

Long-Term Aspen Exclosures in the Yellowstone Ecosystem

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Abstract—Aspen has been declining in the Yellowstone Ecosystem for more than 80 years. Some authors have suggested that aspen is a marginal plant community in Yellowstone and that recent climatic variation has adversely affected aspen, while others contend that excessive browsing by native ungulates is primarily responsible for aspen's widespread decline. To test these hypotheses, I measured all the long-term aspen exclosures ($n = 14$) in the Yellowstone Ecosystem. Aspen stands inside all exclosures successfully produced new stems greater than 2 m tall without fire or other disturbance, while few outside stands successfully regenerated due to repeated browsing. Understory species composition was also significantly different inside and outside exclosures. Protected aspen understories were dominated by tall, palatable shrubs and forbs, while grazed understories were dominated by exotic grasses and unpalatable, low-growing forbs. None of the enclosed aspen exhibited any signs of physiological stress, even on dry south-facing hillsides, an indication that climatic variation has not adversely impacted aspen. Instead, exclosure data suggest that aspen has declined throughout the Yellowstone Ecosystem due to repeated browsing by native ungulates, primarily elk.

Introduction

After Yellowstone was designated as the world's first national park in 1872, a succession of civilian (1872–1886), military (1886–1916), and National Park Service (1916–present) administrators concluded that there were not enough game animals; so they fed wintering elk (*Cervus elaphus*) and other ungulates, and they killed predatory animals such as wolves (*Canis lupus*) and mountain lions (*Felis concolor*). During the 1920s, however, concerns grew that too many elk were overgrazing the park's northern winter range, so the agency began trapping and transplanting elk to areas outside the park. Because trapping alone did not reduce the herd to the range's estimated carrying capacity, rangers began shooting elk in the park to prevent resource damage. This program was called direct reduction, and by 1967 the Park Service had killed over 13,500 elk from Yellowstone's northern herd (Houston 1982).

This upset many people who exerted political pressure to stop the Park Service from shooting elk in the park. After a U.S. Senate (1967) Subcommittee hearing at which the chairman threatened to terminate park funding, the Park Service agreed to abandon its direct reduction program—although the agency still contended that Yellowstone was seriously overgrazed. By 1968, the Park Service had switched to a management program called “natural control” which was changed to “natural regulation” during the early 1970s. These changes occurred without public review or comment (Chase 1986; Wagner et al. 1995). The Park Service originally based “natural regulation” on a presumed “balance-of-nature,” but more recently the agency has cited Caughley's (1976) plant-herbivore model to support its “natural regulation” paradigm (Kay 1990).

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Under "natural regulation," the Park Service completely revised its interpretation of the history and ecology of elk in Yellowstone.

Until 1968, Park Service officials contended that an unnaturally large elk population, which had built up in Yellowstone during the late 1800s and early 1900s, had severely damaged the park's northern winter range, including aspen (*Populus tremuloides*) communities. However, agency biologists now hypothesize that elk and other ungulates in Yellowstone are "naturally regulated," being resource (food) limited, and that the condition of the ecosystem today is much like it was at park formation (Houston 1982; Despain et al. 1986). Elk influences on Yellowstone's vegetation are now thought to be "natural" and to represent the "pristine" condition of the park. According to the Park Service, Yellowstone is not now nor has it ever been overgrazed, and all previous studies to that effect are wrong (Houston 1982).

There are several tenets to the "natural regulation" paradigm (Wagner et al. 1995). First, under "natural regulation," predation is an assisting but nonessential adjunct to the regulation of ungulate populations. If wolves are present, they take only the ungulates slated to die from other causes, such as starvation, and hence predation will not lower ungulate numbers. In the ongoing reintroduction of wolves to Yellowstone, the Park Service has denied that wolves are needed to control the park's elk herds or that wolves will have any significant impact on elk numbers (Boyce 1992). Second, if ungulates and vegetation have coevolved 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, termed ecological carrying capacity, where continued grazing will not change plant species composition or the physical appearance of plant communities. According to the Park Service, thousands of elk starving to death during winter is natural. Third, 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 have been in equilibrium for that period of time (Houston 1982; Despain et al. 1986). The agency now believes that any changes in plant communities since the park was established 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, (3) Yellowstone is marginal habitat for aspen and that recent climatic variation has adversely effected aspen, and (4) elk have not been primarily responsible for the changes that have occurred in the park's aspen communities (Houston 1982; Despain et al. 1986).

