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# ASPEN, ELK, AND FIRE IN NORTHERN YELLOWSTONE NATIONAL PARK[1]

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*Abstract.* Most stands of trembling aspen (*Populus tremuloides*) in northern Yellowstone National Park appear to have become established between 1870 and 1890, with little regeneration since 1900. There has been controversy throughout this century regarding the relative roles of browsing by elk (*Cervus elaphus*) and fire suppression in preventing aspen regeneration. Fires in 1988 burned 22% of the northern ungulate winter range in the park, and created an unusual opportunity to investigate interactions between fire, ungulate browsing, and aspen regeneration. We tested two hypotheses. (1) The fires would stimulate such prolific sprouting of new aspen stems in burned stands that many stems would escape ungulate browsing and regenerate a canopy of large aspen stems. (2) Browsing pressure would be so intense that it would inhibit aspen canopy regeneration in the burned stands, despite prolific sprouting, but increased forage production in the burned areas would attract elk so that they would not seek out remote aspen stands, and hence, aspen regeneration would occur in unburned aspen stands remote from the burned areas.

We sampled aspen sprout density, height, growth form, and browsing intensity in six burned aspen stands, six unburned stands close (<1 km) to the burned area, and six unburned stands remote (>4 km) from the burned area. Density of sprouts was generally greater in the burned stands than in the unburned stands in spring 1990 (2 yr after the fires), but was approaching the density of unburned stands by fall 1991. There were no significant differences in browsing intensity (percent of aspen sprouts browsed by ungulates) in 1990 or 1991 among burned, unburned close, or unburned remote stands, nor were there differences in relation to growth form (juvenile vs. adult sprouts). Unbrowsed sprouts generally were lower than the depth of the snowpack, suggesting that elk browsed nearly all sprouts that were accessible.

The age distribution of 15 aspen stands across the northern winter range indicated that regeneration of large canopy stems had been episodic even prior to the establishment of the park in 1872. The period 1870–1890, when the present-day aspen stands were generated, was historically unique: numbers of elk and other browsers were low, climate was relatively wet, extensive fires had recently occurred, and large mammalian predators of elk (e.g., wolf, *Canis lupus*) were present. This combination of events has not recurred since 1900. The recent paucity of aspen regeneration in northern Yellowstone National Park cannot be explained by any single factor (e.g., excessive elk numbers or fire suppression) but involves a complex interaction among factors.

*Key words:* *aspen* (Populus tremuloides); *elk* (Cervus elaphus); *fire; herbivory; Yellowstone National Park.*

## INTRODUCTION

Much concern has been expressed in recent decades that trembling aspen (*Populus tremuloides* Michx.) is declining in vigor and abundance in Yellowstone National Park (YNP). Aspen is a minor species in YNP, covering only ≈2% of the park area (Despain 1990), yet it is ecologically significant because it is the only deciduous forest type present. Aspen forests support high numbers and diversity of breeding birds and other animals (DeByle 1985*b*), and are visually striking in the fall when the foliage turns yellow.

Many aspen stands in Yellowstone appear to be "deteriorating." These stands are characterized by a canopy of large, mature stems that are gradually thinning

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through the action of various diseases and other natural causes (Hinds and Wengert 1977, Hinds 1985, Hart 1987), and little or no aspen understory (Schier 1975). As the large, old aspen stems die, they are not replaced by new recruitment into the canopy, and various shrubs, grasses, or forbs may eventually come to dominate the site (Kay 1990). Similar aspen "decline" has been reported elsewhere in the Rocky Mountains, e.g., in Jackson Hole 100 km to the south (Krebill 1972, Loope and Gruell 1973, Bartos and Mueggler 1981, Hart 1987, Boyce 1989, Bartos et al. 1994), in the Wasatch Mountains of Utah (Schier 1975), and in Rocky Mountain National Park in Colorado (Olmstead 1979, Hart 1987). A long-term study in Jackson Hole revealed a 39% decrease in stem density from 1970 to 1985, with greatest mortality in the smaller stem size classes (Hart 1987).

Aspen as a species is in no immediate danger of disappearing from YNP. Throughout the Rocky Mountains aspen is a clonal species in which many stems arise from a common root system and are genetically identical (Barnes 1966). Seedling establishment of aspen has been extremely rare in the Rocky Mountains during the 20th century, although aspen seedlings have become established in many parts of YNP that burned in 1988 (Kay 1993; W. H. Romme et al., *unpublished manuscript*). However, seedlings are infrequent in the aspen stands that we studied, and all of the results to be presented below will deal only with aspen root sprouts, not seedlings. Dominant apical meristems produce auxins that inhibit root sprouting, but the root system can produce few to many new stems (referred to as sprouts or suckers) every year in response to small or large injuries that impair the apical dominance of the large stems. Even if all large stems die, the genetic individual (i.e., the root system) can persist for a long time, perhaps indefinitely, in the form of small root sprouts or "shrub aspen" (Despain 1990; but see Kay and Wagner, *in press,* for a dissenting view). DeByle (1964) reported living root systems associated with dead stems in 50-yr-old stands of *Populus grandidentata,* and sites in Yellowstone where all of the mature aspen stems have died in recent decades still support numerous aspen sprouts ≈1 m tall. Nevertheless, the large stems of trembling aspen currently are not regenerating in many parts of YNP, and this raises the question why.

