

Browsing by Native Ungulates: Effects on Shrub and Seed Production in the Greater Yellowstone Ecosystem

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Abstract—Long-term grazing exclosures were used to compare browsed versus unbrowsed shrubs in the Greater Yellowstone Ecosystem. Deciduous shrubs protected from wild ungulates exhibited significantly greater canopy-cover, height, size, and volume than unprotected plants. Browsed shrub populations were dominated by significantly smaller plants than were unbrowsed populations. Protected shrubs increased in canopy-coverage and size while browsed plants remained static or declined. Ungulate browsing in recent times has virtually eliminated shrub seed production in areas frequented by wintering elk. Shrubs measured inside exclosures produced up to 20,000 times more berries than unprotected plants. Individual unprotected shrubs with a few stems beyond the reach of ungulates displayed a similar pattern. Stems above the browse height (2.5 m) produced an abundance of berries while none were produced on that portion of the plants exposed to hrowsing. Old photographs and historical journals indicate that tall shrubs and berries were common prior to park establishment, so the present lack of berries and the browsing-stunted shrub growth form were not the conditions prevailing in pre-European times. The virtual elimination of shrub seed production over much of the ecosystem suggests that ungulate populations are not in equilibrium with their food resources, as required under the “natural regulation” paradigm. These circumstances are not unique to Yellowstone. Similar situations exist in other Western States where wild ungulate numbers are at historical highs. At many locations, large populations of native ungulates are having dramatic impacts on shrub growth and seed production. Without adequate seed production and recruitment, existing plants are not replaced when they die, and plant populations cannot be in long-term equilibrium with herbivores or the environment. By reducing or eliminating seed production, native ungulates may render long-term shrub restoration ineffective. The impact of native ungulates should be carefully considered in the planning and implementation of all shrub revegetation projects.

The relationship between vegetation and native ungulates in the Yellowstone National Park—Jackson Hole region has long been a subject of conflicting opinions and intense debate (Chase 1986, Kay 1990). Until 1968, the National Park Service contended that an “unnaturally” large elk (*Cervus elaphus*) population, which had built up

in Yellowstone during the early 1900s, had severely “damaged” the park’s northern winter range, including deciduous shrub communities. (Terms such as “overgrazing,” “range damage,” and “unnatural” elk populations are common in 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.)

Agency biologists now hypothesize, however, that elk and other animals in Yellowstone are “naturally regulated,” being resource (food) limited (Houston 1982). “Natural regulation” was initially formulated using the logistic-growth equation (Cole 1974), but more recently, agency biologists have also cited Caughley’s (1976) plant-herbivore model to support their paradigm (Houston 1982). Under “natural regulation”: (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 kill the ungulates slated to die from other causes, primarily 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, termed “ecologic carrying capacity,” where continued grazing will not change plant species composition. (3) At equilibrium, competitive exclusion of sympatric herbivores due to interspecific competition will not occur. In Yellowstone, this means elk have not reduced the numbers of smaller-bodied ungulates or other animals such as beaver (*Castor canadensis*).

Park Service biologists now believe that elk, vegetation, and other herbivores in Yellowstone have been in equilibrium for the last several thousand years (Despain and others 1986). Any changes in plant species composition since the park was established in 1872 are believed to be due primarily to suppression of lightning fires, normal plant succession, or climatic change, not ungulate grazing. If deciduous shrub communities have actually declined on the northern range because of ungulate browsing, this would be a basis for rejecting the “natural regulation” hypothesis (Houston 1976). Because “natural regulation” is a global equilibrium model, grazing-induced changes in vegetation height or seed production since park establishment would also indicate that the herbivores have not been in equilibrium with their food resources. Therefore, if ungulate browsing on the northern range has changed what were once tall shrub communities into diminutive shrub types or if ungulate browsing has drastically reduced what was once abundant seed

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production, these would be additional grounds for rejecting "natural regulation."

Historically, the Jackson Hole region of the Greater Yellowstone Ecosystem has had an elk situation similar to that on Yellowstone's northern range (Boyce 1989, Kay 1992). At first, it was thought: (1) Jackson Hole was not a historical elk winter range, (2) European settlement forced elk to winter in the valley, (3) supplemental feeding permitted the growth of an abnormally large elk herd which, (4) caused substantial damage to the winter range. But agency biologists now believe: (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 human developments; (3) therefore, today's elk populations are not unnaturally high, though the distribution of wintering animals may have changed; (4) elk-induced range damage has not occurred; and (5) elk populations would "naturally regulate" if hunting ceased.