The Gallatin is located in the northwest corner of Yellowstone Park and historically has had an elk problem and reinterpretation similar to that on the northern range (Lovaas 1970; Kay 1990). Jackson Hole is situated to the south of Yellowstone Park, and it too has had a long-standing elk situation (Anderson 1958; Beetle 1974, 1979; Boyce 1989). At first, it was thought that (1) Jackson Hole was not a historic elk winter range, (2) European settlement forced elk to winter in the valley, and (3) supplemental feeding permitted the growth of an

abnormally large elk herd, which (4) caused substantial damage to the winter range and a marked decline of aspen (Preble 1911; Murie 1951; Anderson 1958; Krebill 1972; Beetle 1974, 1979). However, federal and state biologists now believe that (1) large numbers of elk have wintered in Jackson Hole for the last several thousand years; (2) feedlots have only replaced winter range lost to modern development; (3) therefore, today's elk population is not unnaturally high, though the distribution of wintering animals may have changed; (4) serious elk-induced range damage has not occurred (Cole 1969; Gruell 1979; Boyce 1989); and (5) the elk herd would "naturally regulate" if sport hunting were terminated (Boyce 1989). Under this interpretation, aspen is thought to be a seral species maintained by fire, and human suppression of lightning fires is believed to be primarily responsible for the observed decline in aspen, not ungulate browsing (Loope and Gruell 1973; Gruell and Loope 1974). Based on repeat photographs, aspen has declined by as much as 95% throughout the Yellowstone Ecosystem since the late 1800s (Gruell 1980a,b; Houston 1982; Kay 1990; Kay and Wagner 1994).

As part of a larger project to test these competing hypotheses and to determine why aspen has declined in Yellowstone (Kay 1990), I measured all the long-term aspen enclosures throughout that ecosystem, because enclosures can be used to study the successional status and trend of plant communities, as well as to evaluate the impact of grazing (Laycock 1975). Enclosures can also be used to evaluate climatic effects since the general climate is the same within the enclosures and on adjacent outside plots. I then analyzed those data to determine whether the aspen stands were seral or climax, whether climatic variation was important in aspen ecology, and what impact ungulate grazing has had on aspen communities. Livestock use does not occur, or is minimal, around the aspen enclosures in the Yellowstone Ecosystem, and all enclosures are situated on big-game winter ranges where elk are the most abundant ungulate.

In addition, to measuring all the aspen-containing enclosures in the Yellowstone Ecosystem, I randomly sampled aspen stands over large areas both inside and outside Yellowstone Park. I also compiled 101 repeat photosets of aspen communities dating to the 1870s, and I evaluated 467 burned and 495 adjacent unburned aspen stands in Jackson Hole. After Yellowstone's 1988 wildfires, I established 865 permanent plots in burned aspen stands. Since those data have been reported elsewhere (Kay 1990, this proceedings), they are here incorporated by reference.

Methods

I first searched agency files to obtain all existing information on each enclosure. Care was taken to locate all prior vegetation data, any written description of permanent vegetation sampling schemes, and any old photographs (Kay 1990). The locations, dates of establishment, and sizes of the aspen enclosures found in the Yellowstone Ecosystem are presented in table 1. At most enclosures, I used multiple 2- x 30-m belt transects to measure aspen stem dynamics on inside and outside plots. To facilitate data collection, I subdivided each 30-m transect into 3-m segments and recorded the number of aspen stems by five size classes within each 3-m segment: (1) <2 m tall, (2) >2 m tall but <5 cm d.b.h. (diameter at breast height), (3) 6–10 cm d.b.h., (4) 11–20 cm d.b.h., and (5) >20 cm d.b.h. I also recorded the number, size, and species of all conifers in each transect. In addition, I visually estimated the percent conifer canopy cover in each stand according to procedures established by Mueggler

Table 1—Location and description of aspen exclosures in the Yellowstone Ecosystem.

Winter range exclosure	Area ^a	Location ^b			Date established	Size	Elevation	Aspect
		T	R	S				
						ha	m	
Northern Yellowstone								
1. Mammoth	YNP	—	—	—	1957	2.116	1,902	N
2. Junction Butte	YNP	—	—	—	1962	2.116	1,890	NW
3. Lamar-East	YNP	—	—	—	1957	2.116	2,027	S
4. Lamar-West	YNP	—	—	—	1962	2.116	2,027	S
5. Range Plot 10	YNP	—	—	—	1934	0.004	1,881	E
6. Range Plot 25	YNP	—	—	—	1936	0.004	1,951	NW
Jackson Hole								
7. East Elk Refuge	BTNF	41N	114W	3	1952	0.110	2,057	SW
8. Upper Slide Lake	BTNF	42N	112W	20	1960	152.376	2,317	S
9. Goosewing	BTNF	41N	112W	3	1942	0.819	2,271	N
10. Uhl Hill	GTNP	44N	114W	1	1963	0.364	2,112	S
Gallatin								
11. Porcupine	GNF	7S	4E	16	1945	1.866	1,920	SE
12. Crown Butte	GNF	9S	5E	7/8	1945	2.066	2,210	S
13. Range Plot 16	YNP	—	—	—	1935	0.004	2,195	W
Pinedale								
14. Soda Lake ^c	BTNF	34N	109W	23	1964	0.431	2,332	S

^aYNP—Yellowstone National Park, GNF—Gallatin National Forest, BTNF—Bridger-Teton National Forest, and GTNP—Grand Teton National Park.

