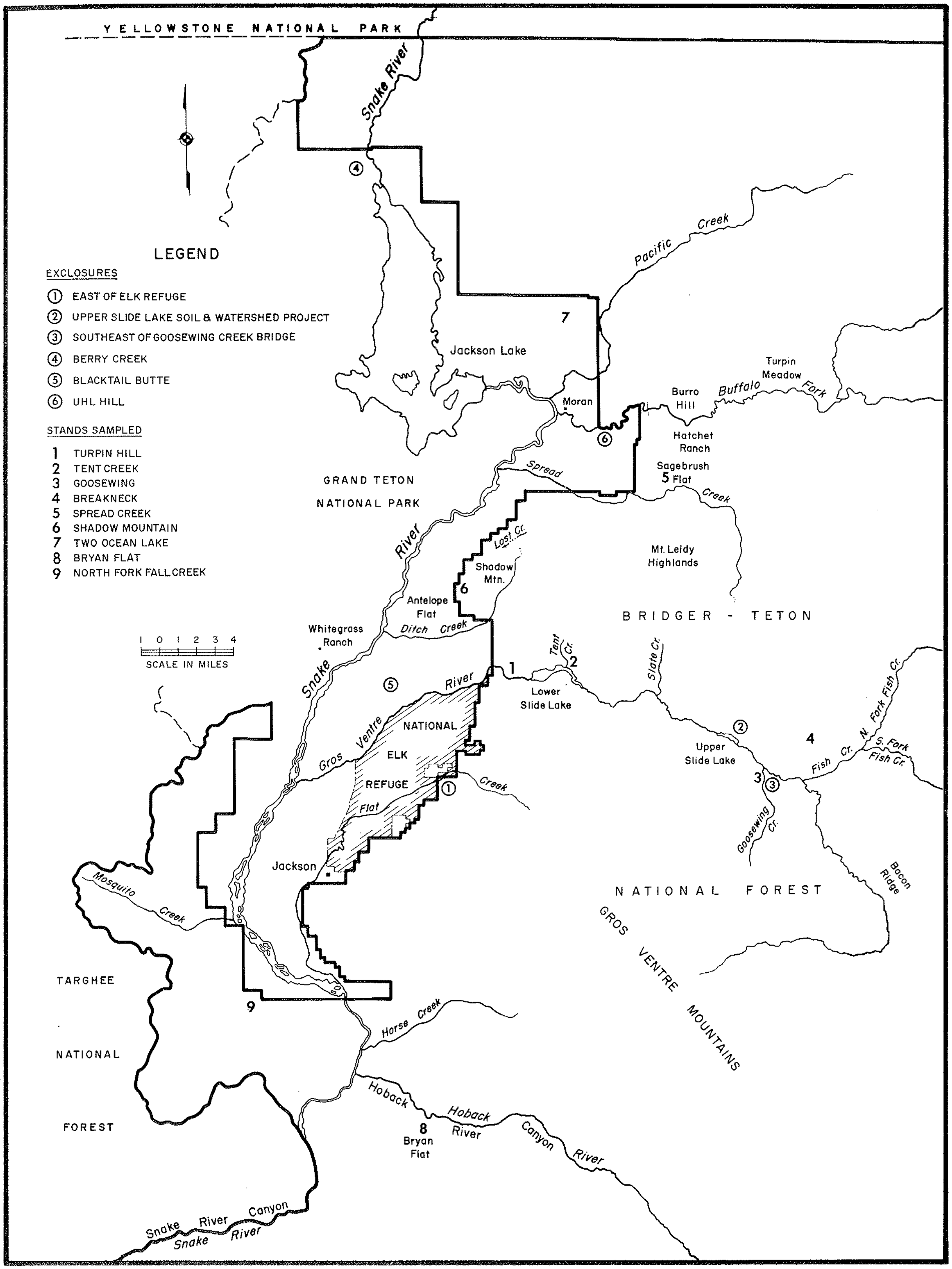


Fig. 3. Location of aspen stands sampled and exclosures.

Acknowledgements

Grateful acknowledgement is made to Douglas Houston of Yellowstone National Park who provided able assistance and critical review of several manuscripts. Appreciation is also extended to Gordon Gullion, University of Minnesota, Cloquet Research Station; William Laycock, Norb DeByle, Joe Basile, George Schier, Intermountain Forest and Range Experiment Station; Richard Krebill, Research, Washington Office; Kimball Harper, Brigham Young University; and Ivan Thorton, Sawtooth National Forest; for helpful discussion and criticism of the manuscript. We thank Edward and Betty Komarek, Tall Timbers Research Station; Don Despain, Yellowstone National Park; Bob Wood and Dale Taylor, Grand Teton National Park; James Yorgason, Wyoming Game and Fish Department; Tom Phillips, Sawtooth National Forest; Paul Shields, Region Four, Forest Service, Ogden; and Jim Connor, Harold Edwards and Gene Benedict of Bridger-Teton National Forest for reviewing the manuscript. manuscript.

General Ecology of Aspen in Jackson Hole

Aspen is a conspicuous tree species in Jackson Hole. Its bright green deciduous leaves and white bark form a contrast to the dark green of conifer forest and light grey of sagebrush vegetation. This contrast is heightened in late September and early October when deterioration of chlorophyll pigments results in yellow foliage of aspen just before leaf fall. In spite of its esthetic importance, aspen plays a relatively minor role here in the total vegetal cover. Baker (1925) pointed out that aspen forest covered less than 0.5 percent of the Teton Division, Bridger-Teton National Forest, whereas some National Forests in Colorado and Utah had 15 percent to 35 percent aspen cover.

Aspen is often found at elevations between 1830 m and 2740 m (6,000 - 9,000 feet) in Jackson Hole, but occurs primarily between 1980 m and 2280 m (6,500 - 7,500 feet). On south-facing slopes of the Gros Ventre Mountains and Mt. Leidy Highlands, it occasionally is found at elevations of 2740 m (9,000 feet).

Aspen cannot survive or reproduce under the shade of competing vegetation. In Jackson Hole it occurs in pure stands, in stands being replaced by conifers, or in stands dominated by conifers. In competition with conifers it thrives for several decades following fire, but is gradually replaced. Primary competing species are Douglas-fir or lodgepole pine. Douglas-fir stands typically contain a few scattered living aspen and numerous dead trunks.

Aspen stands in Jackson Hole are commonly found at ecotones between conifer forest and sagebrush-grass vegetation. Stands are often near the bases of slopes, where they may receive moisture through underground seepage. Optimum development is reached on deep loam soils. Soils of most stands are well drained, but some are subject to saturation or even inundation for a month or more following spring snowmelt. Bailey (1971) noted that aspen stands are often indicators of unstable slopes with active slides in the Bridger-Teton National Forest. Our observations indicate that the majority of stands occur on stable substrates, however.

As in other areas, vegetative root suckering is the primary method of reproduction. Reproduction by seed in the Rocky Mountains appear to be rare even though viable seeds are apparently produced.

Compared to coniferous forests of the area, aspen communities have a lush understory rich in herbaceous and shrub species. Some of the most characteristic understory species include *Epilobium angustifolium*, *Galium boreale*, *Geranium nervosum*, *Lupinus argenteus*, *Rosa woodsii*, *Potentilla glandulosa*, and *Achillea millefolium*. Other common species include *Thalictrum fendleri*, *Fragaria vesca*, *Shepherdia canadensis*, *Amelanchier alnifolia*, *Prunus virginiana var. melanocarpa*, *Syphoricarpos spp.*, *Aster* spp., *Calamagrostis rubescens*, *Bromus anomalous*, and *Agropyron* spp.

Previous Studies Relevant to Disturbance and Aspen Regeneration

The importance of disturbance in the ecology of aspen is well documented. Shirley (1931) recognized that "light" burning following clearcutting stimulates sucker formation. Graham et al. (1963) considered cutting and/or burning of aspen stands necessary for successful regeneration in Michigan. The decline of aspen in Michigan during recent years was shown to be attributable to plant succession following successful suppression of forest fires. Baker (1925) felt from evidence in Utah that fires in earlier years encouraged persistence of aspen. Stahelin (1943) and Daubenmire (1943) recognized the importance of fire in maintaining aspen stands of the Rocky Mountains. Stahelin found that aspen spread by root suckering following fire in the Medicine Bow Mountains of Wyoming and attained dominance in all areas where remnant aspens existed in prefire stands and which conformed to its site requirements.

In an earlier study in Colorado, Clements (1910) found that aspen sprouts grew more rapidly after an intense fire than after a light fire. Sampson (1919) reported that 20,000 to 83,000 aspen sprouts per acre (48,000 to 199,000/ha) occurred after cutting stands in Utah. Smith et al. (1972), in another Utah study, found 30,000 to 50,000 stems per acre (72,000 to 120,000/ha) the first year after clearcutting. In a New Mexico study, Patton and Avant (1970) report a 5 year average of 12,960 sprouts per acre (31,000/ha) after burning *versus* 100 sprouts per acre (240/ha) in adjacent unburned forests.

Horton and Hopkins (1966) summarized the effects of fire on aspen regeneration. Fire can kill established aspen stems without root damage; it can reduce or eliminate the canopy and competing lesser vegetation, thus increasing solar radiation on the ground and increasing soil temperature; it reduces or removes insulating duff layers; and it increases soil heat absorption by exposing and blackening the ground surface. These workers found that to produce prolific suckering, a moderately intense fire which kills all aspen and removes litter and much of the duff layer is desirable and that light burning is undesirable. They felt that rarely, if ever, is a fire in aspen so intense that it kills the root system and prevents suckering.

Investigations by Farmer (1962), Eliasson (1971), and Schier (1973) have indicated that suckers develop on aspen roots after apical dominance, mediated by the action of auxin, has been abolished by killing stems or decreased by a disturbance that altered the environment or damaged stems or roots.

Although the importance of fire in aspen ecology is well documented, disturbance may not be essential for perpetuation of aspen in all instances. Reed (1969; 1971) considered aspen a climax species not needing disturbance for regeneration in the Wind River Mountains of Wyoming. Alder (1970) found that age profiles for aspen stands in Utah and northern Arizona showed a somewhat normal distribution of ages rather than fitting an even-aged pattern and did not regard disturbance as necessary for regeneration.

Past Role of Fire in Jackson Hole and its Apparent Relation to Aspen Ecology

Examination of photographs and narratives from the late 1800's and early 1900's reveals that the decline of aspen in this area has been rather abrupt, since most aspen stands were flourishing prior to 1930.

The widespread occurrence of fires in this area and the role of fire in stimulating aspen regeneration were recognized in the late 1800's during government surveys. Hague (1886) noted that in northern Yellowstone Park aspen was "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." Brandegee (1899) surveyed forest conditions on the Teton Forest Reserve for the U. S. Geological Survey in 1897. His report 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 simply and solely (due) 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."