This paper explores the impact that native ungulates—elk, moose (*Alces alces*), mule deer (*Odocoileus hemionus*), pronghorn antelope (*Antilocapra americana*), bighorn sheep (*Ovis canadensis*), bison (*Bison bison*)—in and around Yellowstone National Park exert on the growth and sexual reproduction of four deciduous shrubs; serviceberry (*Amelanchier alnifolia*), chokecherry (*Prunus virginiana*), buffaloberry (*Shepherdia canadensis*), and bitterbrush (*Purshia tridentata*). Long-term grazing enclosures were used to compare unbrowsed versus browsed shrub communities.

Study Areas

The Greater Yellowstone Ecosystem encompasses portions of northwest Wyoming, southern Montana, and northeastern Idaho (Clark and Zaunbrecher 1987). Study sites were located on the winter ranges of both the northern Yellowstone and Jackson Hole elk herds. Elk presently number around 50,000, comprising approximately 80% of all ungulates in the Greater Yellowstone Ecosystem (Kay 1990). Houston (1982) provides a description of the climate, physiography, and vegetation of Yellowstone's northern range while Boyce (1989) provides similar information for Jackson Hole. Location, dates of establishment, and size of the five enclosures used in this study have been summarized by Kay (1990).

Methods

Shrub Growth and Canopy-Cover

Agency files were searched for existing information on each enclosure. Care was taken to locate (1) all prior vegetation data, (2) any written description of permanent vegetation sampling schemes, and (3) any old photographs. Whenever possible, previously established permanent plots were resampled. Unfortunately, only one enclosure (East Elk Refuge) contained permanent transects to measure shrub canopy-cover. Those transects were remeasured during 1987.

Shrub canopy-cover was measured by multiple 30-m line-intercepts (Hanley 1978) inside and outside each

enclosure. The height, crown length, and crown width of individual shrubs inside and outside each enclosure were also recorded. All serviceberry, chokecherry, and bitterbrush plants within the Camp Creek (constructed in 1932), Uhl Hill (1963), and East Elk Refuge (1952) enclosures were measured. Outside these enclosures, an adjacent comparable area was delineated on which all shrubs of these species were measured. Because the Mammoth (1957) enclosure contained a large number of buffaloberry plants, random samples of 120 shrubs both inside and outside the enclosure were measured. At the Lamar-West (1962) enclosure, random samples of serviceberry and chokecherry plants were measured inside the enclosure, as were all individuals of those species on an adjacent, outside area.

Berry Production

Except for bitterbrush, berry production data were recorded for all plants measured inside and outside the enclosures. For plants appearing to have fewer than 400 berries, all berries were counted. Plants appearing to have more than 400 berries, but less than 2,000, were divided into quarters and a quarter on each plant was randomly selected. All the berries within that quarter were counted and multiplied by four to estimate total numbers on each plant. Plants appearing to have more than 2,000 berries were divided into eighths, an eighth was randomly chosen on which all the berries were counted, and then multiplied by eight to estimate total berries. Berries were counted while green to minimize removal by birds or other animals. The Lamar-West enclosure was sampled in 1989, while the others were sampled during 1987.

Some unprotected shrubs on Yellowstone's northern range have branches beyond the reach of elk, although such shrubs are rare (Chadde and Kay 1991). On those plants, a few tall central stems are surrounded by a large number of lower, repeatedly browsed stems. Several of these "mushroom" chokecherry plants exist along the park highway east of Slough Creek Junction. To evaluate the effect of browsing on berry production of individual shrubs, the number of berries on all stems above and below the browse height (2.5 m) was recorded for each plant in 1989.

Repeat Photographs

Archival photographic collections at Yellowstone National Park, the Montana Historical Society, the University of Montana, Montana State University, 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 were searched for historical photos of the Greater Yellowstone Ecosystem. Approximately 50,000 images were reviewed, but only a small number contained views of deciduous shrub communities. During 1986-1989, the locations in those historic pictures were rephotographed to form sets of comparative photos, a process called repeat photography (Rogers and others 1984). Under magnification, the photo sets were visually evaluated to determine changes in abundance, distribution, and growth form of deciduous shrubs.

Old photographs of the exclosures were obtained from the National Park Service, U.S. Department of Agriculture, Forest Service, and the Montana Department of Fish, Wildlife, and Parks. The locations in those pictures were rephotographed during 1986-1988 to form additional sets of comparative photos. The resulting, multiple-image photo sets were used to evaluate changes inside and outside the exclosures over time.

Results

Shrub Growth and Abundance

Serviceberry, chokecherry, buffaloberry, and bitterbrush inside exclosures had greater canopy-cover, grew significantly taller, and were significantly larger than browsed plants outside exclosures (Table 1). Browsing also affected the height-class frequency distributions of the shrub populations (Figures 1-3). Plant populations outside the exclosures were dominated by significantly shorter height classes than those protected from browsing (all $p < .001$; χ^2 test of inside-outside comparisons). The same was true for size and volume-class frequency distributions (all $p < .001$; χ^2 test of inside-outside comparisons).

