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Response of Shrub-Aspen to Yellowstone's 1988 Wildfires: Implications for "Natural Regulation" Management

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Abstract. Aspen has long been a species of special concern in the Yellowstone Ecosystem. Repeat photographs show that the area visibly occupied by aspen on the northern range has declined approximately 95% since Yellowstone National Park was established and that the number of aspen trees has declined 85% since 1947 due to repeated ungulate browsing, not other factors. Although aspen trees are now absent from many areas they formally occupied, some of those sites still support a low growth of aspen suckers — termed "shrub-aspen." Photographs indicated that aspen can maintain its presence at some locations for up to 60 years without stems ever growing taller than 1 m, again due to repeated browsing by elk and other ungulates.

Park Service biologists have postulated that shrub-aspen is the normal growth form of aspen on Yellowstone's northern range and that it does not represent retrogressive plant succession. This implies that shrub-aspen is a persistent community, and that all tree-type aspen will revert to shrub-aspen. According to this view, aspen will only grow into tree form under ideal climatic conditions or when stimulated by fire.

To test this hypothesis, we used historical photographs to locate early aspen clones on Yellowstone's northern range and then visited those sites to determine what proportion were still represented by shrub-aspen. This also allowed us to compare the area occupied by early aspen stands with the area covered by shrub-aspen today. During the course of this research, the 1988 fires burned several of the shrub-aspen sites we had previously identified. This permitted us to measure the response of those communities to fire.

We found that (1) only two-thirds of aspen clones depicted in early photos, and which today lack aspen trees, are now represented by shrub-aspen; i.e. a third of these aspen clones have completely died out. (2) Where shrub-aspen was found it occupied, on average, only 20% of the area covered by the early aspen clones. (3) Many stands that once contained thousands of aspen trees are now represented by only relatively small numbers of aspen suckers. (4) Burning did not significantly stimulate shrub-aspen height growth, stem density, or clonal spread. Burned shrub-aspen did not revert to a juvenile growth form, as is common when burned tree aspen stands produce new suckers. (5) Shrub-aspen at sites with additional soil moisture were not able to grow into trees even after they were burned, suggesting that climatic effects are unimportant.

These data and recent studies in Colorado on aspen regeneration ecology indicate that Yellowstone's shrub-aspen is not a stable vegetation type. Instead, shrub-aspen is indicative of retrogressive plant succession. Based on vegetation changes in long-term ungulate-proof exclosures, the only known way for shrub-aspen to grow back into the types of aspen communities that existed on Yellowstone's northern range ca. 1870-1890 is if all ungulate browsing were excluded for 100 years or longer. These data do not support current "natural regulation" management.

Keywords: Elk; Aspen; Fire; Yellowstone; Natural regulation.

Introduction

The relationship between vegetation and ungulates in Yellowstone National Park has long been a subject of conflicting opinions and intense debate (Houston 1982, Chase 1986, Despain et al. 1986, Kay 1990). Until 1968, Park Service officials contended that an "unnaturally" large elk (*Cervus elaphus*) population , which had built up in Yellowstone during the late 1800s and early 1900s, had severely "damaged"[1] the park's northern winter

[1]Terms such as "over grazing," "range damage," and "unnatural" elk populations are common in nearly all early, government reports on the elk herds in the Greater Yellowstone Ecosystem. Since these terms are value-laden, they are used throughout this paper only in their historical context.

range, including aspen (*Populus tremuloides*) communities (Tyers 1981). However, agency biologists now hypothesize that elk and other animals in Yellowstone are "naturally regulated," being resource (food) limited (Houston 1982, Despain et al. 1986), and that the condition of the ecosystem today is much like it was at park formation. Elk influences on Yellowstone's vegetation are now thought to be "natural" and to represent the "pristine" condition of the park.