Seventy-five years later, the contrast of ecological conditions from those observed by Brandegee is striking (Fig. 4). Few fires have burned in this area during the 20th century. Abundant photographic evidence shows that coniferous forest cover has increased and conifers continue to invade open areas (Loope and Gruell, 1973). Aspen stands are deteriorating, while successful regeneration is localized. Comparisons between aerial photographs taken in 1967 and those of 1945 show that stand deterioration in given localities has accelerated during recent years (Fig. 5).

The fire history of the Jackson Hole area has been summarized by Loope and Gruell (1973). Aboriginal populations undoubtedly were an ignition source, but the incidence of lightning fires was sufficient to insure recurrent periodic burning and restoration of early stages of plant succession. Removal of aboriginal man has not eliminated the occurrence of man-caused fires. In recent years, lightning has been responsible for between 50 percent and 60 percent of the ignitions. Although the frequency of ignitions since 1900 may differ little from that of previous centuries, the average area burned has been greatly reduced through fire suppression efforts. Removal of light fuels by livestock has also been a factor contributing to rapid suppression of fire in some areas.

In the valley of Jackson Hole, very large fires burned in 1856 and 1879. In the Gros Ventre River valley, some of the largest fires of the 19th century occurred about 1842, 1872, and 1879. Evidence from stand age of lodgepole pine and from ring counts of cross-sections removed from fire-scarred aspens and conifers and of unscarred aspens suggests that the majority of aspen-dominated areas of

Jackson Hole burned between 1840 and 1890. These findings coincide with those of Krebill (1971), who randomly selected 100 aspen stands for sampling while conducting an aspen disease study on the Gros Ventre elk winter range. Increment cores from two mature aspens closest to the center of each plot showed that 46 percent regenerated between 1871 and 1890, while 79 percent had inception dates between 1851 and 1900. Only 9 percent of the sample regenerated before 1850 and 12 percent between 1901 and 1930.

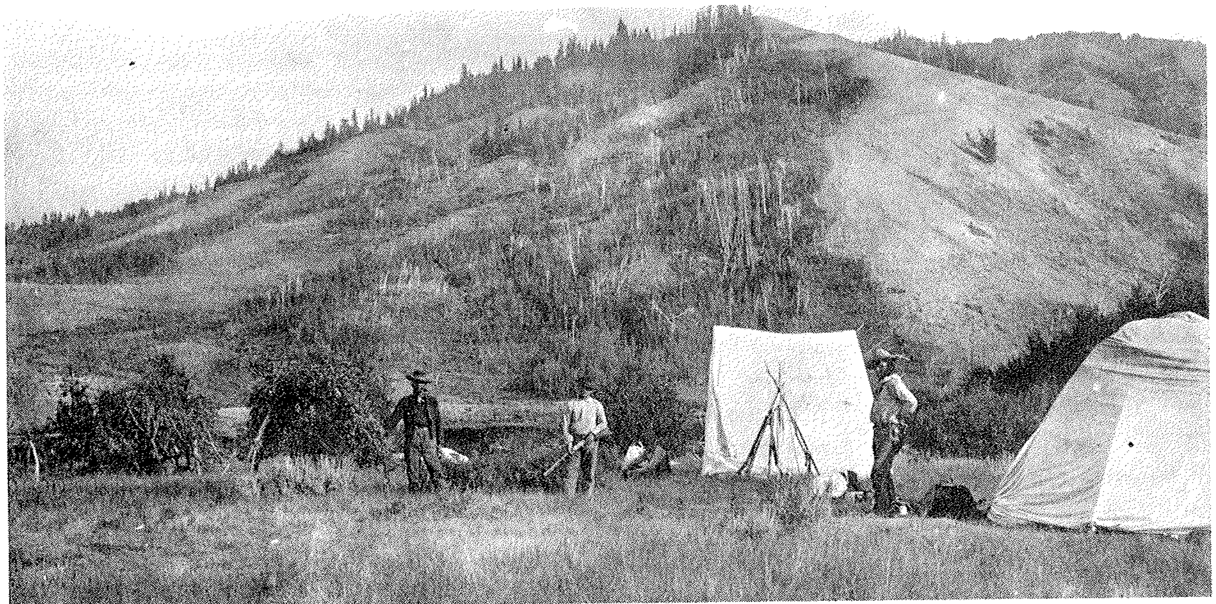
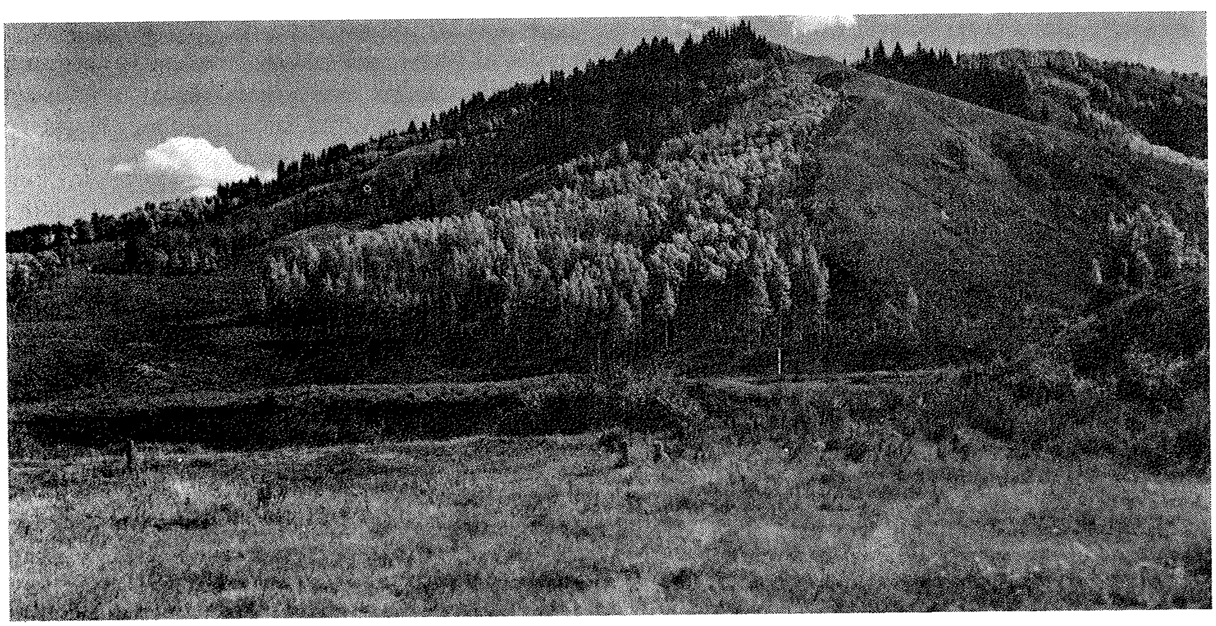


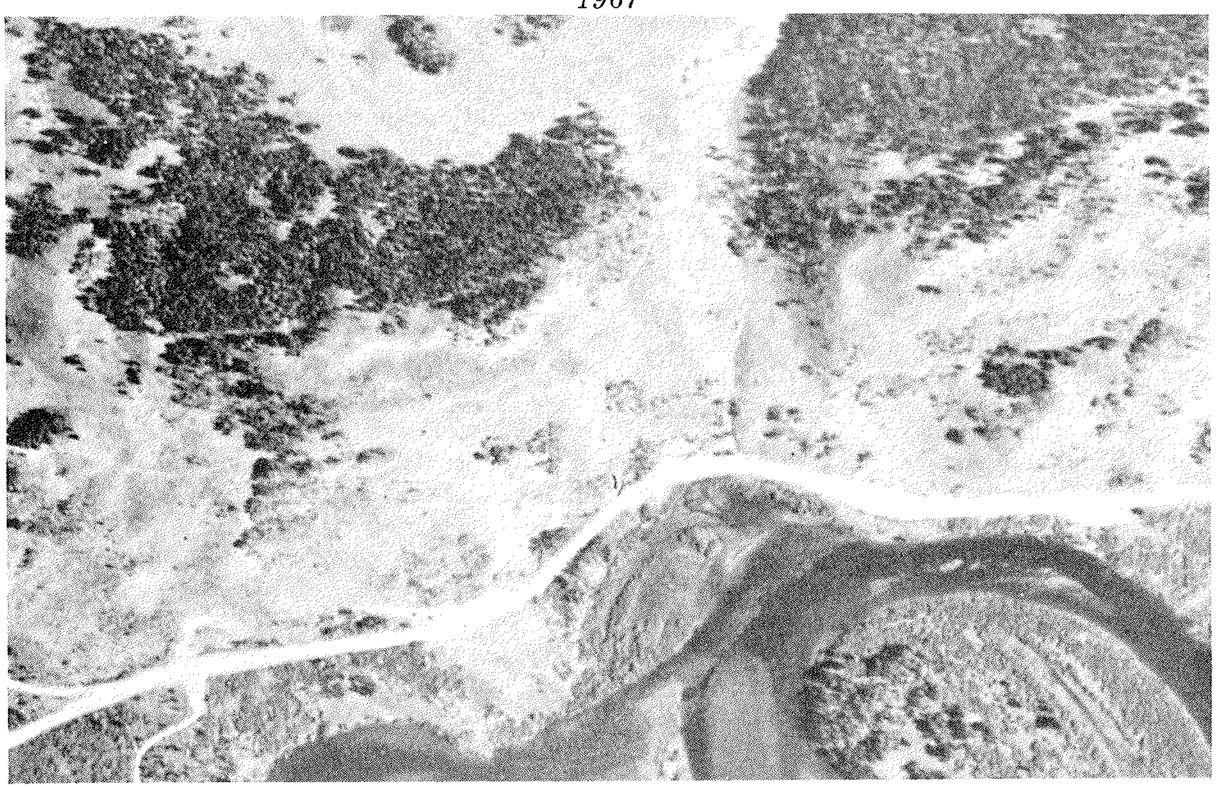
Fig. 4. Near the outlet of Goosewing Creek on the Gros Ventre winter range, Bridger-Teton Forest (above). Circa 1890. Tree cover on near slope is predominately aspen in an early successional stage. Elk trails can be seen where sparsely vegetated slope meets aspen. Courtesy of Western History Department, University of Wyoming. (Below). Sept., 1969. The aspen stand on near slopes is now 90-100 years of age. Spruce are re-invading the aspen. The elk trails are no longer evident since winter supplemental feeding has drawn the elk from this locality.



1945

Fig. 5. Aerial photographs showing decline of aspen stands between 1945 (above) and 1967 (below). East of Jackson Lake Junction at Oxbow Bend of Snake River, Grand Teton National Park.

1967



Effects of Disease on Aspen

Various agents contribute to the natural decline of aspen stands in the absence of major disturbance. Baker (1925) concluded that aspen is extremely susceptible to attack of *Fomes igniarius* (heart rot) and *Fomes applantus* (butt rot), and is commonly injured by many other biotic and climatic agents. Fungi and domestic grazing damage were considered the only influences having a great bearing on management in the central Rocky Mountains.