^bYellowstone Park has not been surveyed.

^cLocated in the Green River drainage to the east of Jackson Hole but within the Yellowstone Ecosystem. Exclosure is behind the Soda Lake elk feedground and was included to maximize sample size.

(1988). Inside the smaller exclosures—Range Plots 10, 16, and 25; East Elk Refuge; and Elk Ranch Reservoir—I made complete counts of all aspen and conifers, as well as on comparable outside areas. Following Mueggler (1988), I estimated understory species composition of shrubs, grasses, and forbs on all inside and outside plots. Finally, I rephotographed all previously established photo sites.

Results

Repeat Photographs

Based on the photosets that were examined (figures 1–3), all enclosed aspen successfully regenerated into multisize-class stands. Aspen did not produce new stems >2 m tall in any of the unprotected stands except at Goosewing and Soda Lake. Aspen outside the exclosures experienced continued mortality and all of the mature trees outside several exclosures had died, including Range Plot 10, Junction Butte, and Lamar-East. Based on the presence of dead, standing trees, all mature aspen outside the Uhl Hill exclosure had also recently died. Aspen clones within all exclosures increased in area, and many expanded into and replaced sagebrush-grasslands within the exclosures (figure 3). Within most exclosures, there was a substantial increase in understory shrubs, but conifers had not encroached upon most of the inside or outside aspen communities.

Aspen Stem Dynamics

Aspen stands inside Yellowstone exclosures (table 2) had a significantly different size-class stem distribution than aspen outside the exclosures ($p < 0.001$, Hotelling's T^2 test) (Kendall 1980). At all but one, East Elk Refuge, there were

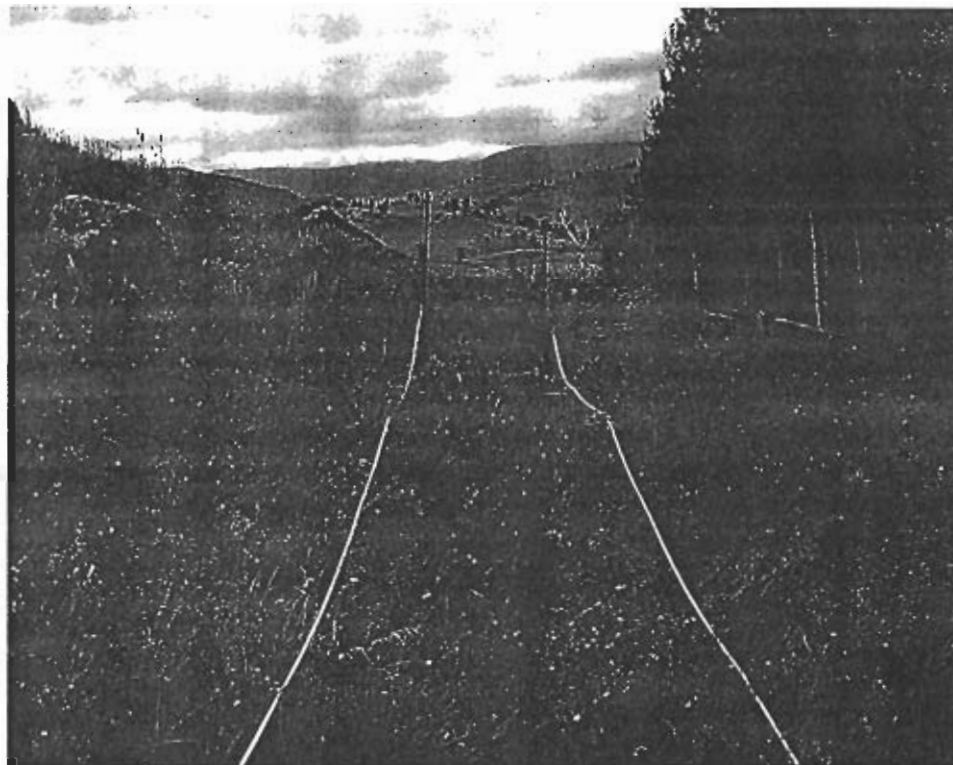


Figure 1—Aspen belt transect outside Yellowstone Park's Junction Butte exclosure in 1962 (top) and 1986 (bottom). The two steel posts mark the north end of the belt transect. Exclosure fence is on the right. Four mature aspen were alive outside the exclosure in 1962, the year this exclosure was built, but all had died by 1986. NPS photo 62-S48, 9/18/62. Charles Kay photo 58, 9/82-12, 7/25/86.

more stems <2 m tall per unit area outside than inside. This was not unexpected since larger aspen often suppress new suckers (Schier et al. 1985). All stands protected from ungulate browsing successfully regenerated and produced stems >2 m tall without fire or other disturbance, and most developed multiple size-classed stems characteristic of stable or climax aspen (Mueggler 1988). In only two instances, Goosewing and Soda Lake, did aspen outside exclosures produce ramets >2 m tall. In those cases, however, there were significantly greater stem densities (>2 m tall but <20 cm d.b.h.) inside the exclosures (table 2).