Under "natural regulation" (Kay 1990:1-31): (1) Predation is an assisting but non-essential adjunct to the regulation of ungulate populations. If wolves (*Canis lupus*) were reintroduced into the ecosystem, they would only take the ungulates slated to die from other causes, such as starvation, and hence predation would not lower ungulate numbers. (2) If ungulates and vegetation have co-evolved for a long period of time and if they occupy an ecologically complete habitat, the ungulates cannot cause retrogressive plant succession or "range damage." The ungulates and vegetation will reach an equilibrium, called ecological carrying capacity, where continued grazing will not change plant species composition or the physical appearance of the plant communities. (3) At equilibrium, competitive exclusion of sympatric herbivores due to interspecific competition will not occur. In Yellowstone, this means that competition by elk has not reduced the numbers of other ungulates or beaver (*Castor canadensis*) since park formation.

The Park Service's "natural regulation experiment" (cf. Despain et al. 1986) is predicated on the assumption that large numbers of elk (12,000 - 15,000) wintered on Yellowstone's northern range for the last several thousand years. Park Service biologists hypothesize that elk, vegetation, and other herbivores in Yellowstone have been in equilibrium for that period of time (Despain et al. 1986). The agency now believes that any changes in plant communities since the park was established in 1872 are due primarily to suppression of lightning fires, normal plant succession, or climatic change, not ungulate grazing. Park service biologists contend that (1) aspen is a seral species in Yellowstone which in the course of plant succession is replaced by conifers or other vegetation, (2) burned aspen stands will regenerate despite heavy utilization by elk and other ungulates, and (3) elk have not been primarily responsible for the changes that have occurred in the park's aspen communities (Houston 1982, Despain et al. 1986).

To test these predictions of the "natural regulation" paradigm, we conducted an extensive study of aspen ecology in the Yellowstone Ecosystem, including inside-outside park comparisons, inside-outside exclosure measurements, aspen burns, and repeat photographs (Kay 1990, Kay and Wagner 1994). During our research, we found that the area visibly occupied by aspen on the northern range has declined approximately 95% since Yellowstone National Park was established and that the number of aspen trees has declined 85% since 1947 due to repeated ungulate browsing, not other factors (Kay 1990). We also discovered that although aspen trees are now absent from many areas they formerly occupied, some of those sites still support a low growth of aspen suckers — a condition we term "shrub-aspen." Repeat photographs indicate that aspen can maintain its presence at some locations for up to 60 years without stems ever growing taller than 1 m, again due to repeated browsing by elk and other ungulates. We also discovered shrub-aspen on other ranges in the Yellowstone Ecosystem where large herds of elk concentrate; e.g., Jackson Hole and the Gallatin (Kay unpub. data).

Park Service biologists, who independently observed this phenomenon (Despain 1991), have postulated that shrub-aspen is the normal growth form of aspen on Yellowstone's northern range and that shrub-aspen does not represent retrogressive plant succession. According to this view, aspen will only grow into tree form under ideal climatic conditions, such as occurred just before Yellowstone Park was established or when stimulated by fire (Despain 1990, 1991). This implies that shrub-aspen is a persistent community and that all tree-type aspen will revert to shrub-aspen.

To test this hypothesis, we used historical photographs to locate early aspen clones on the park's northern range and then visited those sites to determine what proportion were still occupied by shrub-aspen. This also allowed us to compare the area occupied by early aspen stands with the area covered by shrub-aspen today. During the course of this research, the 1988 fires burned several of the shrub-aspen sites we had previously identified. This permitted us to measure the response of those communities to fire.

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Study Area

Our work was conducted on the winter range of Yellowstone's northern elk herd. Houston (1982) provides a description of the climate, physiography, and vegetation of Yellowstone's northern range.

Methods

We searched archival photographic collections at Yellowstone National Park, the Montana Historical Society, the University of Montana, Montana State University, the Museum of the Rockies, the University of Wyoming, the Colorado Historical Society, the Library of Congress, the National Archives, and the U.S. Geological

Survey's Denver Photographic Library for historical photos of the northern range. We reviewed approximately 50,000 images taken in the park and throughout the Yellowstone area. Only a small portion of these were taken on the northern range, and a still smaller number contained views of aspen. During 1986-88, we rephotographed the locations in the historical pictures to form sets of comparative photos, a process called repeat photography (Rogers et al. 1984).