Krebill (1972), identified causes of aspen mortality on the Gros Ventre elk winter range. He states:

> "Death resulting from wind breakage or windfall was infrequent in small trees but rather common in the larger tree classes. *Cenangium singulare*, cause of sooty bark canker, was the single most injurious pathogen found on dead trees . . . and it too was especially prevalent in the larger tree classes. The third group was composed of trees that seemed to have died from a mixture of the following: bark wounding by elk or moose; infestation by stem-boring insects (probably species of *Agrilus* . . .); infection by bark fungi, including *Cytospora sp.*, suppression; and occasional sunscald. Mortality caused by this mixed category was especially prominent among the smaller trees."

Considering an estimated 1,500,000 mature aspens in the study area Krebill concluded:

> "If the 3.6 percent mortality rate of 1970 remains stable in the future, aspen would decline to about 500,000 trees by year 2,000, and to only 40,000 by year 2070."

This trend was hypothesized on the condition that ungulate browsing would continue to prohibit replacement of dying overstory trees and that exclusion of fire would continue to allow invasion of conifers.

Past and Present Status of Ungulate Populations in Jackson Hole

It is impossible to evaluate the influence of browsing by native ungulates on aspen regeneration in Jackson Hole without examining the history of the Jackson Hole elk (*Cervus canadensis nelsoni*) herd. This history has been the subject of much confusion and misinformation. Statements have frequently been made that elk were originally "plains animals" or that, although elk summered in the mountains, there was not a wintering elk herd in Jackson Hole prior to settlement.

Murie's (1940) review of historical information establishes that the Jackson Hole elk were summer residents of the mountains prior to settlement of Wyoming. Osborne Russell, an observant fur trapper, noted the presence of large numbers of elk in the Yellowstone Park region during the 1830's (Haines, 1955). The principal area of summer occurrence as reported by Hague (1893) was the headwaters of the Snake River within what is today southern Yellowstone Park and the Bridger-Teton National Forest.

These elk migrated to valley winter ranges along drainages of the Buffalo Fork, Spread Creek, and Gros Ventre River, and other tributaries of the Snake River. Doane (1877) reported occurrence of elk near Moran and in the hills on the east side of Jackson Hole in December 1876. Emile Wolf, an early settler, in later years described wintering elk in the lower valley of Jackson Hole in the late 1870's (Murie, 1951). Hough (1887) tells of a hunter and trapper reporting 15,000 wintering elk south of Jackson Lake on the Shoshone or Snake River. Early residents of Jackson estimated 20,000 elk on Flat Creek and vicinity in November 1896 after an unprecedented storm (Anderson, 1949; Hedrick, 1952). Irland (1903) reported that a herd of 12,000 elk passed in view of the town of Jackson at one time during the winter of 1902-03. Price (1898) reports that an estimated 10,000 elk wintered in the Gros Ventre Valley during the winter of 1896-97.

Confused speculation has resulted in the account of the Jackson Hole elk migrating through Hoback Canyon to the Red Desert (south of Pinedale, Wyoming) to winter. Cole (1969) suggests the Preble (1911) may have been the originator of this idea. Preble said that the elk had formerly migrated out of Jackson Hole to the plains — without citing an information source. This line of thinking may have been influenced by certain settlers who feared that the United States government would usurp their lands to save the elk herd (Irland, 1903). The idea of Jackson Hole elk migrating to the Red Desert became all but an established tradition when repeated by Graves and Nelson (1919) and Sheldon (1927) without supporting evidence. In subsequent years, many others have perpetuated this idea.

Cole (1969) suggests that much of the confusion over Jackson Hole elk migrating to the Red Desert (by way of the Hoback watershed) stems from a lack of knowledge concerning past relationships between Jackson Hole and Green River winter herds. The evidence is convicing that there was a large winter herd in Jackson Hole before settlement. It is also reasonably certain that the Green River Valley was historic winter range for a large number of elk (Bailey, 1906;

Anthony, 1911). Very often the Green River winter range was referred to as the "Red Desert," since the confines of the Red Desert were rather loosely defined.

There is also evidence that a segment of the Green River herd intermingled with Jackson Hole elk along major hydrographic divide summer ranges in the Upper Gros Ventre, Spread Creek, and Buffalo Fork drainages. These animals were not part of what has been traditionally called the Jackson Hole herd and apparently migrated to winter range in the Green River Valley from the north after crossing the Gros Ventre-Green River divide in the vicinity of Bacon Ridge and the head of Fish Creek. Upon reaching the Green River, many thousands passed each year in the vicinity of Cora, Wyoming, seven miles northeast of Pinedale (Dunham, 1898).

Elk population estimates in Jackson Hole for the circa 1900 elk herd have ranged from 25,000 to 40,000 (Irland 1903; Gunther, 1912; Kneipp, 1915). Which of these estimates is most realistic, cannot be determined. Available evidence suggests the last population high may have occurred in 1896. Heavy losses were reported in the Gros Ventre and in the valley of Jackson Hole in the winter of 1896-97 (Barnes, 1912; Bailey et al., 1915). According to Bailey, the collection of many elk teeth (adult animals) in the spring of 1897 was evidence of a far greater loss than took place during hard winters which followed. These losses, those to poaching, usurption of winter range for ranching and subsequent herd losses during the winters of 1908-09 1909-10 and 1910-11 appear to have contributed to herd reductions which were never made up (Gruell, 1973).

The first quantitative information on Jackson Hole elk was obtained in 1916 when a total of 19,763 were counted. This census data and that in subsequent years up to the winter of 1955-56 are presented by Anderson (1958). Cole (1969) interpreted the results as follows:

> "An average winter count of about 20,000 elk (19,238 to 22,035) was obtained during five winters within the first 20-year period from 1915 to 1935. An average of 16,300 elk per winter (15,014 to 17,902) was counted during six winters within the next 19-year period. An average winter count of about 14,000 elk (11,057 to 17,924) was obtained during six of the winters since 1955-56 (Yorgason, writ. comm., 1968). The counts since 1955 did not always include scattered groups off main wintering areas and the actual average may be slightly higher than shown."

Counts on the Gros Ventre winter range, which is the focal point of this paper, have ranged from highs of 6,273 (1916); 9,128 (1925); 5,543 (1927); 6,079 (1935) and 5,463 (1945) to lows of 2,273 (1921); 2,605 (1941); 2,310 (1949) and 2,104 (1956). The high count in the past ten years was in 1969 when 3,600 were tallied on the three feedground. This count did not include free ranging animals of which there were small groups scattered over a wide area.

The present elk population wintering in areas drained by the upper Snake River (above Alpine, Wyoming) and its tributaries numbers between 15,000 and 20,000, even though about half the former winter range, including many key areas, has been preempted for agriculture and development. Of these, 7,000 to 8,000 are fed supplements on the National Elk Refuge near Jackson, while 6,000 to 8,000 winter at nine smaller feedgrounds operated by the Wyoming Game and Fish Department. The balance free-range on traditional wintering areas consisting of south-facing slopes and adjacent terrain — primarily on the Buffalo Fork, Spread Creek, and Gros Ventre drainages. Local distribution on the winter range has changed with supplemental feeding (Anderson, 1958). Winter feeding has also minimized losses and as a result, population levels are less subject to pronounced fluctuations. Where population control was once by means of periodic heavy winter die-offs, it is now achieved by hunter harvests.

A variety of information suggests that the moose (*Alces alces shirasi*) is a relative newcomer to Jackson Hole. The diary of Osborne Russell (Haines, 1955) indicates that moose were not observed during the trapping era of the 1830's and early 1840's. In the 1870's members of the Hayden Survey rarely encountered moose. Populations increased slowly during settlement of the area in the early 1880's. The low population level of the early 1900's is indicated by the issuance of 27 moose licenses statewide in 1916 with a resulting kill of 17 animals. In 1972, over 900 moose were killed in the Bridger-Teton National Forest.

Mule deer (*Odocoileus hemionus*) populations in Jackson Hole have shown significant increases since settlement (Bridger-Teton National Forest files). As with moose, a variety of information including that of Murie (1951) indicates that deer were scarce before 1930 and that they had increased markedly by 1950. Various information suggests that population levels in the early 1970's have declined from those of the late 1950's and 1960's.

Historic narratives and statements by early settlers indicate that several thousand pronghorn antelope (*Antilocapra americana*) summered in the valleys of the Snake, Gros Ventre and Hoback drainages. Shortly after 1900, numbers had been reduced to a few widely scattered bands numbering only a few animals. In recent years, pronghorns have been frequenting Jackson Hole once again in increasing numbers. The population currently is estimated to exceed 500.

Small herds of bighorn sheep (*Ovis canadensis*) occur in the vicinity of the study area in Jackson Hole. These animals were much more numerous in earlier years. As in other areas of the West, population reductions are believed to have been associated with settlement.

Bison (*Bison bison*) were summer residents of Jackson Hole through the first half of the 19th century, but were eliminated prior to settlement (Fryxell, 1928). Since bison are primarily grazers, their impact on aspen was apparently minimal. Meagher (1973) found that shrubs made up only 1 percent of the diet of Yellowstone bison and did not mention aspen as one of the species browsed.

Any discussion of aspen ecology would be incomplete without mention of beaver (*Castor canadensis*). Though not an ungulate, this rodent was formerly abundant when aspen was in early successional stages. The remains of old dams and aspen cut by beaver attest to a period when impacts on aspen were considerable. Currently, populations are quite low on the Spread Creek and Gros Ventre drainages. Where viable populations exist, they are almost entirely confined to localities where willow species are abundant.

Domestic cattle were first introduced into Jackson Hole in 1883. By World War 1, 15,000 were under permit on what is now the Teton Division of the Bridger-Teton National Forest. Of these, about 9,000 wintered in Jackson Hole (Bailey et al., 1915). Numbers have fluctuated since, currently running about 14,500 on the Teton Division. Domestic sheep have always been confined to lands west and south of the Hoback River. Numbers were reported to have been 45,000 at the time of the establishment of the Teton National Forest in 1908. By 1913, 20,000 were grazed annually, whereas currently only 5,000 are permitted on the Teton Division of the Bridger-Teton National Forest.

Study Methods

Plot Sampling

Sixteen mature aspen stands were sampled for age structure in September and October 1971 (Fig. 3). Those selected were representative of contrasts in stand condition in Jackson Hole. Plots were chosen as representative sites within representative stands. Eight (1A-5B) were on the Gros Ventre winter range and Spread Creek locality where browsing intensity is generally high, successful regeneration of low occurrence, and young stands confined to restricted localities. Six plots (5C, 6A-8B) were in localities where elk browsing intensity is low. One of these plots (5C) was considered an exception for Spread Creek, presumably having developed under low levels of elk foraging. Two plots (5D and 9) were in stands of recent fire origin (Fig.6, Table 1).

All mature aspen were recorded in 5 m x 25 m plots (exception 5D) and felled with a chain saw (245 total). After drying, cross-sections, which had been cut near ground level, were smoothed with a belt sander. Annual rings were counted and diameters measured. Heart rot prevented exact aging of about 10 percent of the samples.

Suckers were also counted in each 5 m x 25 m plot (Table 1). Height and growth form of suckers, intensity of ungulate browsing, species responsible, understory flora, and fire evidence were recorded in each plot.

