REDUCTION OF WILLOW SEED PRODUCTION BY UNGULATE BROWSING IN YELLOWSTONE NATIONAL PARK

Charles E. Kay
Steve Chadde

ABSTRACT

Reports results of a study of the impact that native ungulates had on the production of willow (Salix bebbiana, S. boothii, S. lutea, *and* S. geyeriana) *seeds in Yellowstone National Park. Long-term grazing exclosures were used to compare seed production in unbrowsed versus browsed communities. The number of seeds per m² of female willow canopy coverage inside exclosures ranged from about 109,000 for* S. geyeriana *to over 583,000 for* S. lutea. *Outside the exclosures, no male or female aments (catkins) or willow seeds were produced. Individual willow plants with a few stems beyond the reach of ungulates on Yellowstone's northern range showed an identical pattern. Willow stems above the browse height (2.5 m) produced an abundance of male or female aments. No aments were produced on that portion of the plant exposed to browsing.*

INTRODUCTION

Numerous authors have demonstrated that ungulate browsing impairs the growth of trees and shrubs, which may lead to elimination of those species from their natural habitats (Putman and others 1989; Risenhoover and Maass 1987). In particular, elk (*Cervus elaphus*) can have a major impact on plant communities by reducing woody vegetation and promoting grasses through a combination of grazing and trampling (Edgerton 1987; Gysel 1960; Hanley and Taber 1980; Kay 1990; Tiedemann 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; Krefting and others 1966; Lay 1965). In general, they found that most shrubs, including willows, increase vegetative production under light to moderate clipping. Based on these experiments and field observations, ungulate browsing is thought to stimulate aboveground shrub production. This has been seen as a positive influence by most game managers, who often overlook long-term community relationships.

However, a few researchers 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 (*Chrysothamnus viscidiflorus*) and snowberry (*Symphoricarpos oreophilus*) (Willard and McKell 1978). Hemmer (1975) noted that browsing reduced berry production in serviceberry (*Amelanchier alnifolia*). Shepherd (1971) observed that heavy clipping reduced fruit production in serviceberry, mountain-mahogany (*Cercocarpus montanus*), Gambel oak (*Quercus gambelii*), bitterbrush (*Purshia tridentata*), and big sagebrush (*Artemisia tridentata*).

Seed predation has been shown to influence the species composition of vegetation communities over a wide range of habitats (Andersen 1989; Cavers 1983; Janzen 1971; Louda 1983; Schupp 1988). Most seed predation studies have focused on insects, birds, or small mammals. Reports of ungulate seed predation are uncommon, and few have investigated seed predation by large native ungulates in the Western United States.

This paper explores the impact native ungulates—elk, moose (*Alces alces*), mule deer (*Odocoileus hemionus*), pronghorn (*Antilocapra americana*), bighorn sheep (*Ovis canadensis*), and bison (*Bison bison*)—in Yellowstone National Park are having on the sexual reproduction of willows. Long-term grazing exclosures were used to compare seed production in unbrowsed versus browsed willow communities.

STUDY AREAS

Study sites were located on the winter range of the northern Yellowstone elk herd. Elk, the primary large herbivore, comprise approximately 80 percent of the total number of ungulates in the Greater Yellowstone Ecosystem (Kay 1990). Houston (1982) provides a description of the climate, physiography, and vegetation of Yellowstone's northern range. Location, date of establishment, and size of the exclosures used in this study have been summarized by Kay (1990). Barmore (1981: 453-459), Houston (1982: 415-420), and Chadde and Kay (1991) provide additional information on exclosures in Yellowstone National Park.

Paper presented at the Symposium on Ecology and Management of Riparian Shrub Communities, Sun Valley, ID, May 29-31, 1991.

Charles E. Kay is Graduate Student, Department of Fisheries and Wildlife, Utah State University, Logan, UT. His current address is Wildlife Management Services, 365 South 600 East, Smithfield, UT 84335. Kay's research was funded by the Rob and Bessie Welder Wildlife Foundation, Sinton, TX, and is Contribution No. 371.

Steve Chadde is President, Earthworks Environmental Research, 1115 Martz Rd., Arlee, MT 59821.