At least a part of the answer is heavy browsing by elk (*Cervus elaphus* Erxleben). Most aspen stands in YNP are located in the northern winter range portion of the park, where thousands of elk and smaller numbers of other native ungulates winter each year (Houston 1982). Aspen is a highly palatable food for elk and other ungulates in YNP, as it is elsewhere in the Rocky Mountains (Jones 1974, DeByle 1985*a,* Boyce 1989). Elk eat the tips of aspen sprouts, and sprouts are heavily utilized in many areas, especially where elk congregate in winter or along spring/fall migration routes (e.g., Bartos et al. 1994). Elk also eat the bark of mature trees, except where the smooth white bark has been replaced by thick, black, corky bark in response to injury. Indeed, nearly all large aspen stems in YNP have the thick bark on their bases, extending up as high as elk can reach, with white bark above (Despain 1990, Kay 1990).

Hart (1987) reported that mortality of aspen stems from pathogenic fungi in Jackson Hole was positively correlated with the amount of prior injury by ungulate browsing. Patton and Jones (1977) similarly observed that damage to aspen bark by elk promoted canker infections. In many parts of YNP and Jackson Hole, elk commonly browse nearly all of the root sprouts present in aspen stands (Beetle 1974, 1979, Krebill 1972, Kay 1990, Bartos et al. 1994). Browsing by moose (*Alces alces andersoni* Peterson) has suppressed saplings of balsam fir (*Abies balsamea* (L.) Mill.) in portions of Isle Royale National Park, and various species of wild ungulates are reported to have suppressed tree regeneration in other areas (Brandner et al. 1990). In East Africa, browsing by elephant, impala, and other ungulates has been shown to impair regeneration of *Acacia* and other woody plant species (e.g., Prins and Van der Jeugd 1993). Therefore, several investigators have argued that excessive elk browsing is the major reason why aspen stems are not regenerating in YNP, Jackson Hole, and elsewhere (e.g., Beetle 1974, 1979, Krebill 1972, Kay 1990, Bartos et al. 1994).

Fire is also important in aspen dynamics. Fire kills mature aspen stems, but stimulates abundant production of new sprouts from the root system (e.g., Loope and Gruell 1973, Brown and DeByle 1987). Fire recurred every 20–25 yr in northern YNP prior to the advent of fire control policies in the late 1800s; from 1900 until 1988 there were almost no fires in this area (Houston 1973). There are areas in Jackson Hole where ungulate browsing has been light, both historically and recently, yet few or no tree-sized stems have been produced since the last extensive fires in the late 1800s (Loope and Gruell 1973). Thus, other investigators have argued that elimination of fire is the most important reason for poor regeneration of large aspen stems in YNP and Jackson Hole (e.g., Loope and Gruell 1973, Houston 1982).

The extensive Yellowstone fires of 1988 provided an unusual opportunity to disentangle the interactions of browsing, fire, and aspen regeneration in northern YNP. Fires in that year burned 22% of the northern range, including many aspen stands (Despain et al. 1989). The large scale of the fires may have been especially significant. Earlier work has suggested that ungulates may be capable of browsing all of the new sprouts produced in a small burn or clearcut (≈5–35 ha) and thus preventing regeneration (Jones 1974, Mueggler and Bartos 1977, Bartos et al. 1994). (However, there also are reports of successful aspen regeneration even in very small [2-ha] clear-cut areas [Jones 1975, cited in Mueg-