Age structure of young aspen which were regenerating successfully without fire, was sampled by cutting cross-sections from suckers in 3 m x 3 m plots. Sampling was confined to 5 plots (Fig. 7 and Table 2), which were in widely separated areas. Stands sampled were considered representative, being comparable to those in other restricted localities where aspen establishment in recent years has been successful. New growth was largely confined to stand margins.

Interpretations in Recently Burned and Cut Areas

Observations of aspen stands that regenerated following fires in 1930, 1932, 1934, 1940, 1952, 1963, 1966 and 1972 in the Bridger-Teton National Forest (some located outside the Jackson Hole area) provided an opportunity to study early stages of succession following fire. One stand was found in Grand Teton National Park which had regenerated following cutting.

Interpretations in Exclosures

Observations were made in several fenced range exclosures (.1-150 hectares) in the Bridger-Teton National Forest and Grand Teton National Park. These exclosures made it possible to compare the success of aspen regeneration where ungulate browsing was reduced or excluded with that of adjacent aspen which had been browsed by native ungulates.

Interpretations in the Bridger-Teton National Forest and Grand Teton National Park

A wide cross-section of aspen communities on the Forest was observed by Gruell during the period 1967-71. Contrasts in aspen condition, ungulate distribution, and browsing intensities were recorded. In 1972, we made a concerted effort to examine localities that had not been covered in the Teton Division and to appraise aspen condition in Grand Teton National Park. Interpretations to date were examined and refined.

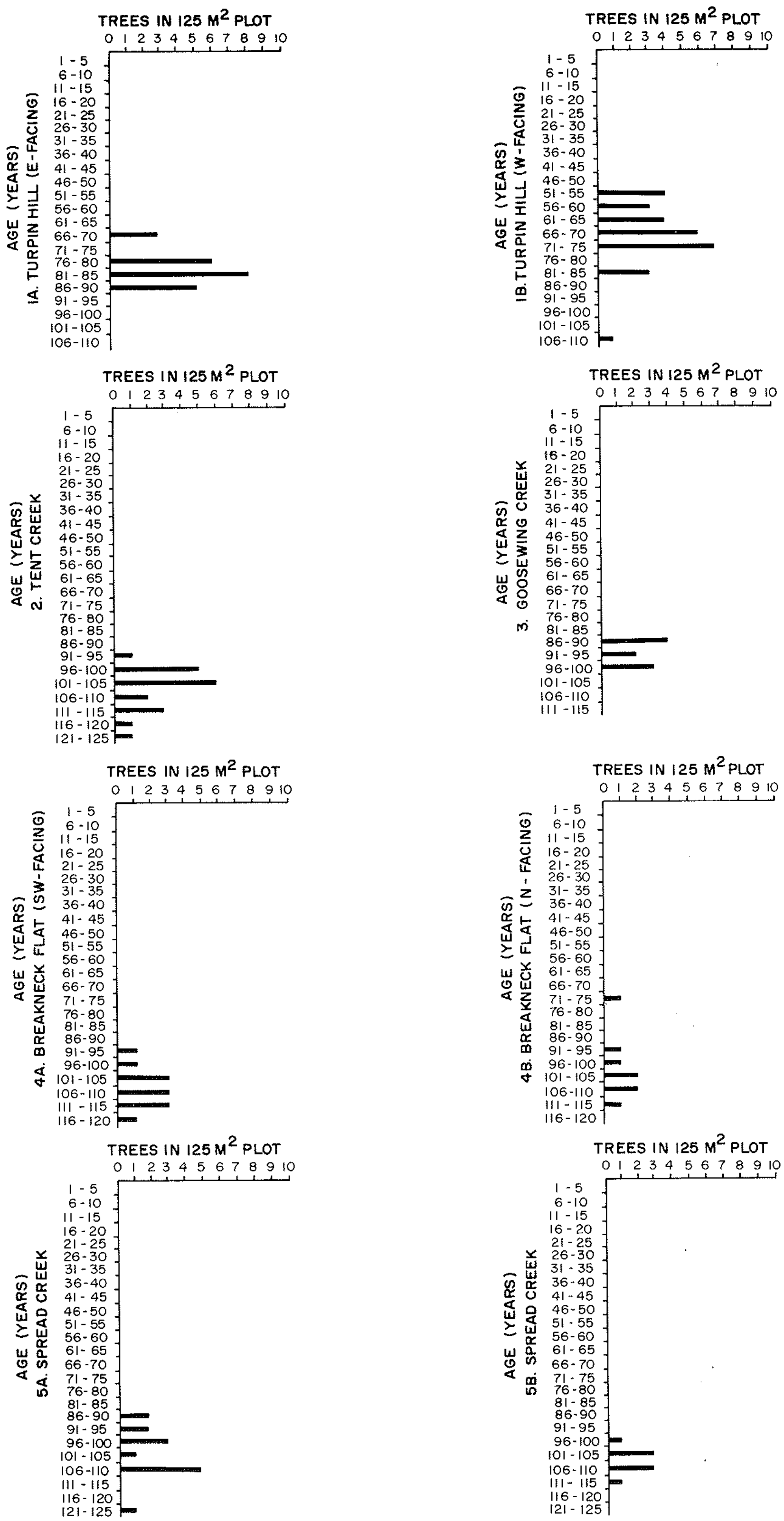


Fig. 6. Age structure (by five-year age classes) of mature aspen stands for all trees over 6.35 cm diameter in 5 m x 25 m plots.

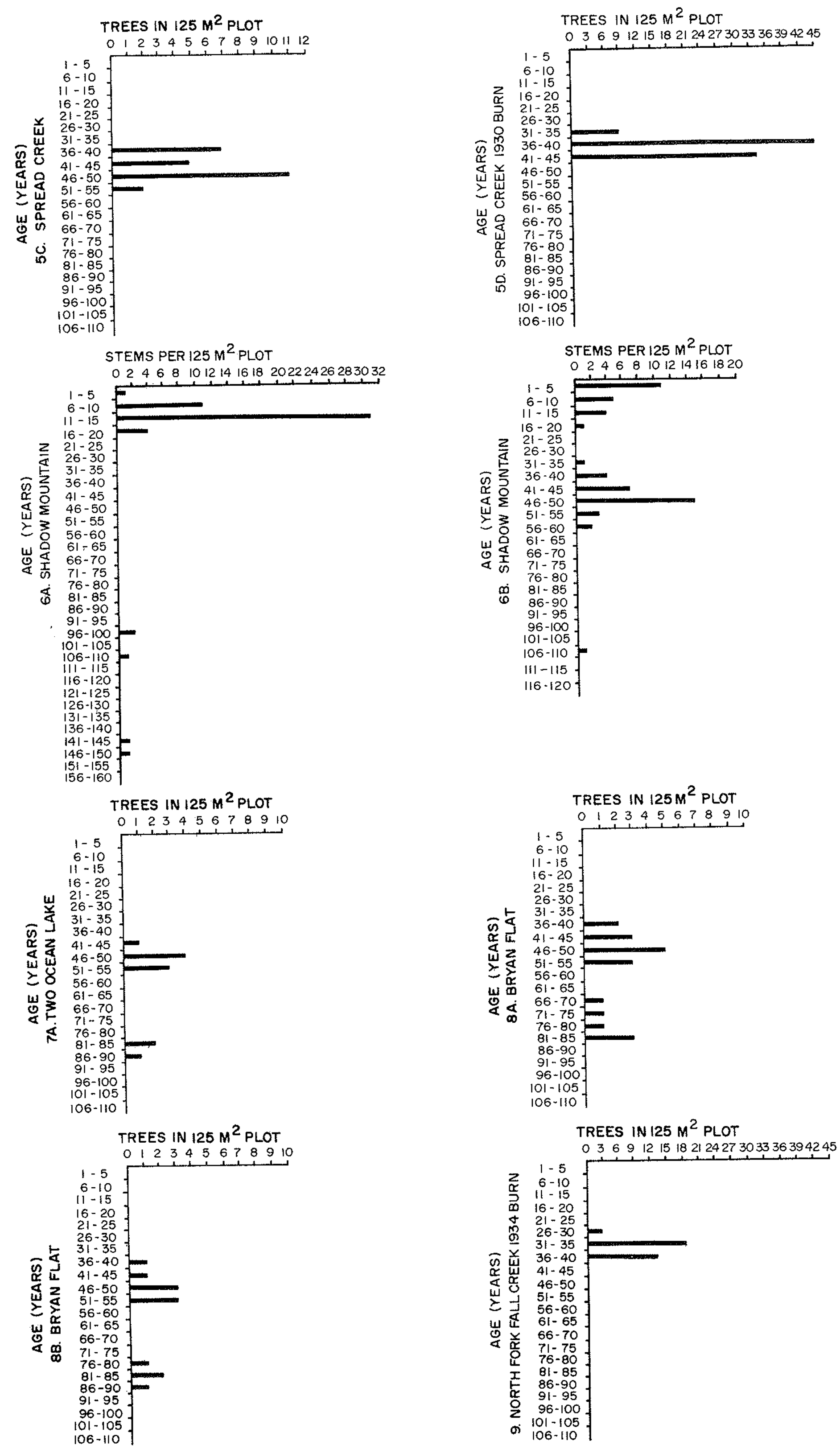


Figure 6. Continued

TABLE 1. Data from 5m x 25 plots in "mature"[1] stands.

Stand No.	Stand Location	Probable date of most recent fires	Number of aspen trees/ plot	Age range of aspen trees in plot (yr)[3]	Mature trees/ hectare	Suckers/ hectare	Maximum height of suckers (m)
1A	Turpin Hill (E-facing)	1879, 1895	26	69-92	2080	14,200	1.2
1B	Turpin Hill (W-facing)	1879- 1895	29	54-85(108)[4]	2320	0	-
2	Tent Creek	?	20	91-121	1600	7,200	0.6
3	Goosewing	1872	9	89-98	720	11,700	0.6
4A	Breakneck (SW-facing)	1850	12	92-116	960	19,300	0.8
4B	Breakneck (N-facing)	1850	10	90-112(70)[4]	800	11,100	0.6
5A	Spread Creek	1850-1890	14	90-109(125)[4]	1120	10,900	1.6
5B	Spread Creek	1850-1890	10	97-113	800	2,400	0.4
5C	Spread Creek	1850-1890	24	38-52	1920	4,600	4.0
5D	Spread Creek	1930	20[2]	34-41	8000	5,600	0.4
6A	Shadow Mountain	1856, 1879	5	96-150	400	3,800	8.0
6B	Shadow Mountain	1856, 1879	34	35-60(108)[4]	2720	1,700	5.0
7A	Two Ocean Lake	1880	11	42-88	880	7,400	5.0
8A	Bryan Flat	1872	19	36-84	1520	800	1.6
8B	Bryan Flat	1872	12	46-86(36)[4]	960	800	3.0
9	N. Fork Fall Creek	1934	36	28-37	2880	700	0.6

[1] Stems over 6.35 cm.
[2] 5m x 5m plot
[3] Trees aged as of end of growing season, 1971
[4] Figure in parentheses refers to age of one extreme individual

TABLE 2. Age-height-diameter relationships in sucker stands occurring at margins of mature stands. Data from 3m x 3m plots.