By field examination, we determined if the aspen clones shown in historical photos were still represented by aspen trees, shrub-aspen, or had completely died out. If shrub-aspen was present, we estimated the area occupied by the original aspen clone, as depicted in the historical photograph, and compared that estimation to the area supporting shrub-aspen at the time of our study. We then randomly placed a single 2x30 m belt transect in each of the shrub-aspen communities and counted the number of aspen stems present. We also recorded the height of each aspen stem and aged a representative sample by cutting the suckers at ground level and counting annual growth rings. Photographs were taken of each shrub-aspen community and of each belt transect, but the plots were not otherwise marked.

After the 1988 fires, our earlier photographs allowed us to establish permanent 2x30 m belt transects as close to the original sites as possible in five of the shrub-aspen communities we had previously measured. The number of aspen stems on those transects was recorded in 1989, 1991, and 1992 as was the height of each sucker. During 1989, we also measured the width of the largest leaf on a sample of shrub-aspen stems to determine if burning had stimulated juvenile-type growth as commonly occurs when tree aspen are subjected to killing fire. A study was also instituted on 131 tree-type aspen clones burned during 1988 to measure the ability of those stands to regenerate via root suckering. Those data, however, will not be reported here except to compare initial sucker density, height, and leaf width with that recorded on shrub-aspen plots.

Where appropriate (Hurlbert 1984), sample means were compared using Student's t test (Sokal and Rohlf 1981).

Results and Discussion

We made 81 repeat photosets of aspen communities on Yellowstone's northern range dating to 1871 (Kay 1990). Only two-thirds of aspen clones depicted in early photos, and which today lack aspen trees, are now represented by shrub-aspen; i.e. a third of the aspen clones have completely died out. There was no correlation between slope, aspect, elevation, distance from surface water, or surrounding vegetation and whether clones either went extinct or reverted to shrub-aspen. Where shrub-aspen was found, it occupied, on average, only 20% of the area covered by the early aspen clones. Many stands that once contained thousands of aspen trees are now represented by only relatively small numbers of aspen suckers. On 22 shrub-aspen plots measured before the 1988 fires, densities ranged from 1,500 to 56,511 stems per ha and averaged 22,551. Individual shrub-aspen stems are also short-lived. The majority were less than four years old while the oldest stem we found was only 15. These results are similar to those reported for the longevity of aspen suckers in tree-type clones on Yellowstone's northern range (Kittams 1952a, 1952b).

Burning did not significantly stimulate shrub-aspen stem density (Table 1); 18,004 per ha before the fires versus 19,170 in 1989. One year after they were burned, tree-type aspen killed by the fires produced sucker densities ranging from 68,847 to 199,040 stems per ha with a mean of 120,941 (Kay unpub. data). This was significantly greater than the density recorded in shrub-aspen communities ($t=22.62$, $p<.001$), and is probably related to clonal vigor; i.e., tree-type aspen is in better condition than shrub-aspen (Bailey et al. 1990).

Burning also did not stimulate shrub-aspen height growth (Table 2). Following fire, mean height growth fell from 41.2 cm to 20.9 cm ($t=3.55$, $p<.01$). In comparison, aspen suckers that sprouted on tree-type, fire-killed aspen plots averaged 70.5 cm ($n=818$) in 1989 (Kay unpub. data), which was significantly taller than what we recorded for shrub-aspen ($t=37.96$, $p<.001$). The 1989 height measurements were recorded before those plants were browsed, as most browsing occurs during winter when animals move on to Yellowstone's northern range. By 1992, however, shrub-aspen on the burned plots were approximately as tall as they had been prior to the 1988 fires. Long-term average aspen sucker height on Yellowstone's northern range appears to be more a function of variable snow depth limiting elk browsing than other factors (Kittams 1952a, 1952b; Barmore 1981).