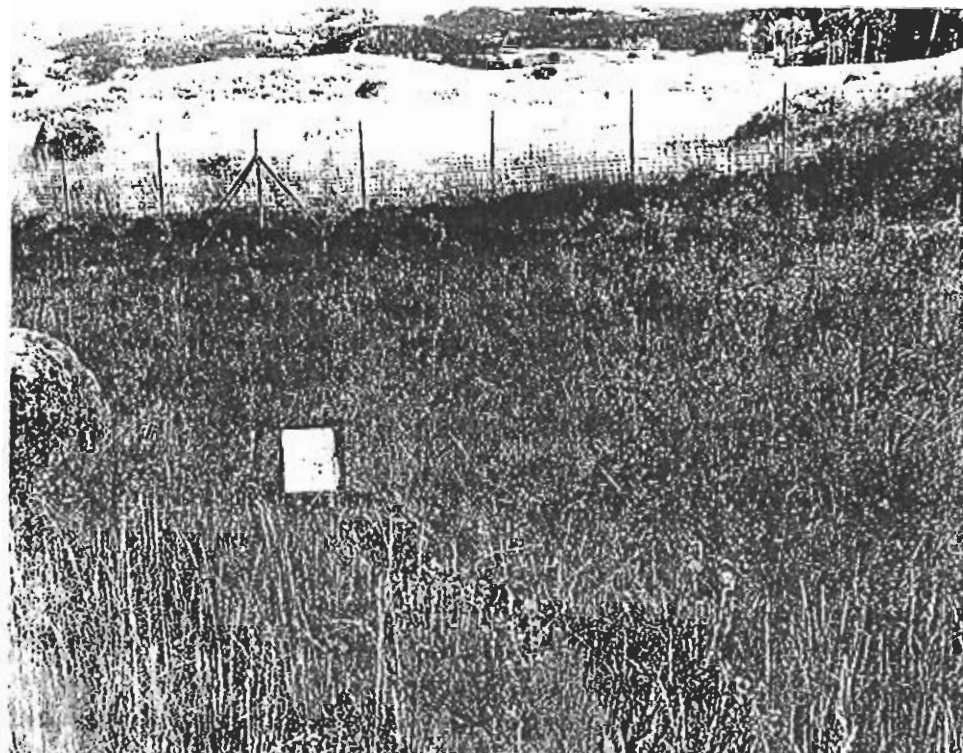


Figure 2—Aspen belt transect inside Yellowstone Park's Junction Butte enclosure in 1962 (top) and 1986 (bottom). Enclosure fence is to the top of the 1962 photo, and the two steel posts mark the west end of the belt transect. NPS photo 62-547, 9/20/62. Charles Kay photo 58, 982-17, 7/25/86.



Conifer Invasion

There were few conifers inside or outside Yellowstone aspen exclosures (table 2). This may be because most exclosures were built on winter range sites where conifers are less common than at higher elevations. A significant proportion of aspen communities throughout the Yellowstone Ecosystem, though, have not been invaded by conifers, including aspen stands immediately adjacent to coniferous forests (Kay 1990).