Stand No.	Stand Location	Number of suckers/ plot	Age range of suckers in plot (years)	Height of suckers(m)	Diameter of suckers(cm)
1C	Turpin Hill (E)	19	6-21	1-4	1-5
5E	Spread Creek	30	3-18	.5-3	.5-4
5F	Spread Creek	21	9-18	.5-5	1-5
7B	Two Ocean Lake	34	8-21	1-10	1-8
10A	Pacific Creek Road	21	5-21	1-9	1-7

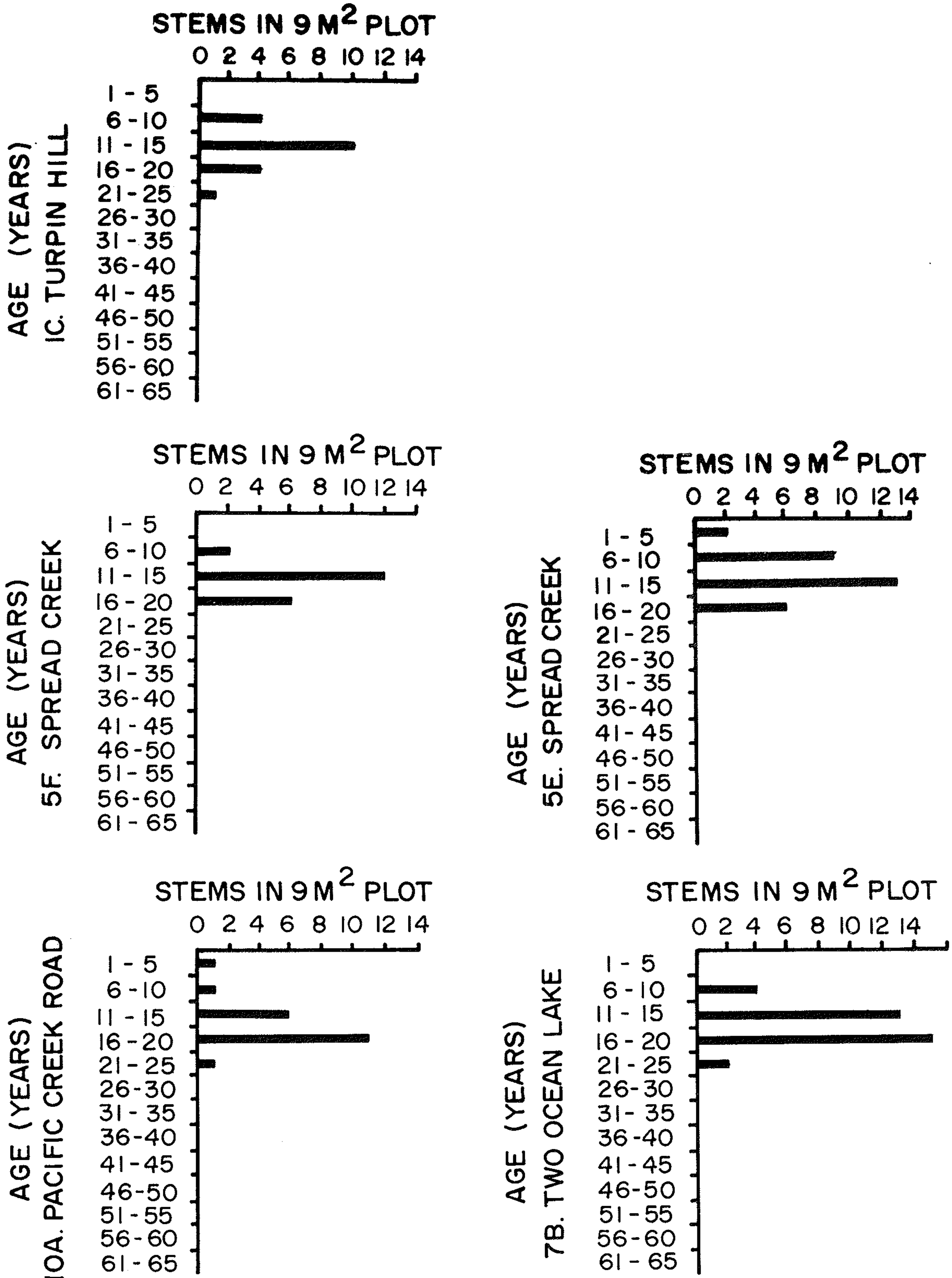


Fig. 7. Age structure of sucker stands (by five-year diameter classes) for all stems in 3 m x 3 m plots.

Results and Discussion

Plot Sampling

Data in Fig. 6 and Table 1 (Gros Ventre and Spread Creek winter ranges) show that age structure of stands 1A-5B varied between 9 and 31 years. The Goosewing stand (3) was the most even aged, originating between 1873 and 1882. Fire scars in the general area suggest the locality burned in 1872. Figure 4 shows a young stand and fire-killed conifer snags in the late 1800's. The widest age spread was that of stand 1B on Turpin Hill which presumably regenerated between 1886 and 1917. Fire scars in the immediate vicinity suggest the stand was influenced by fire in 1879 and 1895. Photographic evidence (Loope and Gruell, 1973) shows a young stand in 1899.

Excepting stand 6B which was 35 to 60 years old, the age structure of stands 6A-8B was more varied. All plots were representative of localities which are not elk winter range and where browsing is primarily by moose. The successful establishment of trees in these stands is evidence that browsing has been light over the years. Fire was not considered a factor in the past 50 years. Some trees in these stands exceeded 80 years and are believed to be of fire origin. Fire evidence was apparent in stand 6A, which included a fire scarred aspen.

Of all stands sampled, 6A contained the fewest mature trees per hectare. The open canopy is characteristic of those stands that have undergone rapid deterioration in the past several decades. As a result of increased sunlight reaching the ground, suckers have attained maximum heights of 8.0 m — the greatest growth measured in 5 m x 25 m plots (Table 1). Age of all suckers in stand 6A and those in 6B were plotted (Fig. 6). These data are representative of the more successful aspen regeneration (without fire influence) in Jackson Hole.

The closest age spread was in stands 5D and 9, which developed following burning in 1930 and 1934. Data show that regeneration started in the first year following fire and continued for 7 and 9 years, respectively. Considering these data, stands of fire origin are initially "even aged." With passing of time, many trees die while some are replaced. This sequence would account for the rather wide age spreads of some old stands — particularly those in localities where browsing levels have been low.

Stand 5C was considered atypical of stand age structure in the Spread Creek area. Few stands appear to be comparable. Successful establishment suggests rapid breakup of the clone, coincident with light ungulate browsing.

Aspen root suckers were present in all but one of the 16 plots sampled (Table 1). Sucker occurrence varied from 0-19,300 stems per hectare (0-7,913 per acre) and averaged 6,400 stems per hectare (2,591 per acre). This level of suckering is materially below that which can be expected on disturbed sites.

The generally heavy intensities of ungulate browsing in stands 1A-5B were reflected in maximum sucker heights ranging between 0.4 m and 1.6 m. Very often repeated browsing

Fig. 8. Aspen suckers on upper slopes of Shadow Mountain which exhibit "hedged" appearance due to repeated removal of apical buds by elk and moose browsing.

of apical buds has altered the growth form to the point where suckers take on a multi-branched or "hedged" appearance (Fig. 8). Lighter browsing levels in stands 1A and 5A allowed greater heights and are representative of low levels of winter elk browsing.

A maximum sucker height of 4.0 m in stand 5C demonstrates that aspen in restricted localities on the margin of elk winter range has the capability of regenerating successfully. This phenomenon is the exception, however.

Lower levels of ungulate browsing intensities (primarily moose) on plots 6A-8B are reflected in sucker heights ranging from 1.6 m to 8.0 m (4.5 m average).

Fire-origin stands 5D and 9 had maximum sucker heights of 0.4 m and 0.6 m. The few suckers produced are being suppressed by parent trees.

Correlation between age and diameter varied considerably depending on location of stands and relative age (Table 3). Correlation coefficients (r) for the eight stands on Spread Creek and the Gros Ventre River average .458. An r-value of .235 for the Tent Creek stand was the lowest attained in our study. The Tent Creek stand had 100-year-old trees with diameters of 11 cm, 19 cm, 23 cm, and 25 cm.

The five plots not on elk winter range averaged .864, while plots in five sucker stands average .736. Alder (1970) found an average within stand age-diameter correlation coefficient of .825 for 44 aspen stands in Utah and northern Arizona.

Our data suggest that qualitative observations or analysis by diameter classes can lead to misinterpretations of the age structure of aspen stands. For example, Reed (1969; 1971) may have underestimated the role of disturbance in aspen stands of the Wind River Mountains (100 to 150 km ESE of Jackson Hole) through use of diameter-class analysis. Diameter-class analysis has the great advantage of convenience over age-class analysis, but close correlation between age and diameter must be established prior to reliance upon diameter.

Recently Burned and Cut Areas

Figure 9 shows the location of ten burns and one cutting which vary in size from 1 or 2 hectares to 5,000 hectares. These are the only significant burns known to have occurred in aspen vegetation since 1930, illustrating the influence of fire suppression.