METHODS

The National Park Service established one permanent willow belt transect inside and another outside the Mammoth (1957), Junction Butte (1962), and Lamar-East (1957) exclosures at the time of construction. At Lamar-West (1962), a willow transect was established only inside the exclosure. The Lamar-East outside willow belt was intended as a control for both the Lamar-East and Lamar-West exclosures. Thus, seven permanent willow belt transects are associated with these exclosures; three outside and four inside. The belt transects at Mammoth, Lamar-East, and Lamar-West are all 1.5 by 30.5 m; those at Junction Butte are 1.5 by 22.9 m. Data on willow canopy coverage and plant height have been collected by the Park Service at various intervals since these exclosures were established. That information, repeat photographs of the belt transects, and additional data collected during 1988 were summarized by Kay (1990) and Chadde and Kay (1991).

Willow Aments

Because there were so few willow aments in areas exposed to repeated ungulate browsing, we recorded the number of aments on the entire belt transect outside each exclosure. In addition, we searched large areas of willow habitat (Chadde and others 1988) adjacent to each exclosure for willow aments and recorded those numbers. However, these procedures were impractical inside the exclosures due to the much greater ament densities that we encountered. Instead, inside the exclosures we counted aments on 1-m^2 plots placed in willow canopies.

Whenever possible, we sampled willows on the inside belt transects, but in most instances we also measured some plants adjacent to the permanent belt transects to obtain an adequate sample. All willows inside the exclosures produced aments, but it was easier to count aments on plants that were in full flower at the time of our visit. Furthermore, our equipment (a 2.5-m stepladder) prevented us from sampling plants taller than 3.5 m. We recorded the sex of all willows on and adjacent to the permanent belt transects. Willows were sampled during spring 1989.

We sampled only the major willow species within exclosures (Chadde and Kay 1991). These included *S. bebbiana*, *S. boothii*, *S. lutea*, and *S. geyeriana* for which we collected samples of female aments from each exclosure. We counted the mature fruits on 60 female aments of each species from each exclosure. Those aments were then air dried in the laboratory and the number of seeds in 10 fruits counted for each species-exclosure. We were unable to make identical measurements on female aments outside exclosures, because ament production was nonexistent there.

As part of another study, Chadde and others (1988) constructed two small exclosures (2 by 4 m) in 1986 adjacent to and sharing a common side with each of the Mammoth and Junction Butte exclosures. A trench 0.5 m deep was dug along the common side and a plastic barrier installed to sever root connections with plants in the older exclosure. Willow stems <30 cm tall were present inside each mini-exclosure when they were erected. We recorded all the aments inside four of these mini-exclosures in 1989 after three seasons of protection from browsing.

Individual Plants

Though rare, some willows and other shrubs on the northern range have branches that are beyond the reach of elk (Kay 1990). On those plants, a few tall, central stems are usually surrounded by a large number of lower, repeatedly browsed stems. Several of these "mushroom" willows exist near Geode Creek. To evaluate the effect of browsing on ament production of individual willows, we recorded the number of male or female aments on all stems above and below the browse height (2.5 m) on each plant. We gathered similar data on river birch (*Betula occidentalis*) near the Mammoth exclosure. These measurements were taken in 1989.

RESULTS

As reported in a previous paper (Chadde and Kay 1991), willows were taller and had greater canopy coverage inside than outside each exclosure. Other less palatable shrubs, such as rose (*Rosa woodsii*) and river birch, exhibited this same pattern. When pooled, these differences were statistically significant across exclosures ($p < 0.01$). Outside these exclosures, the mean height of all willow species was 34 cm while inside it was 274 cm ($p < 0.01$). When the non-willow portions of the belt transects were excluded, willow canopy coverage averaged 14 percent outside the exclosures and 95 percent inside ($p < 0.01$). Thus, willow canopy closure was nearly complete inside the exclosures.

Outside the exclosures, no aments were present in any of the permanent willow belt transects (table 1). Furthermore, only eight male aments were found in an additional 1.13 ha of willow-dominated habitat that we searched adjacent to the four exclosures on Yellowstone's northern range. In contrast, *S. bebbiana*, *S. boothii*, *S. lutea*, and *S. geyeriana* produced an average, respectively, of 1,445, 583, 694, and 1,346 female aments per m^2 of canopy coverage inside exclosures (table 2).

Table 1—Number of aments produced by willows in permanent belt transects and adjacent areas outside Yellowstone exclosures

	Permanent belt transects		Adjacent areas	
Exclosure	Size	Number of aments	Size	Number of aments
	m^2		m^2	
Mammoth[1]	46.5	0	3,000	0
Junction Butte	34.8	0	800	0
Lamar-West	([2])	([2])	3,500	0
Lamar-East	46.5	0	4,500	[3]8
Mean number of aments per m^2		0		0.0007

[1]There were also no male or female aments on *Betula occidentalis* plants in this belt transect.