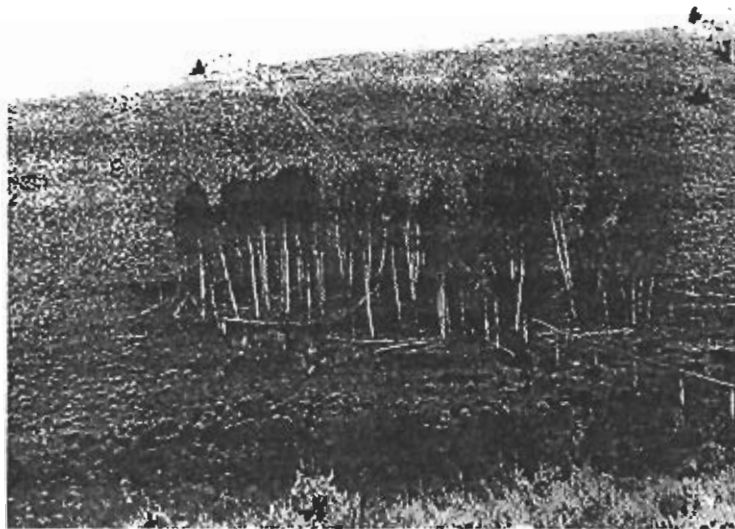


Figure 3—Porcupine Creek enclosure on the Gallatin National Forest. Top: The enclosure was built in 1945, and this photograph was taken 1 year later in 1946. Note that the enclosure fence bisects a single aspen clone. U.S. Forest Service photo. Middle: By 1963, willows in the foreground had increased dramatically in height and canopy cover, but the enclosed aspen showed little apparent change. Photo taken in July by James Peek. Bottom: By 1987, however, aspen inside the enclosure had increased markedly and replaced sagebrush and grasslands on this dry, southeast-facing hillside. Photo taken on August 26 by Charles E. Kay.

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Table 2—Aspen stem densities and estimated conifer canopy cover inside and outside 14 Yellowstone exclosures.

Exclosure ^a	Area sampled <i>m</i> ²	Mean number of live stems per <i>m</i> ² by size classes					Estimate conifer canopy cover
		<2 m	>2 m – ≤5 cm	6–10 cm	11–20 cm	>20 cm	
		number per <i>m</i> ²					percent
1. Mammoth							
Inside	106	0.15	0.16	0.35	0.02	0.00	<5
Outside	106	3.40	0.00	0.00	0.00	0.07	>5
2. Junction Butte							
Inside	95	0.11	0.26	0.49	0.15	0.00	None
Outside	95	0.49	0.00	0.00	0.00	0.00	None
3. Lamar-East							
Inside	106	0.63	0.37	0.27	0.06	0.00	<1
Outside	106	1.91	0.00	0.00	0.01	0.04	None
4. Lamar-West							
Inside	106	0.12	0.29	0.09	0.00	0.00	None
Outside	60	1.63	0.00	0.00	0.00	0.03	None
5. Range Plot 10							
Inside	41	0.00	0.51	0.12	0.34	0.00	None
Outside	41	1.90	0.00	0.00	0.00	0.00	None
6. Range Plot 25							
Inside	45	0.70	0.36	0.36	0.34	0.38	None
Outside	22	3.00	0.00	0.00	0.13	0.00	None
7. East Elk Refuge							
Inside	1,100	2.30	0.05	0.03	0.03	0.01	None
Outside	60	1.28	0.00	0.00	0.10	0.00	None
8. Upper Slide Lake							
Inside	93	0.40	0.20	0.09	0.00	0.01	>50
Outside	93	1.45	0.00	0.00	0.00	0.00	None
9. Goosewing							
Inside	360	0.66	0.94	0.37	0.10	0.05	<2
Outside	360	1.51	0.44	0.00	0.02	0.04	<2
10. Uhl Hill							
Inside	218	0.06	0.09	0.09	0.00	0.00	<1
Outside	180	0.09	0.00	0.00	0.00	0.00	None
11. Porcupine							
Inside	180	0.44	1.12	0.58	0.07	0.03	<1
Outside	180	1.80	0.00	0.00	0.00	0.02	None
12. Crown Butte							
Inside	180	0.07	0.47	0.19	0.13	0.03	<1
Outside	300	0.93	0.00	0.00	0.00	0.03	<5
13. Range Plot 16							
Inside	37	0.16	0.35	0.30	0.05	0.00	>15
Outside	37	1.05	0.00	0.00	0.00	0.00	None
14. Soda Lake							
Inside	180	0.09	0.52	0.27	0.05	0.02	None
Outside	300	0.89	0.03	0.03	0.04	0.01	None
Total (n = 14)							
Inside		0.48	0.41	0.26	0.10	0.04	
Outside		1.52	0.03	0.002	0.02	0.02	
<i>t</i>		4.52	4.22	6.45	2.45	0.70	
<i>p</i>		<0.01	<0.01	<0.01	<0.05	NS	
Total (n = 12) ^b							
Inside		0.43	0.35	0.25	0.10	0.04	
Outside		1.58	0.00	0.00	0.02	0.02	
<i>t</i>		3.37	4.17	4.63	2.10	0.59	
<i>p</i>		<0.01	<0.01	<0.01	<0.10	NS	

^aExclosure numbers correspond to those given in table 1.^bNot including Goosewing and Soda Lake.

Understory Species Composition

At all exclosures, there were major differences in understory species composition between inside and outside plots (table 3). These differences were especially pronounced at exclosures where the inside and outside plots were located within the same aspen clone. This included Range Plots 10, 16, and 25, Junction Butte, Porcupine, Uhl Hill, Soda Lake, and Goosewing. The vegetation inside and outside these exclosures often keyed as entirely different aspen community types (Kay 1990) according to the classification developed by Youngblood and Mueggler (1981).