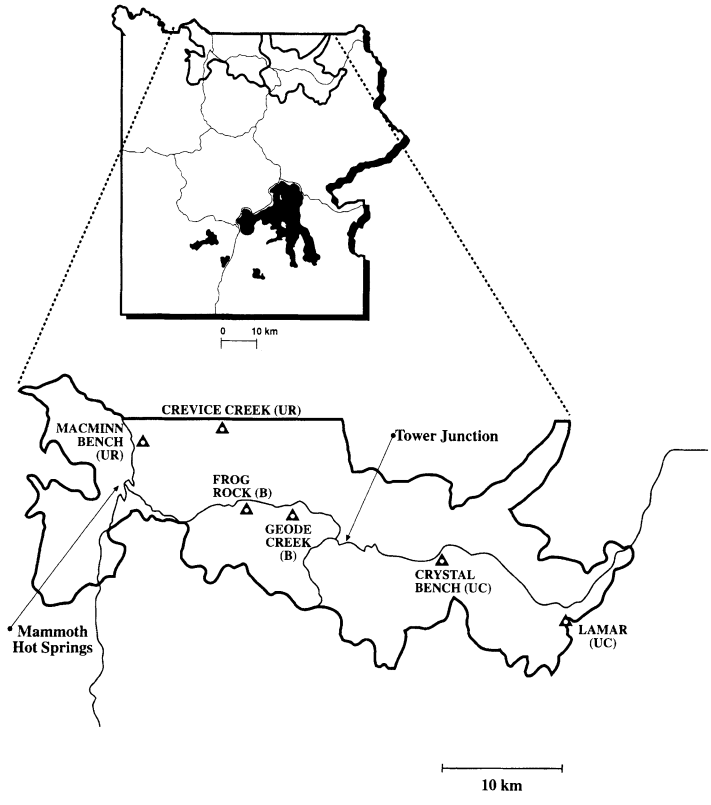


FIG. 1. Aspen stands in northern YNP sampled in this study. Stands designated "B" were burned in 1988 (Frog Rock and Geode Creek sites). Those designated "UC" were unburned and close to the burned areas (Crystal Bench and Lamar sites); "UR" were unburned and remote from the fires (MacMinn Bench and Crevice Creek sites).

gler and Bartos 1977].) With the very large Yellowstone fires in 1988, it became possible to test hypotheses about how the scale of fires may interact with elk browsing to control aspen regeneration in northern YNP.

We designed a sampling program to test two hypotheses. First, we suggested that extensive fires might stimulate the production of so many aspen sprouts that the elk would be unable to browse all of them; some would escape browsing long enough to grow up beyond the reach of browsing elk (≈2 m), whereupon they could grow into large size classes and reestablish an aspen canopy. Such a "predator-satiation" mechanism (e.g., Janzen 1976) could be possible when fires burn a large portion of a landscape. Alternatively, considering that fire usually stimulates an increase in herbaceous production for several years (Blaisdell 1953, Bartos and Mueggler 1981, West and Hassan 1985, Brown and DeByle 1989, Bartos et al. 1994, Wallace et al. 1995), elk might be so attracted to the burned grasslands and forested areas that they would be less likely to seek out small aspen stands remote from the fire. Thus our second hypothesis was that aspen tree regeneration would take place not in the burned areas but in unburned stands far from the fires.

In addition to evaluating spatial effects of the 1988 fires on browsing intensity, we also estimated the dates of establishment of extant aspen stands in northern YNP, and summarized other ecological events and conditions that existed concurrently. The objective of this historical analysis was to uncover correlations and to suggest additional mechanisms of the interaction of fire, elk, and aspen.

## METHODS

We established permanent sampling points within 18 aspen stands distributed throughout northern YNP: 6 stands had been burned in 1988, 6 were unburned but close (<1 km) to large burned areas, and 6 were unburned and remote (>4 km) from the fires (Fig. 1). All stands consisted of a canopy of large, mature aspen stems, a ground layer of small aspen sprouts and herbs, and no intermediate-sized aspen stems or trees of other species. The large stems had all been killed in the burned stands that we sampled. Stands ranged in area from 0.25 to 2.0 ha, and in elevation from 1750 to 2300 m. Most were more or less discrete patches of aspen woodland within an area of sagebrush grassland or adjacent to Douglas-fir forest (see Houston [1982] and Despain [1990] for description of the general vegetation patterns on the northern range).

Each stand was sampled in spring and fall of 1990 and 1991. Spring sampling was carried out in late May to mid-June, just after the buds began to expand. Fall sampling was conducted in September, when the year's stem elongation had stopped.

Within each stand, we established a central transect through the long axis of the stand. This transect was divided into five sections of equal length, and a short transect was started at the midpoint of each section and

extended perpendicularly to the left or right in an alternating pattern. Short transects extended outward as far as aspen sprouts were present within 1 m of the transect, and so were of variable length.

We tallied all aspen sprouts within 1 m of the short transect lines, and recorded for each sprout its height (10-cm classes) and whether it was browsed, unbrowsed, or had a dead tip for other reasons (e.g., fungus disease). During the spring sampling we also classified each sprout as "new" (<1 yr old) or "old" (>1 yr old). "Old" sprouts were recognized by the presence of bud scale scars on the stem. In the fall sampling, when fully expanded leaves were present, we classified each sprout as "juvenile" or "adult," depending on the predominant growth form exhibited (Kramer and Kozlowski 1979, Chapin et al. 1985, Basey et al. 1988, 1990). Juvenile sprouts were characterized by large leaf blades, long internodes, and cordate or truncate leaf bases, and adult sprouts by small blades, short internodes, and obtuse leaf bases. The physiological basis of these morphological differences is not clear in aspen; what we called "juvenile" sprouts may simply be 1st-yr, indeterminate-growth adult sprouts containing a high proportion of late leaves (B. Barnes, *personal communication,* 1993). Nevertheless, the two morphologic forms of sprouts were readily distinguishable in the field, and there were some differences in response of the two forms.