[2]There is no permanent willow belt transect outside this exclosure (see text).

[3]Male *Salix bebbiana* protected from browsing by dead stems.

Table 2—Mean number of aments, fruits, and seeds produced by willows inside Yellowstone exclosures

Species-exclosure	Mean (SEM) aments per m² of canopy coverage: Male	Female	Mean (SEM) matured fruit per female ament (n = 60)	Mean (SEM) seeds per fruit (n = 10)	Mean number of seeds per m² of canopy coverage
Salix bebbiana					
Mammoth	1,878 (102)	1,006 (320)	31.6 (1.2)	5.1 (0.2)	162,127
Junction Butte	1,219 (539)	1,631 (594)	23.7 (1.2)	6.1 (0.4)	235,794
Lamar-West	4,083 (827)	1,482 (216)	46.5 (1.5)	5.8 (0.5)	399,695
Lamar-East	3,080 (0)	1,660 (213)	47.8 (1.4)	6.5 (0.3)	515,854
Subtotals	2,565 (636)	1,445 (151)	37.4 (5.9)	5.9 (0.3)	318,854
Salix boothii					
Mammoth	— —	382 (0)	43.4 (2.0)	6.6 (0.3)	109,420
Lamar-West	1,860 (0)	447 (184)	79.0 (2.0)	6.0 (0.3)	211,878
Lamar-East	— —	920 (0)	71.2 (1.2)	6.0 (0.4)	393,024
Subtotals	1,860 (0)	583 (170)	64.5 (10.8)	6.2 (0.2)	233,142
Salix lutea					
Mammoth	— —	490 (0)	78.4 (2.8)	11.8 (0.4)	453,309
Junction Butte	1,340 (0)	612 (130)	— —	— —	—
Lamar-West	— —	980 (0)	69.2 (3.4)	10.9 (0.6)	739,194
Subtotals	1,340 (0)	694 (147)	73.8 (4.6)	11.4 (0.4)	583,876
Salix geyeriana					
Mammoth	— —	931 (0)	13.0 (0.4)	4.7 (0.3)	56,884
Junction Butte	— —	— —	11.8 (0.5)	3.6 (0.2)	—
Lamar-West	4,300 (0)	1,846 (666)	29.0 (0.9)	5.9 (0.4)	315,850
Lamar-East	3,560 (0)	1,260 (502)	16.4 (0.6)	4.4 (0.3)	90,922
Subtotals	3,930 (370)	1,346 (267)	17.6 (3.9)	4.6 (0.5)	108,972
Total	[1]2,665 (620)	[1]1,001 (241)			306,988

[1] $t = 3.98$, $p < 0.01$.

For all willow species sampled inside exclosures, male aments were 2.7 times more abundant per m² of canopy coverage than female aments. The number of seeds per m² of female willow canopy coverage ranged from a low of about 109,000 for *S. geyeriana* to over 583,000 for *S. lutea* and averaged nearly 307,000. Since no female aments were found outside the exclosures, obviously no seeds could have been produced.

Female willow plants were more common than male plants inside the exclosures and, on average, outnumbered males 1.7 to 1 (table 3). When the mean sex ratio is combined with species canopy coverage (Chadde and Kay 1991) and species seed production values (table 2), an estimate of the total number of seeds produced in the inside and outside willow belt transects can be calculated. Approximately 5,857,000 seeds were produced in the willow transect inside the Junction Butte exclosure and zero outside; Lamar-East had 6,961,000 seeds inside, zero outside; Lamar-West 7,016,000 seeds inside, zero outside; and Mammoth 3,177,000 seeds inside, zero outside.

Individual plants with a few stems beyond the reach of ungulates on Yellowstone's northern range showed an identical pattern. Willow stems above the browse height (2.5 m) produced an abundance of male or female aments; no aments were produced on that portion of the plant exposed to browsing (table 4). Individual river birch (table 5) plants exhibited a similar pattern.