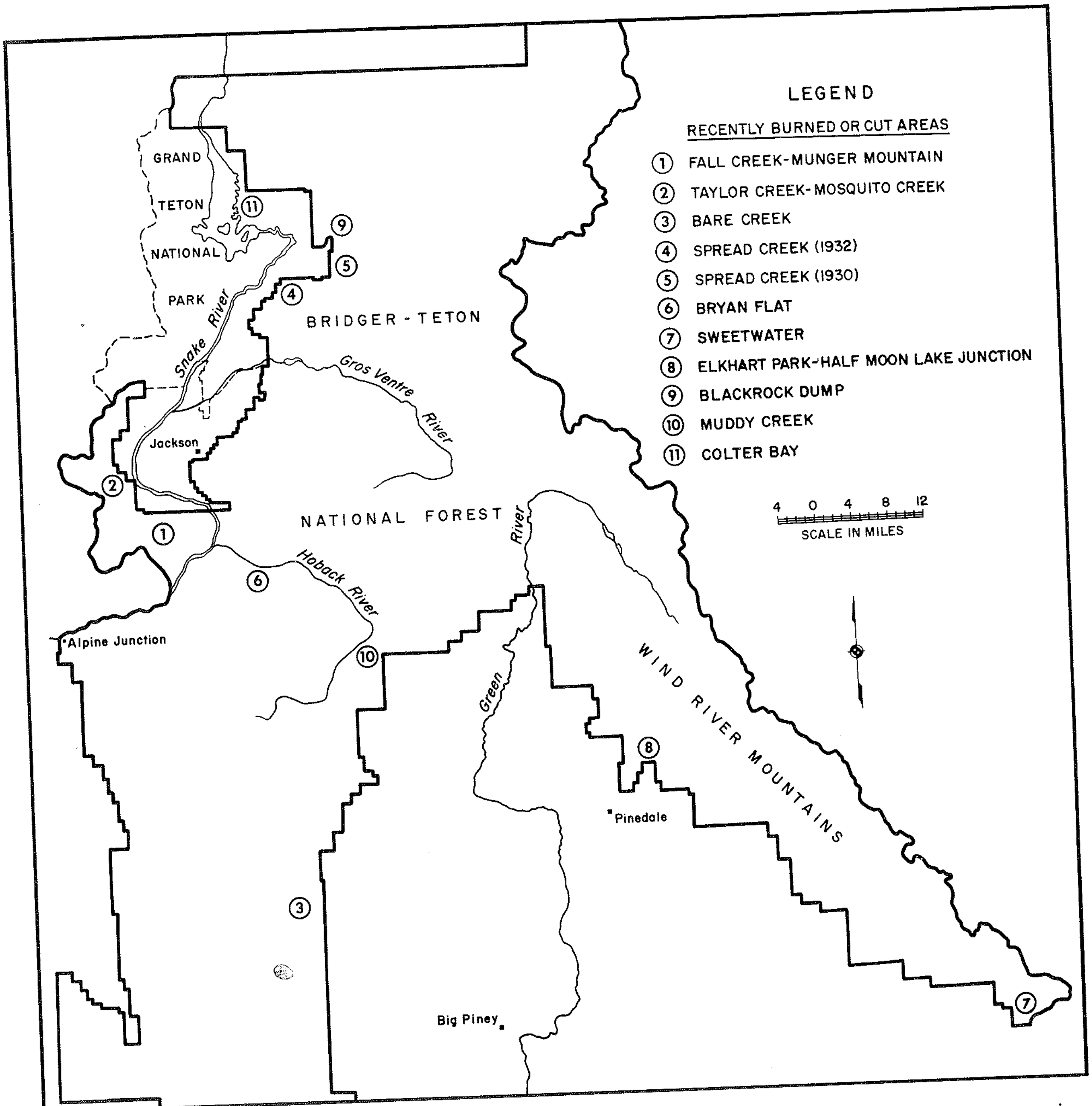


Fig. 9. Location of recently burned areas in the Bridger-Teton National Forest and cut area in Grand Teton National Park.

TABLE 3. Correlation of age and diameter for 21 stands.

Stand No.	Stand Location	Correlation Coefficient Age/Diameter	Probability of no positive Correlation(p)
1A	Turpin Hill (E-facing)	.274	p>0.1
1B	Turpin Hill (W-facing)	.694	p<.001
2	Tent Creek	.235	p>0.1
3	Goosewing	.458	p>0.1
4A	Breakneck (SW-facing)	.590	0.5>p>.02
4B	Breakneck (N-facing)	.630	.05>p>.02
5A	Spread Creek	.708	.01>p>.001
5B	Spread Creek	.876	p<.001
5C	Spread Creek	.562	.01>p>.001
5D	Spread Creek	.368	p>0.1
6A	Shadow Mountain	.751	0.1>p>.05
6B	Shadow Mountain	.913	p<.001
7A	Two Ocean Lake	.870	p<.001
8A	Bryan Flat	.873	p<.001
8B	Bryan Flat	.914	p<.001
9	North Fork Fall Creek	.502	.01>p>.001
1C	Turpin Hill (E)	.663	p<.001
5E	Spread Creek	.704	p<.001
5F	Spread Creek	.692	p<.001
7B	Two Ocean Creek	.752	p<.001
10A	Pacific Creek Road	.869	p<.001

The largest areas examined included the 5,000 hectare Fall Creek-Munger Mountain and 1,900 hectare Taylor Creek-Mosquito Creek burns of September 1934 (T39N, R116 & 117W) and the 700 hectare Bare Creek (T32N, R115W) burn of August 1940. Although the primary vegetation was conifers, these fires swept through substantial acreages of aspen. Well stocked stands have resulted wherever parent stands were killed. Comparison of present young stands with dead logs representing aspen destroyed by fire suggest that many clones have expanded considerably from pre-fire conditions. In each of these areas, aspen regeneration took place in the absence of intense ungulate browsing.

Limited sampling in the Bare Creek burn suggested that most aspen regenerated within a few years following the fire. Today, the burned area includes some of the most vigorous aspen stands in western Wyoming (Fig. 10).

Forest Service records indicate a 1932 fire of 35 hectares on lower Spread Creek (T44N, R114W, S16) burned through an aspen community. According to an individual who witnessed the fire, it progressed at a low intensity in an irregular pattern. The stand has regenerated successfully where parent aspen was killed. Available information suggests winter browsing by elk in this locality has been moderate to heavy. After 40 years, aspen has attained diameters of 7 to 15 cm and heights up to 8 m.

The Spread Creek burn in 1930 of approximately three hectares (T44N, R113W, S11) stimulated regeneration of one of the most vigorous young aspen communities in Jackson Hole. Present stand conditions contrast markedly with dacadent stands in the vicinity (Fig. 11). Growth rings at the center of 20 sections were narrow, indicating crowded suckers during initial stages of growth and/or suppression by ungulate browsing. Current browsing intensities are light to moderate.

Similarly, an aspen burn of approximately five hectares in September 1952 near Bryan Flat Guard Station (T38N, R115W, S9) was responsible for successful stand regeneration. Profuse suckering exists in the burned area with sucker heights varying between 2 and 5 m (Fig. 12). Only at the lower margin of the burn and on an adjacent ridge has ungulate browsing inhibited regeneration. Successful aspen regeneration is negligible outside the fire perimeter. Browsing levels by moose and elk are considerable in this locality.

Observations within a 1963 burn on the Sweetwater drainage southwest slope of the Wind River Range (T29N, R101W), demonstrate that destruction of parent trees does

Fig. 10. Bare Creek burn of 1940, Wyoming Range. Conifer regeneration is inconspicuous 30 years after the fire. Aspen clones have expanded and regeneration is dense.

Fig. 11. Aspen stand in background (5D) regenerated following a fire in 1930. Stand in foreground has not burned since about 1880 and is in advanced stage of deterioration.

Fig. 12. Bryan Flat burn of 1952. Regenerating aspen have reached heights of up to 5 m in spite of fairly intense ungulate browsing.

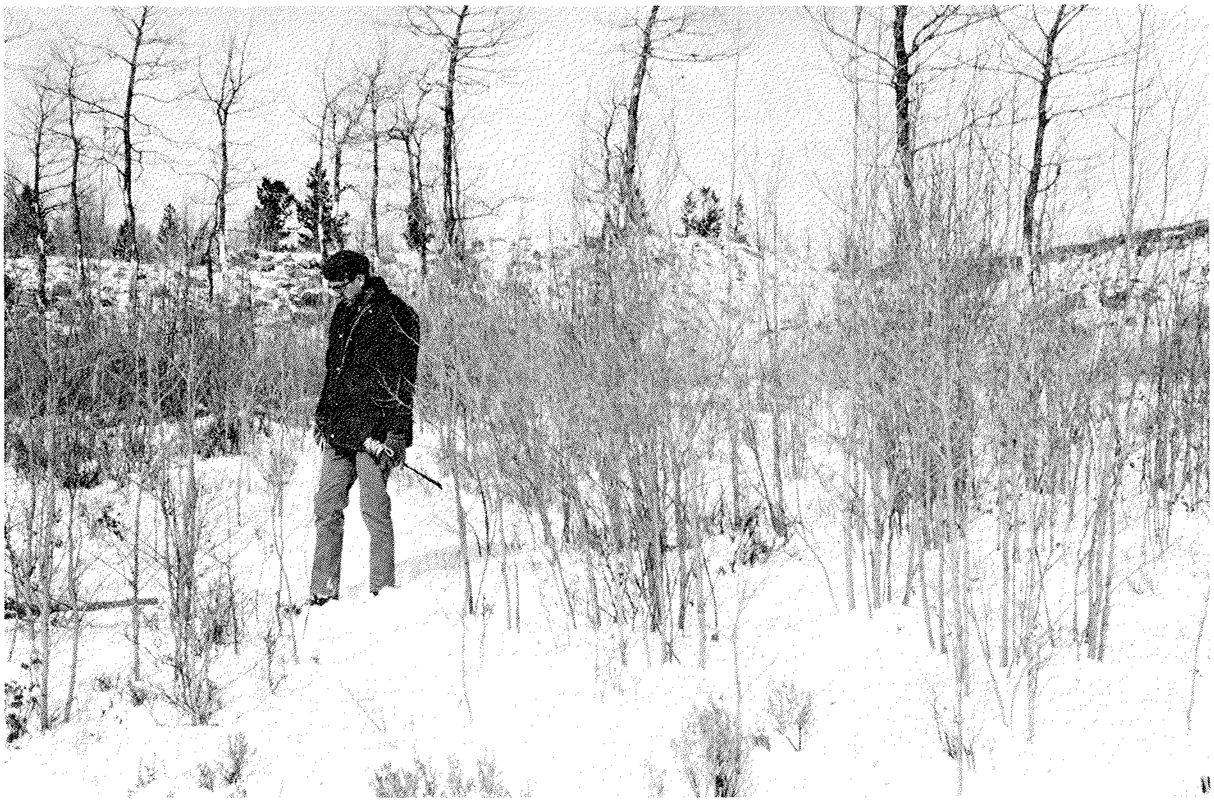


Fig. 13. Regeneration 8 years following fire along Elkhart Park Road, northeast of Pinedale, Wyoming.

not always result in successful aspen regeneration. In this instance, however, the stand was apparently exhibiting no sprouting ability prior to the fire.

A 1963, 150 hectare burn near the junction of the Elkhart Park and Halfmoon Lake roads in the Wind River Range northeast of Pinedale (T34N, R108W) demonstrates that aspen can respond well to fire disturbance even when the site is relatively poor. The soil is shallow and coarse, having developed from granitic substrate of a late-Pleistocene moraine. The parent stand was badly deteriorated at the time of the fire and was completely killed. In 1971, suckers measured 3 to 4 m in height. The level of sprouting has been more than adequate to restock the stand which is in a locality where ungulate browsing is light (Fig. 13).

Observations at the 12 hectare Blackrock Dump burn (T45 N, R113W, S22) of September 1966, showed aspen suckering and establishment to be variable. Near the highway, where browsing is light, suckers have attained 2 to 3 m heights and appear to have potential for establishing a new stand (Fig. 14). Higher on the slopes some distance from the highway, browsing is heavy and clones are small and scattered. In spite of a high suckering incidence, suckers are only 1 m in height and in a suppressed condition due to ungulate browsing.

The most recent aspen burn examined was one of 6 hectares which occurred in August 1972, on Muddy Creek, a tributary of the Hoback River (T36N, R113W, S5). The area was visited on July 27, 1973, to determine the extent of suckering following the fire. The best response occurred where fire-killed parent trees had been more dense. Suckering was relatively sparse where density of parent aspen had been low. Suckers reached 0.5 m to 1 m in height during a portion of the first growing season (Fig. 15). About 5 percent had been browsed by cattle and ungulates.