Since the focus of this study was on potential regeneration of large aspen stems, we recorded both the total number of sprouts present and the number of sprouts that could conceivably grow into mature trees. We often found dense clumps of 2–8 sprouts arising within 0.5 cm of each other, possibly all from one node on the root. Since only one of this cluster was likely to grow into a tree, the clump was counted as a single sprout for the purposes of this study.

Aspen sprout density, relative abundance of new/old or juvenile/adult sprouts, browsing intensity, and height distribution of sprouts were calculated for each stand and sampling period, and a test of skewness and kurtosis was made (Snedecor and Cochran 1956). Differences among stands and years were tested using ANOVA when samples were normally distributed or a Kruskal-Wallis test when samples were either skewed or kurtotic. All statistical analyses were performed using the SPSS statistical package in a VAX environment at Fort Lewis College. We discovered during analysis that the lengths of the short transects had been incorrectly recorded during the spring 1991 sampling; consequently it was not possible to compute sprout density for that sampling period, but the other parameters were unaffected by this field error.

To estimate the dates of origin of extant aspen stands, we collected increment cores from 5–10 dominant canopy trees in similar-appearing stands located close to (within 500 m) 15 of the 18 aspen stands in which browsing intensity was measured (Fig. 1). Three of the unburned remote stands were in an area of difficult access, which was not sampled for age. Cores were taken at a height of ≈1 m because most stems were found to be rotten at the base. We chose not to take increment cores from the same sites in which our permanent plots were located, because coring could cause some mortality of stems and thereby affect future sprout densities.

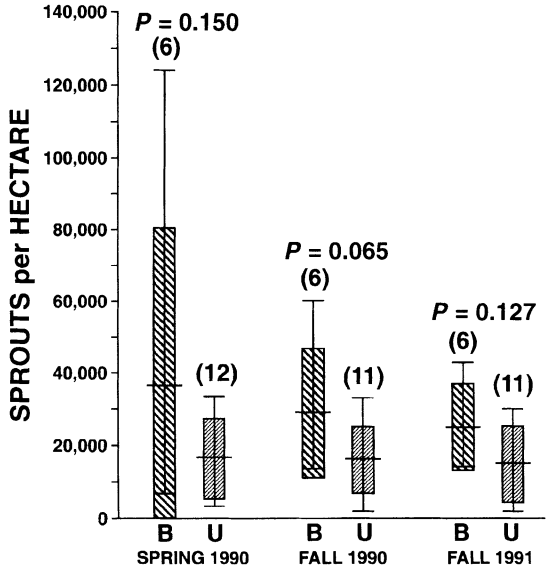


FIG. 2. Density of aspen sprouts in spring 1990, and fall 1990 and 1991 in 6 burned stands (B) and 12 unburned stands (U). (Density was not recorded in spring 1991.) For each variable, the vertical line represents sample range; horizontal lines represent maximum, mean, and minimum values observed; shaded boxes depict one standard error above and below the mean; and number in parentheses is sample size. *P* was determined by Kruskal-Wallis test.

Increment cores were mounted and sanded, and the annual rings were counted under a dissecting microscope. Cross-dating was not performed because the rings were generally complacent and very narrow in the outer portion of the cores. For cores that did not extend directly through the center of the tree but passed close by, we estimated the number of missed rings based on the curvature of the rings closest to the center on the core. We did not add an estimate of age at coring height, because aspen sprouts can elongate ≥1 m/yr. Some of the stems may be older than our estimates because repeated browsing had kept them below breast height (≈1 m) for an unknown length of time. Therefore, our stem ages represent either the approximate ages of the stems or the dates of "release" when they began growing into larger size classes.

## RESULTS

The range and maximum density of aspen sprouts was greater in the burned stands than in the unburned stands in spring and fall of 1990, although the means were not significantly different (Fig. 2). The overlap

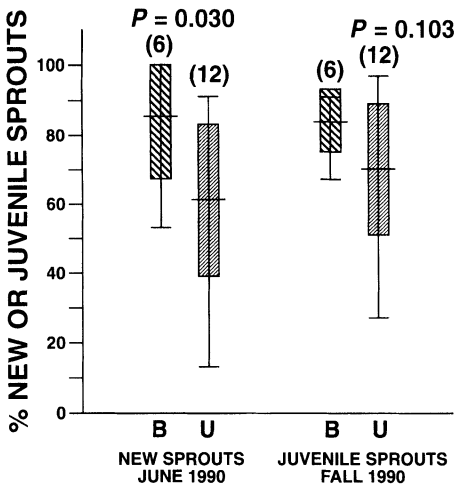


FIG. 3. Relative abundance of new vs. old aspen sprouts in spring 1990, and of juvenile vs. adult sprouts in fall 1990. See *Methods* for distinction between types of sprouts. Symbols as in Fig. 2. *P* was determined by Kruskal-Wallis test.