Table 3—Sex of willow plants inside Yellowstone exclosures

Exclosure-species	Number of plants: Male	Female	Ratio male to female
Mammoth			
S. bebbiana	6	4	
S. geyeriana	0	1	
S. boothii	0	2	
Subtotals	6	7	1:1.2
Junction Butte			
S. bebbiana	6	10	
S. lutea	4	12	
S. geyeriana	2	0	
Subtotals	12	22	1:1.8
Lamar-East			
S. bebbiana	2	8	
S. geyeriana	3	6	
S. boothii	3	2	
Subtotals	8	16	1:2.0
Lamar-West			
S. bebbiana	10	9	
S. boothii	3	6	
S. geyeriana	0	1	
S. lutea	0	5	
Subtotals	13	21	1:1.6
Totals	39	66	1:1.7

Table 4—Number of aments produced above and below browse height (2.5 m) on individual willows in Yellowstone National Park near Geode Creek

Species-plant	Plant size canopy coverage	Number of stems above browse height	Number of aments per plant	
			Below browse height	Above browse height
	m²			
Salix lutea				
A-female	12	5	0	1,680
B-female	2	1	0	78
C-female	2	2	0	170
D-male	3	9	0	1,140
Salix geyeriana				
E-female	4	2	0	160
F-female	1	3	0	1,351
G-female	3	5	0	600
Salix boothii				
H-female	2	2	0	182
Mean			[1]0	[1]670

[1]$t = 2.80$, $p < 0.02$.

Table 5—Number of aments produced above and below browse height (2.5 m) on individual river birch plants near Yellowstone's Mammoth exclosure

Plant	Plant size canopy coverage	Number of stems above browse height	Number of aments on plant			
			Above browse height		Below browse height	
	m²		*Female*	*Male*	*Female*	*Male*
A	4	1	16	280	0	[1]18
B	16	2	0	39	0	0
C	12	2	951	1,291	0	0
D	12	1	272	784	0	[1]3
Mean			310	598	0	5

[1]Protected from browsing by dead stems.

Willows protected for three growing seasons increased in height but produced less than two male or female aments per m² (table 6). It apparently will take several more years for those plants to reach their full reproductive potential.

DISCUSSION

Mechanisms Limiting Seed Production

Winter browsing limits willow seed production in at least three ways. First, browsing removes flower buds that developed the previous fall (Garrison 1953: 315-316; Jameson 1963; Mosseler and Papadopol 1989: 2569). When those plants begin growth the following spring, few flowering buds are present. Lateral buds often produce new leader growth, but they will not produce flowering buds that spring (Childers 1975: 128). Flowering buds are most commonly produced on the previous year's growth. If that woody material is consumed by ungulates, those plants cannot flower the following spring and seeds are not produced. From 1970 to 1978, ungulates on Yellowstone's northern range on average consumed over 91 percent of the current year's willow stem growth (Houston 1982: 149). Willow utilization has not decreased in recent years (Kay 1990).

Second, as Harper (1977: chap. 21) noted, plants allocate resources between vegetal growth and reproduction. Plants that must allocate resources to herbivore-induced vegetative growth are unlikely to produce many seeds (Garrison 1953: 316; Hemmer 1975). 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 willows 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), grazing-induced size limitation also reduces the number of seeds produced. These three mechanisms apparently operate to curtail seed production when plants are exposed to frequent ungulate browsing, as in Yellowstone.

Though we measured seed production only in 1 year, the pattern of virtually no seed production outside the

Table 6—Number of aments produced by willows protected from browsing for 3 years. Mini-exclosures were constructed adjacent to permanent 2.1-ha exclosures in 1986 (see text)

Location/mini-exclosure	Number of aments per m² for total enclosed area			
	Salix bebbiana		*Salix lutea*	
	Female	*Male*	*Female*	*Male*
Mammoth				
M-North	0	1.0	0	0
M-South	0	0	2.8	.4
Junction Butte				
M-West	.5	0	1.4	2.9
M-East	0	1.1	.5	.2
Mean	.1	.5	1.2	.9

exclosures, but abundant seed production within, probably reflects what happens every year. Observations on willows at these exclosures in other years and at other exclosures not included in this study support this conclusion (Kay 1990).

Comparison With Other Studies

Katsma and Rusch (1980) reported that simulated winter deer browsing reduced apple production the following year. Ungulate browsing caused a 61 to 86 percent reproductive depression in *Rosa canina* (Herrera 1984). Allison (1987) concluded that winter browsing by white-tailed deer (*O. virginianus*) affected Canada yew (*Taxus canadensis*) sexual reproduction by reducing pollen production, which, in turn, caused seed production to decline. On Isle Royale, repeated browsing by moose prevented recruitment by balsam fir (*Abies balsamea*), and "no cone production was observed on any browse stunted sapling" (Brander and others 1990: 162).

To the best of our knowledge, no published studies have reported the level of ungulate-induced seed production loss we encountered. Even studies of small mammals, birds, and insects have seldom documented the level 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 percent. However, in Yellowstone Park, ungulate browsing reduced potential willow seed production by 100 percent. Moreover, based on photographic evidence (Chadde and Kay 1991), few willows on Yellowstone's northern range appear to have produced seeds for the last 50 or so years.