Shrub canopy-cover inside the East Elk Refuge exclosure increased over a 35-year period (Table 2). Highly palatable species such as serviceberry and chokecherry increased from 0.5% to 39.5% average canopy-cover. Repeat photographs of this exclosure taken in 1952, 1957, 1967, and 1987 show that shrubs increased inside while remaining relatively static outside. Repeat photographs taken at the other exclosures show an identical trend. Protected shrubs increased in canopy-cover, height, size, and volume while

those outside remained the same or declined. Repeated browsing by native ungulates clearly has had a major impact on Yellowstone's shrub communities and these data support the conclusion of Major and Rejmanek (1992: 149) that the Camp Creek exclosure "illustrates degradation of vegetation ... caused by excessively heavy winter use by large game animals."

Berry Production

Repeatedly browsed shrubs produced practically no berries (Table 1) whereas inside Yellowstone exclosures, there was a positive correlation between the size of individual plants and the number of berries (Table 3). Serviceberry plants outside the Camp Creek exclosure produced an average of 0.07 berries per plant, while protected individuals produced an average of 1,333 berries, a 20,000-fold difference. In most situations, buffaloberry is not eaten by elk (Nelson and Leege 1982), but in Yellowstone this shrub is heavily browsed, as indicated by the plants' severely hedged growth form, as well as their greater canopy-cover and height inside the Mammoth exclosure (Table 1). Buffaloberry plants inside the exclosure produced an average of 1,191 berries per female plant while individuals on the outside produced an average of 2.5 berries, a 476-fold difference. Chokecherry plants outside Yellowstone Park's Lamar-West exclosure produce no berries, while protected individuals produced an average of 2,121 berries (Table 1).

Individual plants with a few stems beyond the reach of ungulates on Yellowstone's northern range showed a similar pattern. Chokecherry stems above the browse height (2.5 m) produced an abundance of berries, while none were produced on that portion of the plant exposed to browsing (Table 4).

Table 1—Effect of ungulate browsing on shrub canopy-cover, height, size (length + width + height), volume (length x width x height), and berry production inside and outside exclosures in the Greater Yellowstone Ecosystem.

Exclosure and species	Mean percent canopy-cover		Mean height (cm)		Mean size (cm)		Mean volume (m ³)		Mean number of berries per plant	
	Outside	Inside	Outside	Inside	Outside	Inside	Outside	Inside	Outside	Inside
Mammoth										
Buffaloberry	1.0	15.0*	48	133**	278	524***	1.08	6.34**	2.50	1191.46**
East Elk Refuge										
Serviceberry	0.4	13.0*	124***	276**	440***	820**	5.54***	30.22**	13.20***	1300.20**
Chokecherry	0.9	11.9*	121***	282**	341***	730**	3.17***	17.27**	33.40***	1517.00**
Uhl Hill										
Serviceberry	0.7	14.0*	60	143**	192	414**	0.42	3.75**	0.00	104.68**
Chokecherry	2.0	6.5	52	130**	126	376**	0.08	2.34**	0.00	65.08**
Camp Creek										
Serviceberry	0.5	18.5*	32	181**	106	528**	0.09	13.15**	0.07	1333.07**
Bitterbrush	1.3	13.0*	36	86**	221	443**	0.46	3.66**	—	—
Lamar-West										
Serviceberry	0.1	7.7*	20	87**	63	246**	0.01	1.48**	0.00	1110.47**
Chokecherry	0.1	9.8*	25	121**	77	545**	0.02	17.28**	0.00	2121.78**

* Outside-inside comparisons $p < .05$; percentages were arcsine transformed; Student's t test.