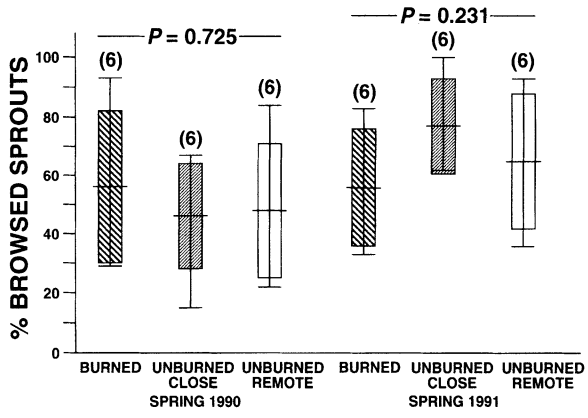


FIG. 4. Winter browsing intensity in burned, unburned close, and unburned remote aspen stands in 1990 and 1991, expressed as percentage of sprouts browsed. Symbols as in Fig. 2. *P* was determined by analysis of variance.

in statistical distributions was in part a result of the tremendous variability among stands, both burned and unburned. Mean density in the 6 burned stands in the spring of the 2nd yr after fire (1990) was 38 000 sprouts/ha, compared to 18 000 sprouts/ha in the 12 unburned stands (Fig. 2). Range and sample mean of sprout density in unburned stands remained relatively constant throughout our sampling period, but range and mean in the burned stands gradually decreased and were approaching the values of the unburned stands by the fall of 1991—the 3rd yr after the fires (Fig. 2).

The percentage of new sprouts in the spring was significantly higher in the burned stands (mean 82%) than in the unburned stands (mean 60%) (Fig. 3). The percentage of juvenile sprouts in the fall was also greater in the burned stands than in the unburned stands (mean 82% compared to 65%), although the difference in the fall was not significant (Fig. 3). Browsing intensity in all stands was much greater in the winter than in the summer; the mean percentage of browsed stems was 45–55% in spring, but only 5–10% in fall (data not shown). Therefore all of our subsequent analyses focused on winter browsing.

There were no significant differences in browsing intensity among the burned, unburned close, and unburned remote stands in the spring of 1991 or 1992; percentage of sprouts browsed was very high (mean 45–75%) in all three kinds of stands in both years (Fig. 4). Nor was there a significant difference ($P < 0.05$) in browsing intensity in new vs. old sprouts in any set of stands in either year (data not shown). Height distributions of sprouts also were not significantly different either between burned and unburned stands or between browsed and unbrowsed sprouts in either year (Fig. 5). Sprouts generally were short in all stands (mean height 21–35 cm) (Fig. 5).

The tree age determinations (Fig. 6) indicated that most of the large aspen alive today in northern YNP originated during a relatively brief period in the 1870s and 1880s. Very few of the stems alive today became established either in the 20th century or earlier in the 19th century. Notice that we cannot infer from the present surviving aspen whether stems did or did not establish in those years for which today there are no survivors. Aspen may have established in those years but subsequently died. This is one of the limitations of a static age distribution.

## DISCUSSION

The peak in density of aspen sprouts during the 2nd yr post-fire that we observed in YNP was comparable to findings reported elsewhere. For example, an experimental burn in Jackson Hole stimulated a doubling

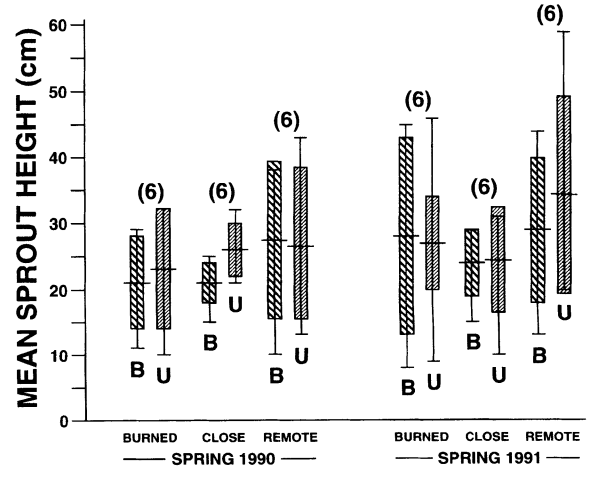


FIG. 5. Height distribution of aspen sprouts in burned, unburned close, and unburned remote stands in spring 1990 and 1991. "B," browsed sprouts; "U," unbrowsed sprouts. Symbols as in Fig. 2.