"Natural Regulation"

The relationship between vegetation and ungulates in Yellowstone has long been a subject of conflicting opinions and intense debate (Chase 1986; Despain and others 1986; Houston 1982; Kay 1990). Prior to 1968, the Park Service contended that an "abnormally" large elk population, which had built up in Yellowstone during the late 1800's and early 1900's, had severely "damaged"[1] the park's northern winter range, including willow communities. However, agency biologists now hypothesize that elk and other animals in Yellowstone are "naturally regulated," being resource (food) limited (Houston 1976, 1982; Kay 1990).

Park Service biologists now believe elk, vegetation, and other herbivores in Yellowstone have been in equilibrium for several thousand years (Despain and others 1986). They also believe that any changes in plant species composition or height are due primarily to suppression of lightning fires, normal plant succession, or climatic change, not ungulate grazing. Houston (1982: 129) concluded that "while ungulates and other herbivores affected the rate of primary succession, changes in distribution of willow were mostly climatically determined."

Houston (1976) indicated that if willow communities had actually declined on the northern range because of ungulate browsing, this would be a basis for rejecting the "natural regulation" hypothesis. Because "natural regulation" is a global equilibrium model, grazing-induced changes in vegetation height since 1872, when the park was created, would also indicate 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 willow communities into short willow types, this would be additional grounds for rejecting "natural regulation."

Based on 48 repeat photosets of willow communities in the park, some dating from 1871, historical accounts, and other data, Chadde and Kay (1991) concluded that Yellowstone's tall willows had declined approximately 95 percent since the park was established, not because of climatic change or succession, but primarily from repeated ungulate browsing. We suggest that the virtual elimination of willow seed production also indicates Yellowstone's ungulates and vegetation are not in equilibrium. Once the existing willows die of old age, disease, insects, or other causes, they cannot be replaced by new plants produced from seed. Under these conditions, willows will eventually disappear. Willows commonly colonize new habitats by producing vast numbers of wind-dispersed seeds. Yet, during a 3-year study to classify wetland communities on the northern range, Chadde and others (1988) observed few willow seedlings on newly created gravel bars and mud flats, which normally provide ideal seed beds.

Several researchers have questioned the importance of seed predation to recruitment in stable populations of

[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 here only in their historical context.

long-lived perennials (Duggan 1985). Anderson (1989) concluded that, "The importance of seed losses to population recruitment at any point in time is related to the abundance of safe sites [for seed germination and seedling establishment]...it is zero when safe sites are absent, negligible when safe sites are rare, and greatest when safe sites are numerous enough for recruitment to be limited by seed supply." He noted that soil seed banks could offset any long-term impacts of seed predation to long-lived perennials.

However, since willow seeds are short lived and are not stored in soil seed banks (Brinkman 1974; Densmore and Zasada 1983), this cannot be an important consideration in willow ecology. Moreover, even if willow seedlings become established outside the exclosures, the level of ungulate browsing that exists would prevent those plants from being recruited into their sexually reproducing populations.

For instance, the few large cottonwoods (*Populus trichocarpa* and *P. angustifolia*) remaining along waterways in Yellowstone Park produce abundant seeds, some of which establish on gravel bars along rivers and streams. However, almost none of those plants has been successfully recruited into their sexually reproducing populations over the last 80 or so years, because repeated ungulate browsing has prevented new cottonwoods from growing taller than 1 m (Chadde and others 1988; Kay 1990). Chadde and Kay (1991) reported that willows established from seed on a gravel bar along Yellowstone's Gardiner River were replaced by grasses and other herbaceous plants within 9 years due to repeated ungulate browsing. During the mid-1970's, a few tall willows were still alive above and below this gravel bar. Those plants probably produced the seeds that became established on this gravel bar. Since that time, continued ungulate browsing in combination with insects and pathogens has eliminated those tall willows (Kay 1990).

Without abundant seed crops, willows cannot take advantage of recruitment opportunities produced by periodic large-scale disturbances such as fire. Yellowstone's 1988 fires occurred under extreme burning conditions during an extended drought and are thought to have been a 100-300-year event (Romme and Despain 1989a, 1989b). Hence, those fires were able to burn normally wet riparian zones (Knight and Wallace 1989), many of which had thick sedge (*Carex* spp.) mats and accumulations of organic matter (Brichta 1987; Chadde and others 1988). These areas, normally unfavorable to willow seed germination and seedling establishment, "were burned down to mineral soil, killing rhizomes and root systems" (Knight and Wallace 1989: 704). This created bare mineral soil and ash substrates that had abundant soil moisture especially after snowmelt in 1989—ideal conditions for germination and seedling establishment of willow (Brinkman 1974). Yet, few willow seedlings were observed in those areas (Kay 1990). Our data indicate that practically no willow seeds were produced on Yellowstone's northern range to colonize this newly created habitat.