On average, shrubs predominated inside exclosures, although forbs and a few grasses were present. In areas exposed to elk and other ungulates, though, there were substantially fewer shrubs and the sites were dominated by grasses (table 3). A large proportion of those grasses were nonnative species, such as timothy (*Phleum pratense*) or Kentucky bluegrass (*Poa pratensis*), which increase under grazing pressure (Mueggler 1988). In Yellowstone Park, timothy and Kentucky bluegrass had an average canopy coverage of 56% outside exclosures and 19% inside ($t = 3.47, p < 0.01$, arcsine transformed data).

While the difference between average percentage of forbs inside and outside Yellowstone exclosures was not statistically significant (table 3), there were major differences in species composition. Forbs that tend to decrease under grazing or trampling such as *Epilobium angustifolium*, *Thalictrum fendleri*, and *Smilacina stellata* averaged 14.9% canopy coverage inside exclosures and 3.0% outside ($t = 2.70, p < 0.02$, arcsine transformed data). Forbs more immune to grazing like Geranium spp. and *Fragaria virginiana* averaged 8.2% canopy coverage inside exclosures and 17.2% outside ($t = 2.50, p < 0.02$, arcsine transformed data). Thus, aspen understories inside exclosures were dominated by species associated with climax communities, while on adjacent outside plots, understories were dominated by species characteristic of grazing disclimaxes (Mueggler 1988).

Discussion

Other Aspen Exclosure Studies

Mueggler and Bartos (1977) reported that shrubs increased inside two, three-part aspen exclosures in southern Utah where mule deer (*Odocoileus hemionus*) and cattle were the primary ungulate herbivores. They (p. 13) concluded that "the most striking difference in understory attributable to animal use was the great reduction in total shrubs.... After 41 years, the ungrazed area at Grindstone Flat produced almost 10 times more shrubs than the area grazed by both cattle and deer and over three times more than that grazed just by deer.

Table 3—Mean canopy coverage of understory plants inside and outside 14 aspen exclosures in the Yellowstone Ecosystem.

Vegetation class	Mean percent canopy coverage		t^a	p
	Inside	Outside		
Shrubs	68	22	3.78	<0.01
Forbs	25	29	0.50	NS
Grasses	15	48	4.06	<0.01

^aArcsine transformed data.

The graminoids increased under grazing at Grindstone Flat." Aspen protected from all grazing developed multisize-class stands while those outside did not.

Coles (1965:38–41) measured the age structure of aspen communities inside and outside a three-part enclosure in central Utah. Where all ungulates were excluded, aspen were multiaged. Where cattle were excluded but mule deer were not, few new stems had grown taller than 2 m. While in South Dakota's Custer State Park, aspen expanded into and replaced grassland inside an enclosure within 2 years following exclusion of grazing (Hoffman and Alexander 1987:15). At South Dakota's Wind Cave National Park, aspen inside an enclosure developed into a multisize-class stand while those subject to ungulate grazing did not (Kay 1990:115). Similarly, Hurlburt and Bedunah (1996:23) measured three-part aspen-containing enclosures in north-central Montana and reported that "grazing solely by wild ungulates dramatically influenced...aspen communities" as elk and deer use tended to eliminate aspen and understory shrubs.

Trottier and Fehr (1982:28–33) reported on an aspen enclosure in Canada's Banff National Park where elk are the most abundant ungulate. They (p. 28) noted that "browsing by elk in this area has a tremendous influence on shrub and tree regeneration in the aspen forest." The protected plot had greater shrub density and a more diverse height class distribution than the browsed plot. "About 97% of the shrubs in the browsed plots were less than 100 cm high and there were no plants taller than 150 cm" (p. 30). Trottier and Fehr (1982:30) concluded that aspen regeneration was limited by ungulate browsing: "Under protection there were plants [aspen] in all height classes indicating that growth to tree stage was proceeding. On the browsed plot all plants were less than 100 cm."

When Banff's aspen enclosure was erected in 1944, two photopoints were established, one inside the protected area and another immediately outside. Retakes 50 years later showed that a dense multiaged aspen stand had grown up inside the enclosure, while no aspen stems had successfully regenerated on outside plots (Kay et al. 1999). Kay et al. (1999) also reported on aspen that had been protected for approximately 10 years within the game-proof fenced Trans Canada Highway right-of-way through Banff's lower Bow Valley. Where elk were excluded, aspen had successfully regenerated, while there was no response on grazed plots.

Milner (1977) measured aspen communities inside and outside four enclosures in Canada's Elk Island National Park where elk and moose (*Alces alces*) are the primary ungulates. Inside each enclosure, aspen "attained a greater basal area, height and d.b.h. class" than on outside plots (p. 52). Moreover, "regeneration of the tree structure was restricted in unprotected areas...[and] shrub height and diameter class were greater in the enclosures" (p. 52–53). Highly palatable shrubs increased significantly inside the enclosures. That is to say, ungulate browsing prevented aspen regeneration and favored grasses over shrubs.