** Outside-inside comparisons $p < .001$; Student's t test.

*** Snowbank site; these plants were partially protected from ungulate browsing by drifted snow.

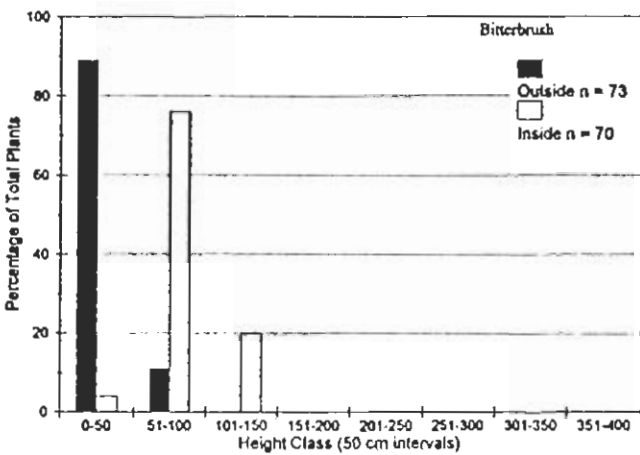
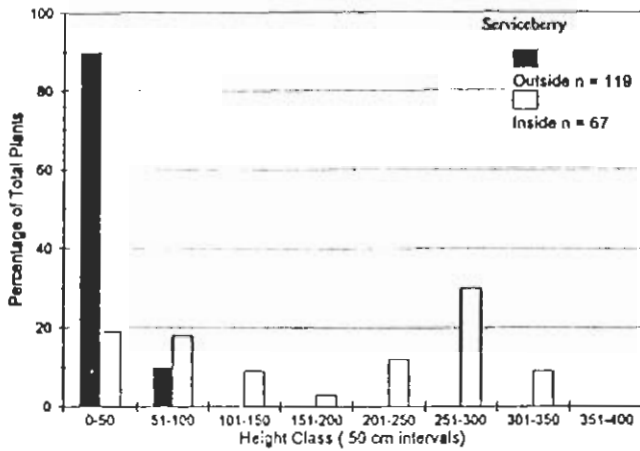


Figure 1—Height-class frequency distributions for shrubs inside and outside the Camp Creek Exclosure in Jackson Hole, Wyoming.

Repeat Photographs

Despite an extensive archival search, few historical photos of Yellowstone's deciduous shrub communities were located. The vast majority of early photographs were of scenic attractions such as hot springs or other thermal features. Relatively few early photographs were taken on low-elevation ungulate wintering areas because hot springs or other scenic attractions, with very few exceptions, are not found there. It also was impossible to identify the species of deciduous shrubs in a number of distant-view photographs taken during the late 1800's. None of the earliest photographers specifically took photographs of vegetation, except when, by chance, their human subjects were posed in front of plant communities (Figure 4).

Nevertheless, I was able to make four repeat photo sets of deciduous shrub communities on Yellowstone's northern range, with the earliest dating from 1872. All the photo sets show that previous tall shrub communities have now been completely eliminated or are presently represented by only a few browsing-stunted stems (Figure 4).

This decline is comparable to that reported for riparian shrub and aspen communities in the park (Chadde and Kay 1991; Kay 1990). Repeated browsing by wild ungulates has virtually eliminated palatable woody plants throughout much of the Greater Yellowstone Ecosystem.

Discussion

Comparison With Other Studies

Numerous authors have demonstrated that browsing by native ungulates can impair the growth of trees and shrubs which may lead to elimination of those species from their natural habitats (Riserhooover and Maass 1987, Putman and others 1989). In particular, elk can have a major impact on plant communities by reducing woody vegetation and promoting grasses through a combination of grazing

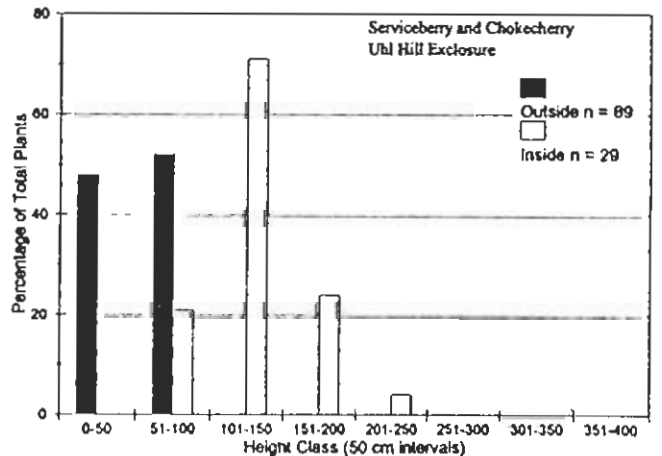
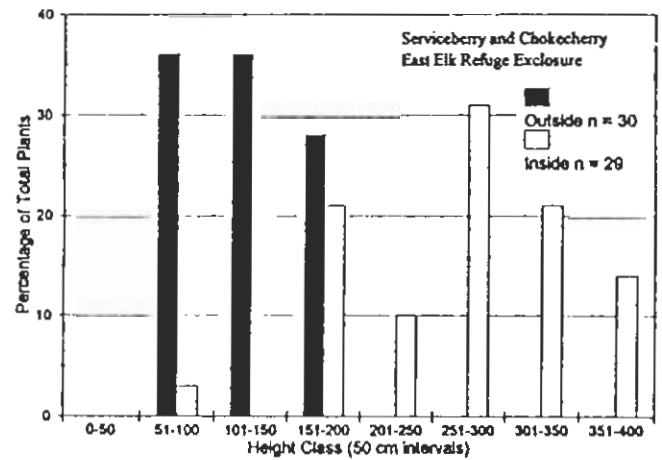


Figure 2—Height-class frequency distributions for serviceberry and chokecherry plants inside and outside two exclosures in Jackson Hole, WY. Plants outside the East Elk Refuge exclosure were taller than shrubs outside other exclosures because they are partially protected from ungulate browsing by drifted snow.