Agency biologists, with little supporting evidence, have assumed that 12,000-15,000 elk wintered on the northern range over the last several thousand years (Despain and others 1986; Houston 1982). However, some measure of pre-European ungulate populations and relative species abundance is needed to determine the level of grazing pressure under which willows have persisted in the Yellowstone area. Based on extensive archaeological research in northwest Wyoming, Wright (1984) concluded that large herds of elk did not inhabit the Greater Yellowstone Ecosystem until the late 1800's. In fact, all the available archaeological evidence suggests that elk were not common in the Yellowstone area over the last several thousand years (Eakin 1986; Eakin and others 1986; Frison 1978; Frison and Walker 1984; Harris 1978; Hoefer 1986; Lahren 1976; Walker 1987). Of ungulate bones unearthed from Yellowstone archaeological sites, elk made up less than 3 percent of the total and elk only accounted for 3 percent of over 52,000 ungulate bones identified from more than 200 archaeological sites throughout the Intermountain West (Kay 1990).

Furthermore, woody plants (including willows) depicted in early (1870-90) Yellowstone photographs show absolutely no evidence of ungulate browsing (Kay 1990). This may explain how willows in Yellowstone were able to maintain viable populations over the past millennia. These data also suggest that some factor besides resource competition was the primary determinant of ungulate abundance and distribution prior to European influence.

Applicability to Other Areas

Though we only measured the impact that native ungulates, primarily elk, have had on willow seed production in Yellowstone National Park, domestic livestock could have a similar effect on willow communities throughout the West. If all the willows are within reach of domestic livestock and if those animals remove a large proportion of the plant's current annual growth, it is highly probable that willow seed production would also show a marked decline under those circumstances.

Browsing impacts on seed production should not be overlooked by managers who are working to restore disturbed riparian areas, especially ones which were degraded by excessive livestock grazing.

REFERENCES

Aldous, S. E. 1952. Deer browse clipping study in the Lake States region. Journal of Wildlife Management. 16: 401-409.

Allison, T. D. 1987. The reproductive biology of Canada yew (*Taxus canadensis*) and its modification by herbivory: implications for wind pollination. Minneapolis, MN: University of Minnesota. Dissertation.

Anderson, A. N. 1989. How important is seed predation to recruitment in stable populations of long-lived perennials? Oecologia (Berlin). 81: 310-315.

Barmore, W. J. 1981. Population characteristics, distribution, and habitat relationships of six ungulate species on winter range in Yellowstone National Park. Mammoth, WY: U.S. Department of the Interior, National Park Service, Yellowstone National Park, Research Office. 677 p. Unpublished report.

Bergstrom, R.; Danell, K. 1987. Effects of simulated winter browsing by moose on morphology and biomass of two birch species. Journal of Ecology. 75: 533-544.

Borchert, M. I.; Davis, F. W.; Michaelsen, J.; Oyler, L. D. 1989. Interactions of factors affecting seedling recruitment of blue oak (*Quercus douglasii*) in California. Ecology. 70: 389-404.

Brander, T. A.; Peterson, R. O.; Risenhoover, K. L. 1990. Balsam fir on Isle Royale: effects of moose herbivory and population density. Ecology. 71: 155-164.

Brichta, P. H. 1987. Environmental relationships among wetland community types on the northern range, Yellowstone National Park. Missoula, MT: University of Montana. 67 p. Thesis.

Brinkman, K. A. 1974. *Salix* L.—willow. In: Seeds of woody plants in the United States. Agric. Handb. 450. Washington, DC: U.S. Department of Agriculture, Forest Service: 746-750.

Cavers, P. B. 1983. Seed demography. Canadian Journal of Botany. 61: 3578-3590.

Chadde, S. W.; Kay, C. E. 1991. Tall willow communities on Yellowstone's northern range: a test of the "natural regulation" paradigm. In: Keiter, R.; Boyce, M., eds. The greater Yellowstone ecosystem: balancing man and nature on America's wildlands. New Haven, CT: Yale University Press: 231-262.

Chadde, S. W.; Hansen, P. L.; Pfister, R. D. 1988. Wetland plant communities on the northern range of Yellowstone National Park. Final contract report to National Park Service, Yellowstone National Park. Missoula, MT: University of Montana, School of Forestry. 81 p.