Gysel (1960), Olmsted (1977), Stevens (1980), and Baker et al. (1997) reported on aspen enclosures in Colorado's Rocky Mountain National Park where elk and mule deer are the most common ungulates. Inside three out of four enclosures, aspen developed into multisize-class stands while those outside did not. In the fourth, aspen was completely replaced by conifers, but conifers did not establish in the other enclosures (Olmsted 1977:27). Inside the three enclosures, aspen spread into and replaced grasslands while outside, grazing changed aspen communities into grasslands (Gysel 1960; Stevens 1980; Baker et al. 1997). Shrubs were more common inside the enclosures than out (Stevens 1980). A temporary reduction of elk numbers in that park allowed some aspen

stems to escape browsing and to grow into larger size classes (Olmsted 1977, 1979; White et al. 1998).

Harniss and Bartos (1990) and Bartos and Harniss (1990) reported on an exclosure in eastern Utah where the mature aspen trees had been killed by herbicide to stimulate resprouting. "Where livestock were excluded, aspen were essentially eliminated from the site by deer and elk" (Harniss and Bartos 1990:37). While in Arizona, treated aspen had to be protected by game-proof fencing, and when the fencing was removed from a 6.5-ha aspen stand that had produced 50,000 stems per ha more than 3 m tall, the regenerated aspen were severely damaged by elk (Shepperd and Fairweather 1994; Fairweather and Tkacz 1999).

More recently, Kay and Bartos (2000) measured all known aspen exclosures on the Dixie and Fishlake National Forests in south-central Utah. Five of the exclosures were of a three-part design with a total-exclusion portion, a livestock-exclusion portion, and combined-use portion that permitted the effects of mule deer and elk herbivory to be measured separately from those of livestock. Aspen within all total-exclusion plots successfully regenerated and developed multiaged stems without the influence of fire or other disturbance. Aspen subjected to browsing by wildlife, primarily mule deer, either failed to regenerate successfully or regenerated at stem densities significantly lower than that on total-exclusion plots. On combined wildlife-livestock-use plots, most aspen failed to regenerate successfully, or did so at low stem densities. Aspen successfully regenerated on ungulate-use plots only when deer numbers were low. Similarly, ungulate herbivory had significant effects on understory species composition. In general, utilization by deer tended to reduce shrubs and tall palatable forbs while favoring the growth of various grasses. There was no evidence that climate variation affected aspen regeneration. Instead, observed differences were attributed to varied histories of ungulate herbivory.

Thus, aspen exclosure studies throughout the Western United States and Canada support the results reported here—namely, that native ungulate use can have a significant effect on aspen regeneration and understory species composition. Moreover, aspen stands dominated by old-age or single-age aspen, which are common in the Yellowstone Ecosystem and across the West (Mueggler 1989, 1994), are not a biological attribute of aspen, but an artifact of excessive ungulate browsing.

Climate Change

The decline of aspen on Yellowstone's northern range has been attributed by some to climatic change and especially the drought during the 1930s (Houston 1982). That supposition, though, is not sustained because newly enclosed aspen in Range Plots 10, 16, and 25 grew vigorously during and after the 1930s drought, while aspen outside did not (Kay 1990). Similarly, if as Despain et al. (1986:109) claimed, "Yellowstone is not the center of good aspen habitat and even a slight change in climate could have significant effects on aspen here," then aspen inside exclosures should show signs of physiological stress such as stunted growth or twisted trunks. But, none of the aspen inside any exclosure in the Yellowstone Ecosystem show signs of physiological stress. Aspen 60 years old inside Range Plot 25 were approximately 20 m tall, over 20 cm d.b.h., and had straight trunks (Kay 1990:108). Furthermore, aspen stands on south-facing hillsides inside several exclosures (Lamar-East, Crown Butte, Porcupine; figure 3) had expanded and replaced grass-sagebrush, which would not have been possible if those aspen had been in physiological stress or if the climate

had been limiting or marginal for aspen. It is also clear that it is not climate that prevents aspen from reaching its biological potential outside Yellowstone exclosures. Instead, repeated browsing by elk and other ungulates has kept aspen from successfully regenerating, and it is ungulate browsing that is primarily responsible for the decline of aspen throughout the Yellowstone Ecosystem.

The more profuse vegetation inside the exclosures does, itself, alter the microclimate, but that is an incorporated variable caused by the plants' response to the elimination of ungulate browsing, not the cause of the vegetation's response. Such microclimatic conditions would prevail in any aspen stand not subject to heavy ungulate use, whether in an exclosure or not. Moreover, Baker et al. (1997) and White et al. (1998) reported no correlation between climatic variation and aspen regeneration anywhere in western North America.