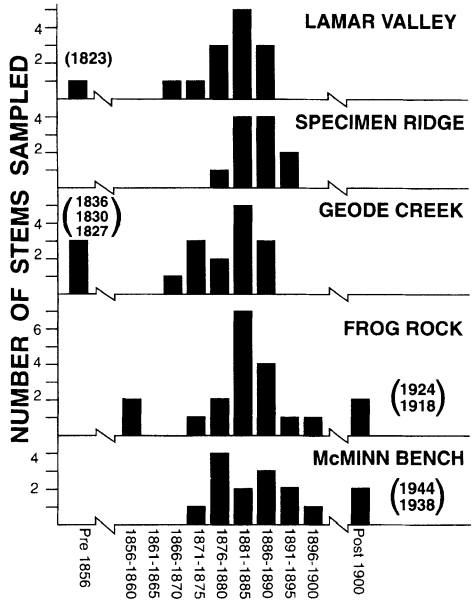


FIG. 6. Number of aspen stems established in 5-yr periods in 15 stands distributed across northern YNP (Fig. 1). A single bar is provided for the small number of stems established before 1856 and after 1900; individual dates are shown in parentheses.

of sprout density in the 2nd yr after the fire, but by the 3rd yr density was only slightly higher than before the fire (Bartos and Mueggler 1981). Brown and DeByle (1987, 1989) observed maximum sprout density 1–2 yr after fire, and Jones and Trujillo (1975) reported that maximum sprout density usually is seen the year after a fire with a gradual decrease thereafter. We sampled only in the 2nd and 3rd yr after fire, and so cannot rule out the possibility that sprout densities were somewhat higher in the 1st yr; nevertheless we clearly saw a decrease by the 3rd yr. Changes in soil temperatures and related auxin production may account for this temporal pattern in sprout production after fire (Schier 1975, Hungerford 1988).

The range in maximum sprout densities following fire that we found in Yellowstone (7000–125 000 sprouts/ha) also was roughly within the range reported elsewhere in the Rocky Mountains. Other reports include 26 000–38 000 sprouts/ha in New Mexico (Patton and Avant 1970), 35 000–250 000 sprouts/ha in the southwest (Jones and Trujillo 1975, Patton and Jones 1977), 27 000–35 000 sprouts/ha in Jackson Hole (Bartos and Mueggler 1981), and 9000–58 000 sprouts/ha in Idaho and western Wyoming (Brown and DeByle 1987, 1989).

Although the sprouting response that we measured was expected on the basis of previous studies, the lack of significant differences in browsing intensity among burned, unburned close, and unburned remote stands was unexpected, and caused us to reject both of our hypotheses about aspen regeneration. It appears now that regeneration of large aspen stems will not be stimulated by the 1988 fires, either in burned stands or in unburned stands remote from the fires. On the contrary, the fires actually may have hastened the process of "deterioration" of Yellowstone's aspen stands by killing most of the remaining large stems in many stands without producing a new cohort that will grow into large size classes (Bartos et al. 1994, Kay and Wagner, *in press*). What is the cause of this?

Studies in Alaska and in Utah have demonstrated that browsing by snowshoe hare, beaver, and other vertebrates stimulates increased production of the juvenile growth form in aspen, and that these juvenile sprouts contain high levels of resins and other substances that deter browsers (e.g., Bryant 1981, Chapin et al. 1985, Basey et al. 1988, 1990). It is possible that the juvenile sprouts in Yellowstone's burned aspen stands also contained higher levels of herbivore deterrents, but the elk did not appear to browse older sprouts or adult forms selectively. Rather they browsed all sprouts heavily, apparently with little discrimination. This may be because of the high density of ungulates on the northern Yellowstone winter range in the winters of 1989–1990 and 1990–1991 (≈12 000 and 18 000, respectively) (Singer et al. 1989; J. Mack, *personal communication,* 1992). With lower elk densities, browsing may be more selective. For example, food-limited hare populations in Alaska consumed greater quantities of twigs coated with extracts of juvenile sprouts than did less food-limited populations, but all populations tested still showed a significant avoidance of the coated twigs (Bryant 1981).

This suggestion of relatively indiscriminant browsing by Yellowstone elk is further supported by the height distributions of browsed and unbrowsed aspen sprouts. In all stands these distributions were not significantly different (Fig. 5). Moreover, mean heights of browsed and unbrowsed sprouts in the spring of 1990 and 1991 were only 21–35 cm—approximately the depth of an average snowpack in this area. This suggests that most of the unbrowsed sprouts were missed by ungulates simply because they were beneath the snow and thus unavailable. Aspen sprouts in some parts of Jackson Hole also remain generally $<1$ m because of heavy and sustained browsing by elk and moose (Bartos and Mueggler 1981, Hart 1987, Bartos et al. 1994). In contrast, aspen sprouts produced after the 1988 fires in another portion of Jackson Hole where ungulate browsing is very light are elongating rapidly (K. Doyle, *personal communication,* 1992). Aspen sprouts protected from browsing may grow $\geq 1$ m in 1 yr on good sites (Jones 1974, Jones and Trujillo 1975, Crouch 1981).