Chase, A. 1986. Playing God in Yellowstone: The destruction of America's first National Park. Boston: Atlantic Monthly Press. 446 p.

Childers, N. F. 1975. Modern fruit science. 6th ed. New Brunswick, NJ: Rutgers University, Horticultural Publications. 976 p.

Densmore, R.; Zasada, J. 1983. Seed dispersal and dormancy patterns in northern willows: ecological and evolutionary significance. Canadian Journal of Botany. 61: 3201-3216.

Despain, D. G. 1989. Interpretation of exclosures in riparian vegetation. In: Gresswell, R. E.; Barton, B. A.; Kershner, J. L., eds. Practical approaches to riparian management: an educational workshop. Rep. BLM-MT-PT-89-001-4351. Billings, MT: U.S. Department of the Interior, Bureau of Land Management, Montana State Office: 188.

Despain, D.; Houston, D.; Meagher, M.; Schullery, P. 1986. Wildlife in transition: man and nature on Yellowstone's northern range. Boulder, CO: Roberts Rinehart. 142 p.

Duggan, A. E. 1985. Pre-dispersal seed predation by *Anthocaris cardamines* (Pieridae) in the population dynamics of the perennial *Cardamine pratensis* (Brassicaceae). Oikos. 44: 99-106.

Eakin, D. H. 1986. Results of additional archaeological investigations along sections of the North Fork of the Shoshone River, Highway 14, 16, 20. Highway project SCPF-031-1 (21). Project No. WY-49-84. Laramie, WY: Office of Wyoming State Archaeologist. 58 p. + appendix.

Eakin, D. H.; Darlington, D.; Peyton, L. 1986. Results of archaeological investigations along sections of the North Fork of the Shoshone River, Highway 14, 16, 20. Highway project SCPF-031-1 (21). Project No. WY-49-84. Laramie, WY: Office of Wyoming State Archaeologist. 135 p.

Edgerton, P. J. 1987. Influence of ungulates on the development of the shrub understory of an upper slope mixed conifer forest. In: Provenza, Frederick D.; Flinders, Jerran T.; McArthur, E. Durant, compilers. Proceedings—symposium on plant-herbivore interactions; 1985 August 7-9; Snowbird, UT. Gen. Tech. Rep. INT-222. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 162-167.

Elmquist, T.; Ericson, L.; Danell, K.; Salomonson, A. 1987. Flowering, shoot production, and vole bark herbivory in boreal willow. Ecology. 68: 1623-1629.

Frison, G. C. 1978. Prehistoric hunters of the high plains. New York: Academic Press. 457 p.

Frison, G.; Walker, D. N., eds. 1984. The Dead Indian Creek site: an archaic occupation in the Absaroka Mountains of northeastern Wyoming. Wyoming Archaeologist. 27(1-2): 11-122.

Garrison, G. A. 1953. Effects of clipping on some range shrubs. Journal of Range Management. 6: 309-317.

Gysel, L. W. 1960. An ecological study of the winter range of elk and mule deer in the Rocky Mountain National Park. Journal of Forestry. 58: 696-703.

Hanley, T. A.; Taber, R. D. 1980. Selective plant species inhibition by elk and deer in three conifer communities in western Washington. Forest Science. 26: 97-107.

Harper, J. L. 1977. Population biology of plants. New York: Academic Press. 456 p.

Harris, A. 1978. The Mummy Cave tetropods. In: McCracken, H., ed. The Mummy Cave project in Northwestern Wyoming. Cody, WY: Buffalo Bill Historical Center: 146-151.

Hemmer, D. 1975. Serviceberry: ecology, distribution, and relationships to big game. Project W-120-R-5 and 6. Helena, MT: Montana Fish and Game Department; Job Completion Report. 76 p.

Herrera, C. M. 1984. Seed dispersal and fitness determinants in wild rose: combined effects of hawthorn, birds, mice and browsing ungulates. Oecologia (Berlin). 63: 386-393.

Hoefer, T. 1986. Archaeological data recovery at site 48 SW 1242: La Barge natural gas project. Cultural Resour. Manage. Rep. 21. Rock Springs, WY: Western Wyoming College, Archaeological Services.

Houston, D. B. 1976. Research on ungulates in northern Yellowstone National Park. In: Research in the parks: Transactions of the National Park Centennial Symposium; 1971 December; National Park Service Symposium Series No. 1. Washington, DC: U.S. Department of the Interior, National Park Service: 11-27.