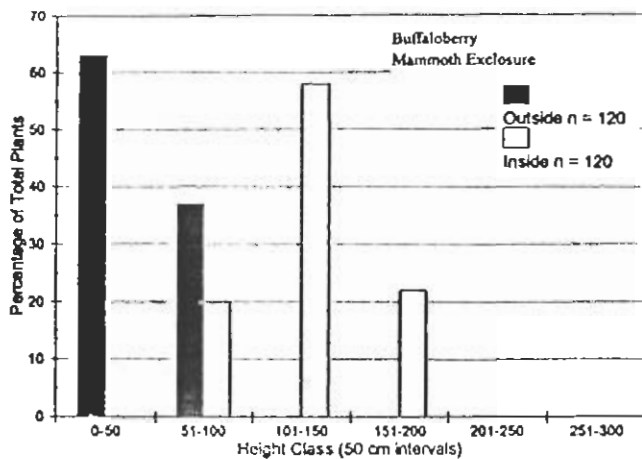


Figure 3—Height-class frequency distributions for shrubs inside and outside two exclosures in Yellowstone National Park.

and trampling (Edgerton 1987; Hanley and Taber 1980; Tiedmann and Berndt 1972).

In response to this concern, wildlife biologists have conducted numerous clipping experiments to determine "proper use" levels for many shrubs because those plants are often key foods for big game during critical winter periods (Aldous 1952; Julander 1937; Lay 1965). In general, they found that most shrubs increase vegetative production under light to moderate clipping. Based on these experiments and field observations, ungulate browsing is thought to stimulate above-ground shrub production. This has been seen as a positive influence by most game managers who often overlook long-term community relationships.

A few researchers, however, have cautioned that browsing may depress seed production and thereby negatively impact plant populations over several generations (Verkaar 1987). Clipping suppressed flowering in many common browse species and most plants produced flowers only on their upper, unclipped branches (Garrison 1953). Simulated winter browsing reduced female ament production in birch (*Betula pendula* and *B. pubescens*) (Bergstrom and Danell 1987), as well as seed production in rabbitbrush

Table 2—Shrub canopy-cover inside the East Elk Refuge exclosure 1952-1987.

Transect and species	Percent canopy-cover by year			
	1952	1959	1967	1987
G-9				
<i>Artemisia tripartita</i>	2	4	2	0
<i>Symphoricarpos oreophilus</i>	9	7	6	5
<i>Rosa woodsii</i>	8	10	17	43
<i>Chrysothamnus nauseosus</i>	3	2	0	1
<i>Chrysothamnus viscidiflorus</i>	0	0	4	0
<i>Prunus virginiana</i>	1	3	8	35
<i>Ribes</i> spp.	0	3	8	22
<i>Amelanchier alnifolia</i>	0	0	2	16
Subtotals	23	29	47	122
G - 10				
<i>Artemisia tripartita</i>	0	0	3	2
<i>Symphoricarpos oreophilus</i>	18	19	20	22
<i>Rosa woodsii</i>	6	8	16	49
<i>Chrysothamnus nauseosus</i>	11	5	0	10
<i>Chrysothamnus viscidiflorus</i>	0	2	15	0
<i>Prunus virginiana</i>	0	0	2	11
<i>Tetradymia canescens</i>	1	1	1	0
<i>Amelanchier alnifolia</i>	0	2	2	17
Subtotals	36	37	64	111

(*Chrysothamnus viscidiflorus*) and snowberry (*Symphoricarpos oreophilus*) (Willard and McKell 1978). Hemmer (1975) noted that browsing reduced berry production in serviceberry, while Shepherd (1971) observed that heavy clipping reduced seed production in serviceberry, mountain mahogany (*Cercocarpus montanus*), Gambel's oak (*Quercus gambelii*), bitterbrush, and big sagebrush (*Artemisia tridentata*).

Rodriguez and Welch (1989) reported that ungrazed big sagebrush "produced not only significantly longer seed stalks, but greater numbers of seed stalks per plant than grazed plants." Ungrazed big sagebrush also produced significantly more seeds than grazed plants (Wagstaff and Welch 1991). The shrubby legume engordacabra (*Dalea bicolor*) responded to "moderate browsing by shifting its resources from reproduction to vegetative growth.... Heavily browsed populations sacrifice[d] the ability to increase population size through seedling recruitment in order to tolerate excessive browsing" (Romero-Manzanares and Garcia-Moya 1990).