Our tree-age data indicate that most of the extant aspen trees in northern YNP became established in the 1870s and 1880s (Fig. 6). It is possible that additional large aspen stems originated before and after this period, but have died and are no longer evident. However,

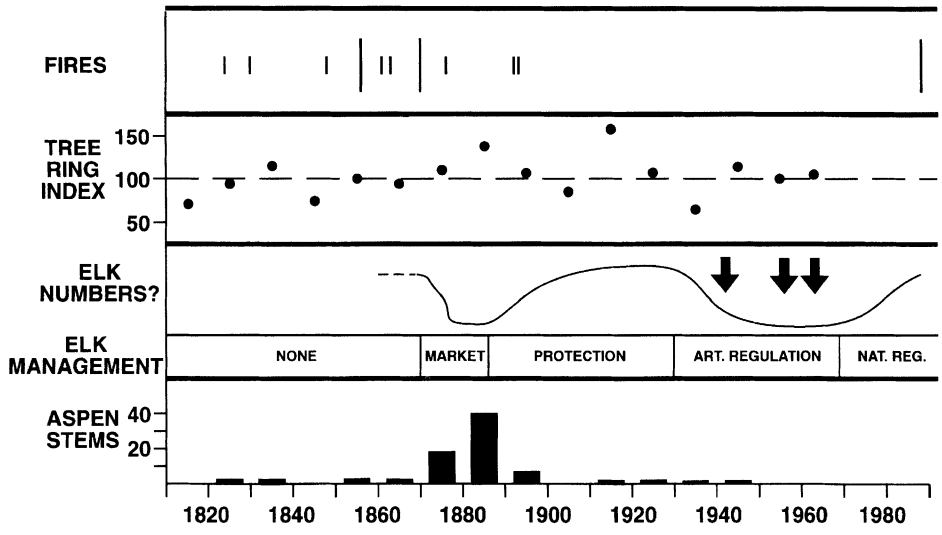


FIG. 7. Preliminary summary of changes since 1810 in ecological factors that appear to influence aspen tree regeneration in northern YNP. Dates of fires from Houston (1973), mean tree-ring index in each decade calculated from data in Drew (1975), relative numbers of elk from Houston (1982) and Schullery and Whittlesey (1992), general emphasis in elk management from Houston (1982), and establishment of aspen stems modified from Fig. 6.

we believe that very few stems grew to large size either in the several decades prior to 1865 or after ≈1900, based on historical records, photos, and observations (Warren 1926, Houston 1982, Schullery and Whittlesey 1992). For example, Warren (1926:179) determined the age distribution of an aspen stand in northern YNP, and reported that all but 2 of 31 sampled trees had become established between the mid-1860s and mid-1880s. He also expressed concern that aspen stands were being decimated by beaver (*Castor canadensis* Kuhl) and were not regenerating. The paucity of aspen regeneration prior to 1860 (Fig. 6) could be an artifact related to the short life span of aspen stems. However, aspen stems 170–200 yr old have been reported in the southwest (Mueggler and Bartos 1977, Patton and Jones 1977), and the presence in our study sites of a few stems from the 1830s indicates that trees can live at least 150 yr in this area. Moreover, early photographs of the Yellowstone area from the late 1800s consistently show young aspen stands with few or no older stands (Houston 1976, 1982; M. Meagher, *personal communication,* 1992). Therefore, we believe that the relative lack of trees from the period 1840–1860 in our samples reflects poor recruitment during that time.

### *A historical perspective*

The age distribution of extant aspen stands in northern YNP suggests that regeneration of large aspen trees was episodic even before the park's establishment in 1872. The situation appears similar in Jackson Hole, where most of the extant aspen stands there became established between 1850–1890 (Krebill 1972, Loope and Gruell 1973). How then was it possible for large-stem aspen stands to become established in northern YNP during the period 1870–1890 when they evidently cannot do so today? We cannot yet answer this question definitively, but we can tentatively identify some of the critical factors involved (Fig. 7). We suggest that this historical analysis is valuable in studying such a complex problem because it can uncover correlations among factors and thereby suggest testable hypotheses about mechanisms.

It seems certain that elk were present in what is now northern YNP in the 1800s and earlier, but we probably will never know their exact numbers or how those numbers fluctuated from year to year (Houston 1982, Schullery and Whittlesey 1992; but see Kay 1990 for a dissenting view). Market hunting in the 1860s and 1870s reduced elk numbers, probably substantially (Fig. 7). Protection of wildlife and other resources became more effective in the 1880s, and elk numbers began to rise (Houston 1982, Schullery and Whittlesey 1992). There is considerable uncertainty about actual elk numbers from 1886 to 1930, but they probably were numerous throughout that period (Houston 1982).