Fig. 14. Blackrock Dump burn of 1966, Buffalo Fork Valley. Six years after fire, reproduction appears capable of establishing new stands in portions of the burn.

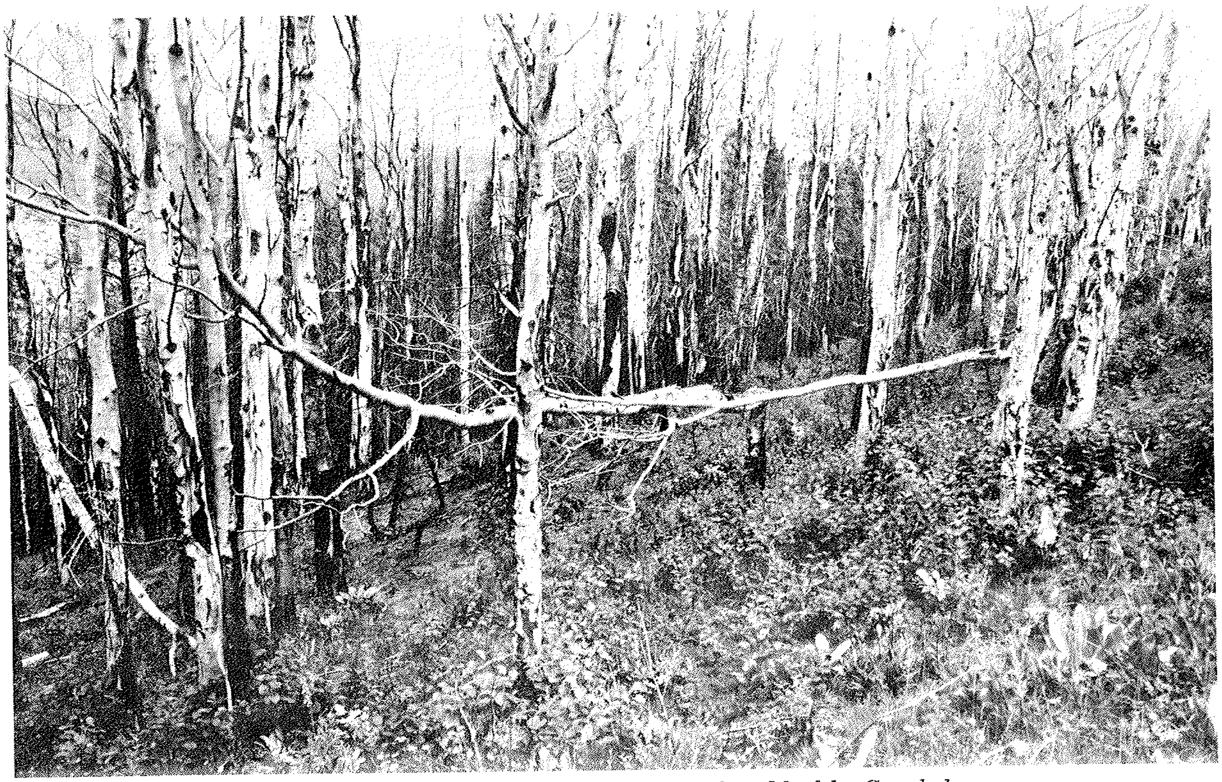


Fig. 15. Aspen reproduction one year after Muddy Creek burn.

Fig. 16. Colter Bay Campground, Grand Teton National Park. An 18 year-old aspen stand which regenerated following cutting. Aspen suckers in foreground have been suppressed by moose browsing.

Aspen response to cutting is evidenced in a 5 hectare area on the western edge of Colter Bay Campground in Grand Teton National Park (T46N, R115W, S34). Lodgepole pine and aspen were cleared from a swampy area in the mid-1950's during campground construction, and the terrain was slightly modified to facilitate drainage. Aspen regenerated vigorously following this disturbance, attaining heights of 6 to 7 m (Fig. 16). Moose browsing has inhibited reproduction at the margin of the stand, but has had a negligible effect within the stand. Aspen is not a common species elsewhere in the Colter Bay area. Where it does occur, browsing by moose is sufficient to suppress suckers.

Exclosures

Observations were made at six exclosures in the Bridger-Teton National Forest and Grand Teton National Park (Fig. 3, Table 4). The three exclosures in the Bridger-Teton National Forest and the Uhl Hill exclosure in Grand Teton National Park are on elk winter range. Excepting the UHL Hill exclosure, supplemental winter feeding of elk in the vicinity has artificially concentrated animals and intensified browsing. The Berry Creek and Blacktail Butte exclosures on Grand Teton National Park have been removed and were not on elk winter range. All exclosures were constructed between 1942 and 1964 and represented the only sites in Jackson Hole where aspen had been artificially protected from ungulate browsing for purposes of studying growth response.

The best data base on aspen response under protection was obtained in the Upper Slide Lake exclosure. Over the eight year period 1961-68 suckers had reached an average height of 81 inches (2.1 m) on two transects. Measurements on two transects outside the

TABLE 4. Characteristics of aspen regeneration in exclosures.

Location	Size (hectares)	Date Established	FORMER STATUS: Condition of Parent Stands	FORMER STATUS: Condition of Reproduction	CURRENT STATUS
East of National Elk Refuge T41N, R115W, S.3	0.1	1952	Seven mature aspen trees alive in 1952.	Numerous suckers kept at less than 0.5m tall due to elk browsing.	Most parent trees dead. Clone has expanded; suckers have attained heights of 4-5 m.
Upper Slide Lake[1] Soil and Watershed Project T42N, R112W, S.20	150	1960	Aspen stand appeared to have closed canopy in 1918 photograph.	Numerous suckers in 1960 less than .5m tall; browsed by elk and moose.	Parent stand has deteriorated to about 50 scattered trees. Numerous suckers have attained heights of 3-5 m.
Southeast of Goose-[1] wing Creek Bridge T47N, R116W, S.24	0.8	1942	Parent stand appeared largely intact in 1952 photograph.	Reproduction was not conspicuous in 1952 photograph.	Reproduction has reached sapling size, averaging 5-6m tall. Some saplings are 8-10m tall. Parent stand is deteriorating.
Berry Creek T47N, R116W, S.24	2.5	1964	Several dozen mature trees within exclosure. Stand not deteriorating rapidly.	Moderate browsing pressure by elk and moose kept suckers at heights less than 0.5m.	Several dozen suckers 1-3m high, present in 1972.
Blacktail Butte[1] T44N, R113W, S.5	0.4	1964	Intact aspen canopy in portion of exclosure.	Suckers .5-2m tall. Subject to browsing primarily by moose.	In 1972, suckers in exclosure ranged from 1-3m in height.
Uhl Hill T44N, R113W, S.6	0.4	1964	A few stunted parent trees (only 5m high) occurred at the SE corner; very poor site for aspen growth.	No suckers over 0.2m in height. Heavy Browsing in winter by elk in the area.	About 30 suckers occur just inside SE corner of exclosure (height up to 3m). Most parent trees are dead.

[1] *Exclosure had been subject to significant periodic foraging. Drifting snow allowed ungulate entry.*

exclosure showed average heights over the same period ranging between .2 m and .5 m. The high measurement was made in 1964.

Sucker response within exclosures is evidence that aspen will regenerate successfully when protected. Best sucker densities and growth rates have occurred in deteriorated stands with open canopies.

Webb (1957) reports similar results in the lower Bow Valley in Banff National Park, Alberta. An exclosure fenced in 1944 and examined in 1953 showed aspen two to eight feet in height. Heavy elk browsing had totally suppressed regeneration outside the exclosure.

Bridger-Teton National Forest and Grand Teton National Park

Observations over the past seven years agree with earlier workers that elk are the primary ungulates utilizing aspen regeneration. Browsing occurs mainly in early winter, although during some years free ranging animals make use of aspen late into the winter. There is little evidence that browsing of suckers is significant during the spring period. By spring most suckers have been utilized and the diet has shifted to herbaceous species. Summer browsing of suckers by elk is generally insignificant, since aspen is a minor vegetal component on elk summer ranges. The most notable exception occurs in valley areas in Grand Teton National Park where summer elk densities are high (Martinka, 1969).

With few exceptions, aspen stands on elk winter range have not regenerated successfully since 1900. The Spread Creek locality and Gros Ventre drainage comprise the largest contiguous areas in this category. Browsing intensities have been sufficiently heavy to inhibit escapement of suckers to tree size (Fig. 17). In instances where escapement of suckers has occurred on elk winter range, it is confined to localities where elk densities are low. In some areas successful aspen regeneration appears to be related to highway traffic which keeps browsing levels down. Construction may have also been a factor by disturbing roots and releasing food energy.

Some investigators have assumed that the deterioration of the aspen type is related to unnaturally high elk populations resulting from artificial winter feeding (Beetle, 1968). This is not supported by past narratives which describe the aspen in the Gros Ventre drainage as "highlined" with little or no regeneration prior to any appreciable winter feeding of elk (Olson, 1938; Woods, 1942; Doman, 1953) and the historic accounts of elk numbers in the area. Plot data from the Gros Ventre drainage suggest that this condition has prevailed for at least 50 years.

The barking (i.e., eating of bark) of aspen by elk has been recognized for many years (Bailey, 1906). In some instances the intensity was so great as to completely girdle whole stands (Bailey et al., 1915). Barking of this intensity appears to be exceptional and occurs only where elk are concentrated. In the Gros Ventre drainage, where concentrations have been common, there is little direct indication that mature trees have been lost by barking.