Table 1. Density of shrub-aspen stems on Yellowstone's northern range before and after the 1988 fires.

	Year — Stems per ha			
Plot	1986	1989	1991	1992
SC-1	34,173	42,008	30,006	20,337
SC-2	23,171	20,504	20,671	14,836
SC-3	20,171	11,669	7,668	4,668
A-8	3,667	833	500	667
SC-10	8,668	21,171	13,169	12,336
Mean	18,004	19,170	14,336	10,502
SEM	5,501	6,835	5,168	3,667

Table 2. Mean height (cm) of shrub-aspen stems on Yellowstone's northern range before and after the 1988 fires.

	Year — Mean (SEM) height			
Plot	1986	1989	1991	1992
SC-1	33.7 (0.9)	16.8 (0.6)	16.3 (0.6)	30.2 (1.0)
SC-2	30.9 (0.8)	22.7 (0.7)	22.2 (0.6)	30.7 (0.8)
SC-3	46.7 (2.6)	30.8 (1.8)	31.3 (1.5)	42.6 (2.8)
A-8	42.9 (2.9)	23.6 (7.4)	34.7 (7.4)	49.6 (2.6)
SC-10	51.7 (6.8)	11.0 (0.4)	38.0 (1.7)	43.5 (6.0)
Mean	41.2	20.9	28.6	39.3
SEM	3.9	3.3	4.0	3.8

Measurements of aspen leaf widths further indicate that fire did not stimulate shrub-aspen. The width of the largest leaf on aspen suckers that sprouted in burned tree-type aspen the first year after Yellowstone's fires averaged 79 mm (n=127) while that of shrub-aspen averaged 26 mm (n=159) (t=34.71, p<.001). There was also no indication that burning stimulated the spread of the shrub-aspen clones. Instead, declining stem-densities (Table 1) suggest the opposite trend. This is not surprising since other research in Yellowstone has shown a positive correlation between above-ground aspen biomass and aspen suckering following fire (Renkin and Despain 1991). Aspen stands with the lowest above-ground biomass, such as shrub-aspen, produced the lowest amounts of sucker biomass after they were burned (Renkin and Despain 1991).

Recently, Park Service biologists have attributed the demise of aspen in Yellowstone National Park to a drying climatic trend unrelated to ungulate use of the northern range. There is no evidence, however, to support that contention especially since aspen located inside long-term, ungulate-proof exclosures has expanded and replaced grasslands (Kay 1990). Moreover, shrub-aspen located along streams or in other areas with supplemental moisture have not achieved tree status. In addition, with the loss of aspen trees, soil chemistry often is modified to such an extent that normal aspen communities may not be able to become reestablished even if grazing is excluded (Cryer and Murray 1992). This suggests that it may be difficult to restore aspen to its former status in the park. Moreover, aspen seedlings which grew after Yellowstone's 1988 fires will not reverse this trend because ungulate browsing is limiting aspen seedling height growth and will probably prevent any of those plants from growing into trees, let alone establishing new clones (Kay 1993). This is not surprising since others have shown that elk (Bartos et al. 1991, 1994) or cattle (Fitzgerald and Bailey 1984, Fitzgerald et al. 1986, Walker 1993) can prevent regeneration of even burned tree-type aspen.

Conclusions

These data indicate that Yellowstone's shrub-aspen is not a persistent vegetation type. Instead, the decline of aspen on Yellowstone's northern range, including the creation of shrub-aspen, is indicative of retrogressive plant succession caused by repeated ungulate browsing. Based on vegetation changes in long-term ungulate-proof exclosures (Kay 1990), the only known way for shrub-aspen to grow back into the types of aspen communities that existed on Yellowstone's northern range ca. 1870-1890 is if all ungulate browsing were excluded for 100 years or longer. These data do not support current "natural regulation" management.

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