The period from 1930 to 1968 was a time of artificial reductions of the elk herd to maintain what was thought to be an appropriate herd size (3000–6000 animals (Houston 1982)). In 1969 YNP began its policy of natural regulation, in which no artificial reductions were attempted (Despain et al. 1986). The elk population grew rapidly during the early part of this period, and then leveled off around 15 000–20 000 in the late 1970s (Houston 1982).

Climatic variation in northern YNP (Fig. 7) was inferred from tree-ring indices developed from Douglas-fir (*Pseudotsuga menziesii* var. *glauca* Franco) near Gardiner, Montana, adjacent to YNP. We computed mean tree-ring index in each decade from yearly values reported in Drew (1975). Based on documented re-

sponses of Douglas-fir to climatic variation elsewhere in the Rocky Mountains (e.g., Fritts et al. 1965), we assumed that tree-ring indices >100 indicated generally moist conditions, whereas indices <100 indicated generally dry conditions. This analysis suggested that the period 1870–1890 was characterized by generally moist conditions (Fig. 7). This could have enhanced aspen tree regeneration via better summer growing conditions and more rapid elongation of root sprouts beyond browsing height. Alternatively, deeper winter snows could have made it more difficult for wintering ungulates to reach aspen sprouts, especially considering that many aspen stands in northern YNP are located in small depressions and drainages where wind-blown snow tends to accumulate.

Several fires were documented in northern YNP prior to 1886, some of them very extensive, but no large fires occurred from that time until 1988 (Fig. 7). Other possibly important factors in aspen regeneration are densities of wolf (*Canis lupus* L.), beaver, and moose (not shown in Fig. 7). Numbers of wolves were reduced greatly by 1880, though they were not finally extirpated until the 1920s (Schullery and Whittlesey 1992). It is unlikely that wolves altered the overall geographic distribution of wintering elk herds, but they may have caused the elk to move about more frequently on the winter range and browse individual stands less heavily. Beaver, which may browse aspen heavily, appear to have been reduced substantially by trapping and shooting in the periods 1820–1840 and 1870–1900, but apparently they were abundant in the early 1900s; their numbers have been low since about 1940 for unknown reasons (Schullery and Whittlesey 1992). Moose, which also browse aspen, apparently were absent or rare in the Yellowstone region prior to the early 1900s but have been present in low numbers since then (Schullery and Whittlesey 1992).

### *Conclusions*

We suggest that a complex interaction, involving elk abundance, climatic variation, fire, and possibly also mammalian predators and other herbivores, controls the dynamics of aspen tree regeneration in northern YNP. None of these factors is sufficient in itself to explain the temporal patterns we observed. The last major episode of aspen tree regeneration apparently occurred in 1870–1890, a historically unique period when numbers of elk, beaver, and moose were low, fires had occurred recently, climatic conditions were moist, and wolves were present. This combination of conditions has not occurred again since then (Fig. 7). For example, the dramatic elk reductions in the 1950s and 1960s occurred during dry climatic periods with no fires. A moist decade in the 1910s coincided with numerous elk, numerous beaver, and no fires. The extensive fires of 1988 were accompanied by high elk densities and generally dry climatic conditions.

We are not yet able to disentangle the mechanistic bases of all of these interactions, or even to say confidently which are of greatest importance, but we suggest that two important conclusions arise from this present study. First, regeneration of large-stem aspen in northern YNP (and perhaps elsewhere in the Rocky Mountains) evidently occurred episodically even before the arrival of Europeans in the region. This idea is counter to a prevailing popular conception that presettlement ecosystems and landscapes were somehow constant and unchanging before Europeans arrived to alter them (Sprugel 1991). A similar situation has been described in parts of East Africa, where episodic regeneration of *Acacia* bush during the last 200 yr has coincided with periods when a major browser, the impala, was decimated by disease (Prins and Van der Jeugd 1993; also see Krebs [1988:106–111] and Walker [1989] for other interpretations of the ungulate/plant "problem" in Africa). It follows that the paucity of aspen tree regeneration in YNP during the 20th century is not necessarily a major departure from "natural" conditions. It also may not be necessary, on ecological grounds, to regenerate tree-sized aspen stands in northern YNP; they apparently were rare in the mid-1800s, and possibly at other times in the past as well.

Our second conclusion is that a single-factor approach to understanding and managing aspen dynamics in YNP is not sufficient. If managers do decide that they want to regenerate the stands that now appear to be "declining"—for reasons of aesthetics, wildlife habitat, landscape diversity, or otherwise—then it is not enough to focus solely on elk numbers, fire occurrence, or any other single factor. Additional research is needed to more clearly identify the critical variables in the aspen equation and to elucidate the mechanisms of their interactions.

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