Houston, D. B. 1982. The northern Yellowstone elk: ecology and management. New York: MacMillan. 474 p.

Jameson, D. A. 1963. Responses of individual plants to harvesting. Botanical Review. 29: 532-594.

Janzen, D. H. 1971. Seed predation by animals. Annual Review of Ecology and Systematics. 2: 465-492.

Julander, O. 1937. Utilization of browse by wildlife. Transactions of the North American Wildlife Conference. 2: 276-287.

Katsma, D. E.; Rusch, D. H. 1980. Effects of simulated deer browsing on branches of apple trees. Journal of Wildlife Management. 44: 603-612.

Kay, C. E. 1990. Yellowstone's northern elk herd: a critical evaluation of the "natural regulation" paradigm. Logan, UT: Utah State University. 490 p. Dissertation.

Knight, D. H.; Wallace, L. L. 1989. The Yellowstone fires: issues in landscape ecology. BioScience. 39: 700-706.

Krefting, L. W.; Stenlund, M. H.; Seemel, R. K. 1966. Effect of simulated and natural browsing on mountain maple. Journal of Wildlife Management. 30: 481-488.

Krugman, S. L.; Stein, W. I.; Schmitt, D. M. 1974. Seed biology. In: Seeds of woody plants of the United States. Agric. Handb. 450. Washington, DC: U.S. Department of Agriculture, Forest Service: Chapter 1.

Lahren, L. A. 1976. The Myers-Hindman site: an exploratory study of human occupation patterns in the upper Yellowstone Valley from 7000 BC to AD 1200. Livingston, MT: Anthropologos Researches International. 195 p.

Lay, D. W. 1965. Effects of periodic clipping on yield of some common browse species. Journal of Range Management. 18: 181-184.

Louda, S. M. 1983. Seed predation and seedling mortality in the recruitment of a shrub, *Haplopappus venetus* (Asteraceae), along a climatic gradient. Ecology. 64: 511-521.

Mosseler, A.; Papadopol, C. S. 1989. Seasonal isolation as a reproductive barrier among sympatric *Salix* species. Canadian Journal of Botany. 67: 2563-2570.

Peters, R. H.; Cloutier, S.; Dube, D.; Evans, A.; Hastings, P.; Kaiser, H.; Kohn, D.; Sarwer-Foner, B. 1988. The allometry of the weight of fruit on trees and shrubs in Barbados. Oecologia (Berlin). 74: 612-616.

Putman, R. J.; Edwards, P. J.; Mann, J. C. E.; How, R. C.; Hill, S. D. 1989. Vegetational and faunal changes in an area of heavily grazed woodland following relief of grazing. Biological Conservation. 47: 13-32.

Risenhoover, K. L.; Maass, S. A. 1987. The influence of moose on the composition and structure of Isle Royale forests. Canadian Journal of Forest Research. 17: 357-364.

Romme, W. H.; Despain, D. G. 1989a. Historical perspective on the Yellowstone fires of 1988. BioScience. 39: 695-699.

Romme, W. H.; Despain, D. G. 1989b. The Yellowstone fires. Scientific American. 261(5): 37-46.

Schupp, E. W. 1988. Seed and early seedling predation in the forest understory and in treefall gaps. Oikos. 51: 71-78.

Shepherd, H. R. 1971. Effects of clipping on key browse species in southwestern Colorado. Tech. Publ. 28. Denver, CO: Colorado Division of Game, Fish and Parks. 104 p.

Tiedemann, A. R.; Berndt, H. W. 1972. Vegetation and soils of a 30-year deer and elk exclosure in central Washington. Northwest Science. 46: 59-66.

Verkaar, H. J. 1987. Population dynamics—the influence of herbivory. New Phytologist. 106(Suppl): 49-60.

Walker, D. N. 1987. Late Pleistocene/Holocene environmental changes in Wyoming: the mammalian record. In: Graham, R. W.; Semken, H. A.; Graham, M. A., eds. Late quaternary mammalian biogeography and environments of the Great Plains and prairies. Illinois State Museum Scientific Papers Vol. 22. Springfield, IL: Illinois State Museum: 334-393.

Willard, E. E.; McKell, C. M. 1978. Response of shrubs to simulated browsing. Journal of Wildlife Management. 42: 514-519.

Wright, G. A. 1984. People of the high country: Jackson Hole before the settlers. New York: Peter Lang. 181 p.

Zimmerman, R. H. 1972. Juvenility and flowering in woody plants: review. Hortscience. 7: 447-455.