Aboriginal Overkill

How then was aspen able to flourish in Yellowstone and throughout the Intermountain West for the last 10,000± years? Simple: The large elk and other ungulate populations assumed under "natural regulation" (Houston 1982; Despain et al. 1986; Romme et al. 1995) did not exist until after Yellowstone was designated a national park. Historical journals, old photographs, and archaeological data all indicate that there are now more elk in Yellowstone than at any point prior to 1872 (Kay 1990, 1994, 1995a,b, 1996, 1997a,b,c,d,e, 1998; Kay and Walker 1997). Archaeologically, elk are rare to nonexistent from sites in the Yellowstone Ecosystem and throughout the Intermountain West (Kay et al. 1999). Historically, elk and other ungulates were also rare there. Between 1835 and 1876, for instance, 20 different expeditions spent 765 days in the Yellowstone Ecosystem on foot or horseback, yet reported seeing elk only once every 18 days. Today there are over 100,000 elk in that system. Similarly, bison (*Bison bison*) were only seen three times by early explorers, none of which were in the present confines of Yellowstone Park, while recently there have been as many as 4,000 bison in the park. Moreover, if elk and other ungulates were as abundant in the past as they are today, then late 1800s photographs of preferred forage species such as aspen and willows (*Salix* spp.) should show that those plants were as heavily browsed historically as they are today. But early photos of aspen and other species in Yellowstone show no evidence of ungulate browsing, unlike present conditions (Kay and Wagner 1994). Thus, there is no evidence to support the view that large numbers of elk were ever common in Yellowstone until after 1900.

Before park establishment, Yellowstone's elk population was limited at low densities by predation, primarily by Native Americans. Contrary to prevailing beliefs, Native Americans were not conservationists (Kay 1994, 1998). Because native peoples could prey-switch to small mammals, plant foods, and fish, they could take their preferred ungulate prey to low levels or extinction with little adverse effect on human populations. In fact, once Native Americans killed off most ungulates, human populations actually rose. As explained elsewhere, Native Americans were the ultimate keystone species, and their removal has completely altered ecosystems, not only in Yellowstone, but throughout North America (Kay 1994, 1995a, 1997a,b,c, 1998).

It must also be remembered that large numbers of native peoples inhabited the Yellowstone Ecosystem for the last 10,000± years (Hultkrantz 1974; Wright 1984). The claim that Native Americans seldom visited Yellowstone because they feared the park's geysers and hot springs is false—that myth was invented by early park administrators to promote tourism (Hultkrantz 1979).

Yellowstone's original inhabitants were forcefully removed ca. 1878 to reservations in Idaho and Wyoming for the same reason (Haines 1974, 1977).

Conclusions

1. Aspen stands inside all Yellowstone exclosures successfully regenerated without fire or other disturbance.
2. Aspen inside all exclosures developed multisize-classed stands characteristic of stable or climax aspen communities.
3. Few aspen stands, inside or outside exclosures, had been heavily invaded by conifers—another characteristic of stable or climax aspen.
4. Inside exclosures, aspen understories were dominated by shrubs and tall forbs characteristic of stable or climax aspen, while outside plots were dominated by nonnative grasses and unpalatable forbs representative of grazing disclimaxes.
5. Aspen stands dominated by old-age or single-age class trees are not a biological attribute of aspen, but an artifact of excessive ungulate browsing.
6. Yellowstone is not marginal habitat for aspen nor has climatic variation had any measurable effect on that ecosystem's aspen communities.
7. Instead, aspen has declined and is declining in Yellowstone Park and throughout the ecosystem due to repeated browsing by unnatural numbers of elk and other native ungulates.
8. As explained elsewhere (Kay, this proceedings), fire cannot be used to successfully regenerate aspen communities subject to high levels of ungulate herbivory. In fact, burning only hastens the demise of aspen subjected to even moderate levels of ungulate use (White et al. 1998; Kay et al. 1999). Instead, the only way for aspen to maintain its historic presence in Yellowstone is to reduce ungulate herbivory to more natural levels (Kay 1998; White et al. 1998). One way to accomplish this objective would be to honor existing treaties and to allow Native Americans to hunt in Yellowstone, as they did for more than 10,000 years (Kay 1998).

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Abstract

The current status and trend of aspen is a topic of debate; some studies have claimed dramatic reductions in aspen stands while others have found no major changes. The actual picture of aspen forests across the West is variable, and the presence of conifers and ungulates in aspen may or may not indicate a progressive loss of aspen. These proceedings summarize the state of knowledge about aspen ecology, the condition and trends in aspen ecosystems in the West, and human dimensions and management options for sustaining aspen.

Keywords: ecosystem management, ecosystem research, sustainable forests, quaking aspen, *Populus tremuloides*

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