Katsma and Rusch (1980) reported that simulated winter deer browsing reduced apple production the following year. Ungulate browsing caused a 61-86% reproductive depression in *Rosa canina* (Herrera 1984). Allison (1990a,b) concluded that winter browsing by white-tailed deer (*O. virginianus*) affected Canada yew (*Taxus canadensis*) sexual reproduction by reducing pollen and seed production. On Isle Royale, repeated moose browsing prevented recruitment by balsam fir (*Abies balsamea*) and "no cone production was observed on any browse stunted sapling" (Brander and others 1990). Native ungulates reduced willow seed production from an average of 307,000 seeds per

Table 3—Effect of plant size on berry production inside Yellowstone area exclosures.

Species and size class*	n	Mean (SE) number of berries per plant	
Camp Creek Exclosure			
Serviceberry			
< 254cm	26	0.0	(0)
255 - 635cm	7	299.4	(114.2)
636 - 889cm	19	1285.6	(169.1)
> 889cm	13	2573.5	(183.1)
Lamar-West Exclosure			
Serviceberry			
< 127cm	18	40.7	(15.1)
128 - 254cm	30	455.8	(78.5)
255 - 381cm	21	1583.2	(130.3)
382 - 508cm	5	2883.6	(373.0)
> 508cm	4	6135.8	(1001.0)
Chokecherry			
< 254cm	9	341.1	(109.3)
255 - 508cm	16	769.7	(288.0)
509 - 762cm	9	3277.3	(762.3)
> 762cm	7	6016.7	(861.0)
Uhl Hill Exclosure			
Serviceberry			
< 254cm	3	0.0	(0)
255 - 508cm	10	52.9	(16.8)
> 508cm	5	166.4	(39.1)
East Elk Refuge Exclosure			
Serviceberry			
< 508cm	2	0.0	(0)
509 - 1016cm	7	841.3	(150.1)
> 1016cm	4	2750.0	(603.5)
Chokecherry			
< 508cm	2	80.0	(16.0)
509 - 762cm	7	656.0	(162.5)
763 - 1016cm	5	1652.8	(504.9)
> 1016cm	2	5228.0	(755.9)

*Size class = crown length + crown width + plant height (cm).

m² of female willow canopy-cover to zero in Yellowstone Park (Kay and Chadde 1992).

To the best of my knowledge, no studies of native ungulates have reported the level of reproductive depression in plants encountered in Yellowstone. Even studies of small mammals, birds, and insects have seldom documented the magnitude of seed loss observed in Yellowstone. For instance, Elmquist and others (1987) reported stem girdling by mice reduced willow seed production a maximum of 94%. In Yellowstone, however, ungulate browsing reduced berry and willow seed production by nearly 100%, and based on photographic evidence, few willows on the park's northern range appear to have produced seeds for the last 50 or so years (Kay and Chadde 1992). Similarly, serviceberry and chokecherry plants apparently have produced few berries since the early 1900's (see below).

Mechanisms Limiting Seed Production

Winter browsing limits seed production in at least three ways. First, browsing removes flower buds which developed

Table 4—Number of berries produced above and below browse height (2.5 m) on individual chokecherry plants in Yellowstone National Park.

Plant	Plant size canopy-cover (m ²)	Number of stems above browse height	Number of berries on plant	
			Within the browse zone	Above browse height
1	6	1	0	50
2	9	4	0	278
3	4	1	0	67
4	12	1	0	96
5	2	1	0	42
6	2	1	0	217
7	12	4	0	461
8	50	5	0	519
9	50	2	0	162
10	70	5	0	329
Mean			0	222

^t = 3.88, p < .01

the previous fall (Garrison 1953: 315-316, Mosseler and Papadopol 1989: 2569). When those plants begin growth the following spring, few flowering buds remain. Lateral buds propagate new leader growth, but they do not produce flowering buds that spring (Childers 1975: 128). Flowering buds most commonly develop on the previous year's growth. If that woody material is consumed by ungulates, those plants cannot flower the following spring and berries or seeds are not produced. Winter browsing removes virtually all of the previous summer's growth on serviceberry, chokecherry, and other deciduous shrubs throughout much of the Greater Yellowstone Ecosystem (Boyce 1989, Houston 1982).

Second, as Harper (1977: Chapter 21) noted, plants allocate resources between vegetative growth and reproduction. Plants which must allocate resources to herbivore-induced vegetative growth are unlikely to bear many berries or seeds (Watson 1984, Watson and Casper 1984). Further, woody plants pass through a juvenile or vegetative phase during which they cannot be induced to flower (Krugman and others 1974; Zimmerman 1972). On Yellowstone's northern range, repeatedly browsed shrubs often exhibit juvenile characteristics (Despain 1989).