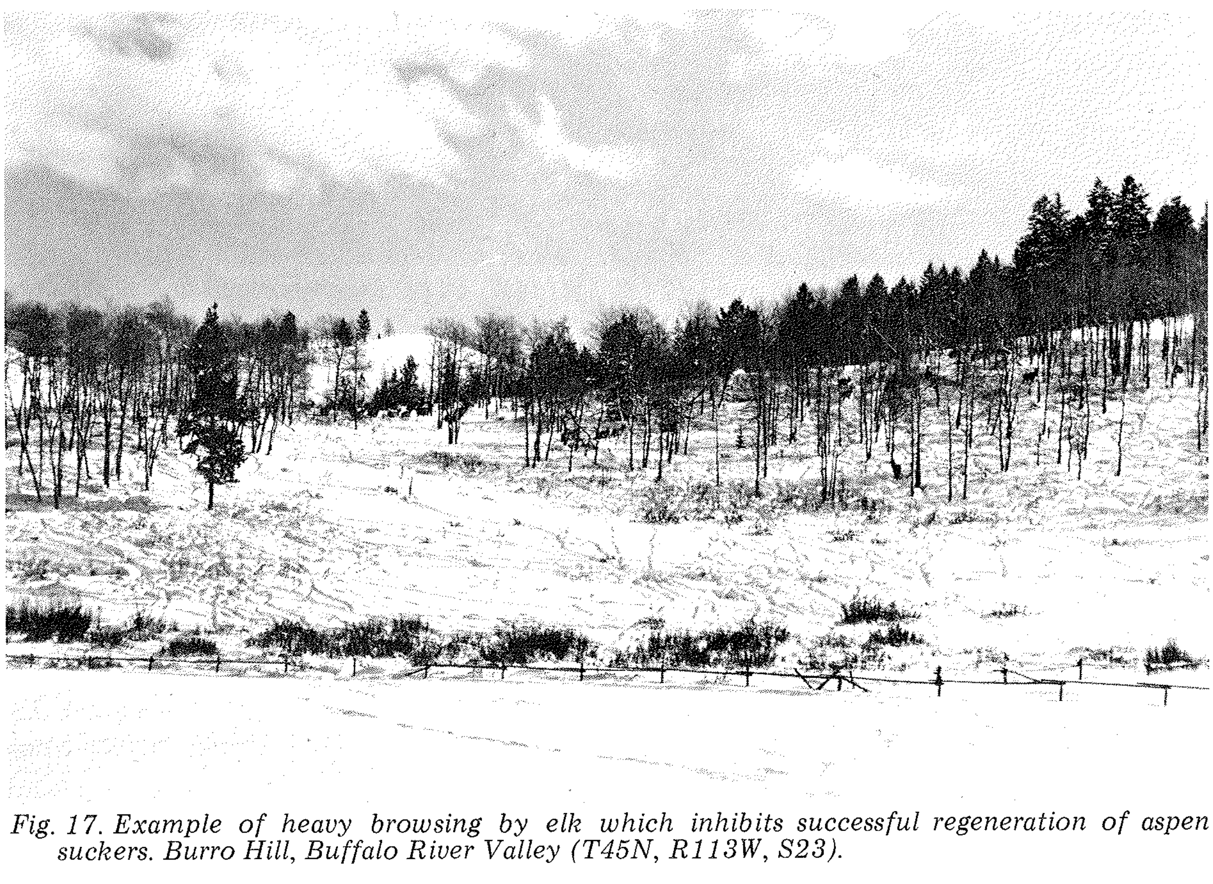


Fig. 17. Example of heavy browsing by elk which inhibits successful regeneration of aspen suckers. Burro Hill, Buffalo River Valley (T45N, R113W, S23).

Fig. 18. Lower Shadow Mountain road (T43N, R115W, S11). Aspen regeneration is attaining sapling size under open canopy without disturbance.

Krebill (1972) suspects that barking may indirectly cause tree losses by affording insects and pathogens an avenue of attack.

Our observations indicate that aspen suckers up to 8 cm in diameter sometimes are completely girdled and killed, but such girdling is not common in Jackson Hole. Mortality of stems of this size appears to have been the result of attack by pathogens and/or shading. This impression is supported by the presence of comparable numbers of dead stems in localities where ungulate browsing is minimal.

The most successful aspen regeneration occurs in localities which are not associated with wintering elk (Fig. 18). The more conspicuous areas in Jackson Hole, include low lying slopes in the vicinity of Bryan Flat, Horse Creek, Shadow Mountain — south to the Gros Ventre road; Hatchet Ranch vicinity and slopes west draining into Buffalo Fork; headwaters of Uhl, Coal Mine and Eynon Draws west of Sagebrush Flat; and localities adjacent to the highway between Moran and Turpin Meadow. The lower slopes of the Teton Range between Mosquito Creek and the Whitegrass Ranch exhibit similar conditions.

Moose are the primary browsers in areas not frequented by wintering elk. Foraging by moose on elk winter range has also been a major contributor to the high level of utilization. They appear to have less potential than elk for suppressing aspen regeneration when it occurs in quantity, even though population densities in Jackson Hole are among the highest in North America.

The significance of moose browsing on aspen regeneration may have been underestimated in the past. They readily browse aspen (Houston, 1968) and it is apparent that they are responsible for suppressing regeneration in many localities. Their impact is felt especially on summer range where aspen stands are small and localized.

The barking of aspen by moose occurs, but is usually confined to occasional trees. An extreme example was noted in the valley of the lower Buffalo Fork where well stocked aspen stands showed barking of most trees.

Excepting elk and moose, native ungulate browsing of aspen is of low intensity. The most significant utilization of aspen is made by mule deer in the Snake River Canyon where deep snow restricts forage availability.

Domestic sheep have not been a factor in browsing of aspen on native ungulate winter ranges, since sheep grazing has not been permitted.

Domestic cattle have been permitted to graze elk winter range on a restricted basis. On the whole, the impact of this grazing on aspen reproduction appears to have been negligible. A short grazing period, large quantities of available forage, and light-to-moderate stocking levels preclude appreciable browsing of aspen. The browsing of aspen on summer range is also negligible. Aspen occurrence is marginal over much of the summer range. Where it does occur on cattle allotments, large quantities of forage precludes appreciable browsing.

Discussion and Conclusions

The importance of disturbance in aspen ecology is well documented. Investigators in various parts of the country have recognized the rejuvenating influence of fire and cutting on aspen succession.

It has been established that prior to suppression efforts, fire was a major force shaping ecosystems in Jackson Hole (Loope and Gruell, 1973). There is convincing photographic evidence that early fires burned aspen communities. Observations by T. S. Brandegee in 1897 indicate that aspen in early stages of succession was a common feature of the landscape.

Aspen age sampling on the Gros Ventre drainage has suggested that the great majority of stands regenerated between 1840 and 1900. Fire occurrence as determined by fire scars was widespread during this era.

The evidence is strong that large numbers of elk wintered in Jackson Hole and on the Gros Ventre drainage prior to 1900. It appears reasonably certain that these elk were a major biotic influence on aspen during early successional stages.

Sampling on the Gros Ventre drainage showed that only a small percent of parent trees regenerated after 1900. These data coincide with reports from 1938-1953 which state that elk browsing was inhibiting successful aspen regeneration. Since supplemental feeding had been insignificant to date, the prevailing condition must have been the result of browsing by large numbers of free-ranging elk with an assist by moose in the absense of fire.

Aspen stands are more even-aged on the Spread Creek and Gros Ventre winter ranges when compared to outlying areas which are not frequented by wintering elk. The more even-aged structure of these stands appears to be the result of profuse suckering and high survival up to 30 years following fire. With closing of the canopy in succeeding years, intraspecific competition had a marked influence in reduction of sprouting rates. It is probable that suckers produced were more vulnerable to elk browsing and the stand ceased to regenerate.

Presumably the stands exhibiting wider age structures are those which have received less browsing. Under decreased browsing levels, suckers have been able to regenerate successfully over extended time periods. Suckering intensity has been greater when most of the parent stand succumbed over a short time interval (Fig. 19). It is believed that the increase in reproductive vigor exhibited by such stands is directly attributable to the rapid deterioration of parent clones which have reached advanced age in recent years.

Observations in aspen communities which burned since 1930 indicate that suckers will regenerate successfully on limited acreage if browsing levels are not intense. It is evident that there is little likelihood of successful regeneration within small burns on heavily browsed winter range. Houston (1973) suggests that fires which kill most overstory aspens over large areas may be necessary to produce successful regeneration in northern Yellowstone National Park.

Fig. 19. Along Pacific Creek Road (T45N, R114W, S12). Intense suckering response of aspen clone following rapid demise of mature stand. Location of stand 10A.

Aspen growth response within exclosures demonstrates that stands on heavily utilized winter range would regenerate if not subjected to the influence of ungulates. A suckering incidence of 0-19,300 stems per hectare (0 to 7,813 per acre) suggests that this incidence of suckering would not be adequate in restocking stands to former levels. Stands which would respond are those which have open canopies.

Exclosures present a highly atypical picture, since they show response of vegetation when not exposed to heavy ungulate browsing. Removal of the influences of both fire disturbance and ungulate browsing leads to a response of vegetation within exclosures which is undoubtedly unique in the vegetational history of northwestern Wyoming.

This study has established that aspen has regenerated successfully on some "climatic climax" sites in Jackson Hole without the influence of fire. The degree of success varies by site and condition of parent stand. When compared with the total Jackson Hole aspen community, the acreage where successful regeneration has occurred is minimal. A large portion of the aspen in this region is seral to conifer and will not replace itself without major disturbance.

We postulate that suckering of aspen and growth of palatable grasses, herbs, and shrubs following extensive fires, particularly on winter range, produced a forage supply sufficiently large to overcome biotic effects of ungulates — thereby allowing successful regeneration of aspen stands. Because of the advanced stage of plant succession, current production of aspen suckers and associated palatable forage is drastically reduced from former levels on elk winter range. This reduced forage supply places a heavier demand on aspen than would exist were stands in early succession. It has been noted that in late succession, heavy browsing often causes multi-stemmed suckers, which dissipate growth potential. This contrasts with early successional stages when release of large amounts of food energy allow accelerated growth of suckers.

How vegetation would respond to burning under current levels of browsing is not understood. A great increase in the moose population has added to browsing intensities. However, trend counts indicate a reduced elk herd on the Gros Ventre winter range. The picture is further complicated by supplemental feeding at three feedgrounds. Impacts on aspen in the vicinity of feedgrounds are undoubtedly greater now than formerly. On the other hand, the feeding of elk has had a compensating effect by reducing browsing intensities on outlying winter range. Whether current browsing by elk and moose is capable of suppressing aspen regeneration following burning can only be answered through large-scale return of fire to aspen communities.

Considering the evidence, we conclude that the current decline of aspen stands, particularly in the Spread Creek locality and Gros Ventre drainage is primarily due to virtual elimination of fire as an ecological agent in this century. With continued exclusion of fire on the Spread Creek and Gros Ventre winter range, many aspen stands will be reduced within a half century to a point where they no longer contribute significantly to the vegetal cover. Adoption of fire management policies which would allow the reintroduction of fire into the aspen-sagebrush habitat type of Jackson Hole is the most promising means of maintaining aspen communities. Such a policy should include prescribed burning, as well as taking advantage of natural ignitions which occur in approved fire management planning areas. Stimulation of aspen clones by cutting or herbicide application are alternatives to burning. These methods are more expensive and do not appear to have as desirable ecological effects as fire.

Aspen is a significant component of the natural vegetation, provides habitat for many wildlife species, contributes to the ungulate food source, and is clearly an esthetic asset to the area. The necessity for its preservation seems obvious in a National Park, where a primary management goal is maintenance of ecosystems in as pristine a condition as possible (Houston, 1971). In the Bridger-Teton National Forest, the perpetuation of aspen communities can be justified on esthetic grounds alone, as well as by its important contribution to the habitat needs of many wildlife species.

The conclusions of this study contrast with previous interpretations which imply that successful regeneration of aspen in Jackson Hole is possible only with substantial decreases in elk foraging. The ability of aspen to reproduce after fire coincident with current levels of ungulate browsing must be tested by burning pre-sampled stands on diverse sites. Bridger-Teton National Forest and Grand Teton National Park have plans for the prescribed burning of aspen in several localities whenever proper burning conditions occur. Data have been recorded for preburn ecosystems for comparison with post-burn response.

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