Finally, since there is a positive correlation between size of individual plants and size of the fruit crop (Herrera 1984: 390, Peters and others 1988, Table 3), grazing-induced size limitation also reduces the number of berries produced. Because plants outside exclosures in Yellowstone were significantly smaller (Figures 1 - 3), this factor also works to limit berry production. These three mechanisms operate to curtail seed production when plants are exposed to frequent ungulate browsing, as occurs in the Yellowstone Ecosystem.

While this study only measured berry production, there is a correlation between chokecherry, buffaloberry, and serviceberry fruits and seed production. Since chokecherry fruits are a one-seeded drupe and buffaloberry bear drupelike ovoid fruits (achenes enveloped in fleshy perianth), fruit and seed production are equivalent in these



Figure 4—Repeat photo set of aspen and chokecherry on Yellowstone's northern range. (a) In 1893, aspen and chokecherry (solid arrow) showed no evidence of ungulate browsing. Shown are soldiers in Company D of the Minnesota National Guard on patrol. Yellowstone was under military administration from 1866 until 1916 when the National Park Service was established. Photograph by F. Jay Haynes (H-3069), courtesy Haynes Foundation Collection, Montana Historical Society, Helena, MT. (b) That same area 95 years later in 1988. Only a few aspen trees remain and the chokecherry plant depicted in the earlier photo is now represented by a handful of browse-stunted stems. In the absence of fire, conifers have increased markedly and show the effect of repeated ungulate browsing or high-lining. Charles Kay photo No. 3,049-27.

species (Schopmeyer 1974). Serviceberry fruits each contain from 4 to 10 small seeds (Robinson 1986; St. Pierre and Steeves 1990).

Despite a consistent yearly bloom in most shrubs, fruit production is highly variable due to weather and especially late frosts during flowering (Kendall 1986). "In any given

locality, heavy crop years are often interspersed by years in which few fruit can be found" (St. Pierre 1989). Thus, seed production probably varies inside the exclosures, but since the shrubs' current annual growth is annually consumed outside the exclosures, few if any seeds could ever be produced by those plants. So, although seed production was only measured in 1 year, the pattern of virtually no seed production outside the exclosures, but seed production within, probably reflects what happens every year. Observations of shrubs at these exclosures in other years and at other exclosures not reported here support this conclusion (Kay 1990). Even after 3 years' protection from browsing, willows in Yellowstone produced few seeds, and it apparently takes newly protected shrubs 10 to 15 years, or longer, to regain their full reproductive potential (Kay and Chadde 1992).

"Natural Regulation"

As has been shown, some serviceberry and chokecherry plants persist on the northern range, but nearly all are less than 0.5 m tall and bear almost no fruit (Table 1). According to the "natural regulation" hypothesis, conditions which exist today are thought to reflect the pristine or pre-European condition of the Yellowstone Ecosystem and, by inference, other ungulate wintering areas throughout the Western United States. Gruell (1979: 67, 1980: 8) contended that a "suppressed growth form from persistent browsing was the historical norm" for serviceberry and other shrubs in Jackson Hole; implying that berries were always rare. Contrary to this claim, however, the Reverend Samuel Parker (1967: 85-86), who traveled through Jackson Hole in 1835, found an abundance of serviceberries and other shrub fruits along the Hoback River near where the Camp Creek exclosure is now located.

In September 1869, the Cook-Folsom-Peterson Expedition encountered Native Americans who were gathering and drying large quantities of chokecherries at the mouth of Tom Miner Creek a few kilometers north of Yellowstone Park. "Here we found a wickiup inhabited by two old squaws who were engaged in gathering and drying chokecherries . . . they had two or three bushels drying in the sun" (Haines 1965: 16). The Washburn Expedition of 1870 reported that near Yellowstone Park "we crossed a small stream bordered with black cherry trees [chokecherries], many of the smaller ones broken down by bears, of which animal we found many signs" (Langford 1972:13). Since shrubs have to be at least 2 m tall before branches are commonly broken down by feeding bears, chokecherry plants in 1870 not only produced abundant berries, but were also much taller than today's plants. Thus, early records suggest that berries were once common in the Greater Yellowstone Ecosystem, and that the present lack of berries was not the condition prevailing in presettlement times. Moreover, all ethnohistoric accounts indicate that Native Americans once gathered large quantities of berries throughout the West, especially serviceberries and chokecherries (Chamberlin 1911; Franzen 1978; Janetski 1987; Lowie 1909, 1924; Murphy and Murphy 1960).

Resource-limited ungulate populations and large quantities of berries are mutually exclusive on most western ranges. Even moderate numbers of ungulates curtail

berry production because these plants provide highly preferred forage, especially in winter (Nelson and Leege 1982). Ungulate-induced berry reduction is even reflected in grizzly bear (*Ursus arctos*) food habits. While grizzlies throughout western North America commonly consume large quantities of berries (Dood and others 1986; LeFranc and others 1987), bears in the Yellowstone Ecosystem eat few berries. From 1977 to 1989, over 6,500 grizzly bear scats were collected and analyzed in Yellowstone, yet chokecherries were only reported in one scat, serviceberries in two, and buffaloberries in 51 (Kay 1989).

Without seed production and recruitment, plants cannot be in long-term equilibrium with their ungulate herbivores (Crawley 1992). Repeat photographs dating back to the 1880's of deciduous shrubs in the Greater Yellowstone Ecosystem show that tall shrubs were common when Yellowstone Park was established, but that they have now virtually disappeared. Those photos also demonstrate that shrubs inside today's enclosures have the same height and physical structure as that of shrubs on the open range during the 1870's-1890's. So, present conditions inside the enclosures more closely approximate the level of ungulate use existing when Yellowstone Park was established than do contemporary conditions.

Based on 48 repeat photographs of tall willows (Chadde and Kay 1991) and 81 of aspen (*Populus tremuloides*) (Kay 1990; Figure 4), aspen and tall willow communities decreased approximately 95% since Yellowstone Park was established, due, primarily, to repeated ungulate browsing, not succession, climatic change, or fire suppression. Furthermore, aspen, willows, conifers, and deciduous shrubs depicted in early (1870-1890) photographs show no evidence of ungulate browsing and suggest that large numbers of resource-limited elk did not winter there during the late 1700's up until after park establishment (Kay and Wagner, in press, Figure 4).

Agency biologists have postulated that 12,000-15,000 elk wintered on the northern range for the last several thousand years (Despain and others 1986; Houston 1982), while Boyce (1989) contends that another 15,000 or so elk wintered in Jackson Hole. Some objective measure of pre-European ungulate populations and relative species abundance is needed, however, to determine the level of grazing pressure under which deciduous shrubs have persisted in the Yellowstone Ecosystem. Based on extensive archeological research into aboriginal subsistence patterns in western Wyoming, Wright (1984) concluded that large herds of elk did not inhabit Jackson Hole until the late 1800's.

The available archeological evidence suggests that elk were actually quite rare in the Yellowstone area over the last several thousand years (Frison 1978; Frison and Walker 1984; Harris 1978; Hoefer 1986; Lahren 1976; Walker 1987). Of more than 52,000 ungulate bones identified from over 200 archeological sites in the Intermountain West, only 3% were elk (Kay 1990, 1992). Few elk bones have ever been identified from any of the archeological sites excavated in Jackson Hole (Wright 1984) and only 1% of the ungulate bones found in Yellowstone-area archeological sites have been identified as elk (Kay

1990). Furthermore, aboriginal subsistence patterns indicate that all ungulates were rare throughout this area for the last 9,000-10,000 years (Wright 1984).

This may explain how deciduous shrubs and other woody plants were able to maintain viable populations over the past millennia. These data do not support the "natural regulation" paradigm and would also suggest that some factor besides resource competition was the primary determinant of ungulate abundance and distribution prior to European influence. Elsewhere, I have developed an "Aboriginal overkill" hypothesis to explain the absence of large, pre-Columbian ungulate populations in the Intermountain West (Kay, in press a, b).

Implications for Revegetation and Restoration

Although I measured the impact of native ungulates on shrub growth and seed production only in Yellowstone, those circumstances are not unique to that ecosystem. Similar situations exist in other Western States where big game numbers are at historic highs (Cundy 1989; Davis and Brotherson 1991; Duncan 1975; Schultz and others 1990). At many locations, large populations of native ungulates are having dramatic impacts on shrub growth and seed production (Kay, unpublished photos). Without adequate seed production and recruitment, existing plants are not replaced when they die, and plant populations cannot be in long-term equilibrium with herbivores or the environment. Even where seedlings become established, repeated ungulate browsing can prevent those plants from being recruited into their sexually reproducing populations. Unless corrective measures are taken, I predict that many shrub species will be eliminated from these ranges in the years to come.

Native ungulates may also render long-term shrub revegetation or restoration ineffective by repeated browsing and by reducing or eliminating seed production. The impact of native ungulates should be carefully considered in the planning and implementation of all shrub revegetation projects. In this regard, excessive grazing by native ungulates can be just as damaging as heavy grazing by domestic livestock (Crisp 1978; Crisp and Lange 1976; Roundy and Ruyle 1989; Silander 1983).

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