CHAPTER VII

SEED PRODUCTION OF DECIDUOUS SHRUBS

INTRODUCTION

Seed predation has been shown to influence the species composition of vegetation communities over a wide range of habitats (Janzen 1970, 1971, 1975; Rockwood 1973; Mares and Rosenzweig 1978; Borchert and Jain 1978; Inouye et al. 1980; Boucher 1981; Jensen 1982; Cavers 1983; Louda 1983; DeSteven and Putz 1984; Hobbs 1985; Kjellsson 1985; Andersen 1987; Smith 1987; Sork 1987; Schupp 1988; Smith et al. 1989). Predispersal seed predation has also been identified as an important process in structuring plant communities (Janzen 1970, Thompson 1985). 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.

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 (Julander 1937, Young and Payne 1948, Aldous 1952, Garrison 1953, Lay 1965, Krefting et al. 1966, Shepherd 1971, Willard and McKell 1978, Wolff 1978, Danell et al. 1985). In general, 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.

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 1953:315-316). Simulated winter browsing reduced female ament (catkin) 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 while Shepherd (1971) observed that heavy clipping reduced fruit production in serviceberry, mountain mahogany (Cercocarpus montanus), Gambel oak (Quercus gambellii), bitterbrush (Purshia tridentata), and big sagebrush. Austin and Burgess (1990) reported that Cornus racemosa plants inside a 5-year old exclosure produced significantly more flowers and fruits than plants exposed to white-tailed deer browsing. Anderson (1990) found that Trillium grandiflora grazed by white-tailed deer produced significantly fewer flowers and fruits than ungrazed plants.

This chapter explores the impact that "naturally regulated" ungulate populations in the Greater Yellowstone Ecosystem are having on the sexual reproduction of seven shrubs and one forb. Ungulate exclosures were used to compare seed production and plant growth in unbrowsed versus browsed shrub communities (see Chapter 2 above).

RESULTS

Berry Production Inside-outside Exclosures

Serviceberry, chokecherry, and buffaloberry inside exclosures had greater canopy-coverage (Table 37), grew significantly taller (Table 38), and were significantly larger (Table 39) than outside browsed plants. Furthermore, shrubs repeatedly browsed produced practically no berries (Table 40). Serviceberry plants outside the Camp Creek exclosure produced an average of 0.067 berries per plant while protected individuals produced an average of 1,333 berries; a 20,000-fold difference.

In most situations, buffaloberry is not preferred by elk,

Table 37. Effect of ungulate browsing on shrub canopy-coverage as recorded inside and outside exclosures in the Greater Yellowstone Ecosystem.

	Mean (SEM) canopy-coverage (%)			
Exclosure and species	n	Inside	n	Outside
Mammoth				
Buffaloberry	3	15.0 (7.6)	3	1.0 (0.7)
East Elk Refuge				
Serviceberry	9	13.0 (4.6)	8	0.4 (0.4)*
Chokecherry	9	11.9 (4.7)	8	0.9 (0.5)*
Uhl Hill				
Serviceberry	4	14.0 (3.1)	3	0.7 (0.4)*
Chokecherry	4	6.5 (2.1)	3	2.0 (0.6)
Camp Creek				
Serviceberry	6	18.5 (5.0)	12	0.5 (0.2)*

*All $p < .01$, t-test on arcsine transformed data.

Table 38. Effect of ungulate browsing on shrub height as recorded inside and outside exclosures in the Greater Yellowstone Ecosystem.

Exclosure and species	Mean height (cm) Inside	Outside	*t***
Mammoth			
Buffaloberry	133.1	48.0	19.02
East Elk Refuge			
Serviceberry	276.1	124.5*	4.95
Chokecherry	281.9	121.2*	9.38
Uhl Hill			
Serviceberry	143.0	60.2	8.26
Chokecherry	130.0	51.8	16.56
Camp Creek			
Serviceberry	181.4	32.0	14.97
Lamar-West			
Serviceberry	86.6	19.8	11.34
Chokecherry	121.2	25.4	5.55

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

** All $p < .01$.

Table 39. Effect of ungulate browsing on shrub growth as recorded inside and outside exclosures in the Greater Yellowstone Ecosystem.

Exclosure and species	Mean [height plus crown length and crown width] (cm)		
	Inside	Outside	*t***
Mammoth			
Buffaloberry	523.5	277.9	7.77
East Elk Refuge			
Serviceberry	820.4	440.2*	3.07
Chokecherry	730.0	341.4*	4.99
Uhl Hill			
Serviceberry	414.3	192.3	5.93
Chokecherry	376.4	126.2	13.65
Camp Creek			
Serviceberry	527.6	105.9	12.67
Lamar-West			
Serviceberry	246.1	62.7	7.18
Chokecherry	544.6	77.2	4.01

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

** All $p < .01$.

Table 40. Effect of ungulate browsing on berry production as measured inside and outside exclosures in the Yellowstone area.

Exclosure and species	Mean number of berries per plant		*t*	*p*
	Inside	Outside		
Mammoth				
Buffaloberry*	1191.46	2.50	2.87	< .001
Camp Creek				
Serviceberry	1333.07	0.07	13.69	< .001
Uhl Hill				
Serviceberry	104.68	0.00	6.74	< .001
Chokecherry	65.08	0.00	8.64	< .001
East Elk Refuge				
Serviceberry	1300.20	13.20**	3.86	< .001
Chokecherry	1517.00	33.40**	3.03	< .001
Lamar-West				
Serviceberry	1110.47	0.00	4.86	< .001
Chokecherry	2121.78	0.00	2.89	< .001

* Dioecious; mean includes only female plants and assumes a 50:50 sex ratio.

** Protected by snowbank which tends to reduce ungulate use.

especially if more palatable shrubs are present (Nelson and Leege 1982). However, in Yellowstone elk utilize buffaloberry heavily, as indicated by the severely hedged growth form and the greater canopy-coverages and heights inside the Mammoth exclosure. Buffaloberry plants inside the exclosure produced an average of 1,191 berries per female plant while individuals outside the exclosure produced an average of 2.5 berries per female plant; a 476-fold difference.

Willow Seed Production Inside-outside Exclosures

As discussed in Chapter 6 (above), willows are taller and have greater canopy-coverage inside than outside each exclosure. Outside the exclosures, no aments were present on any of the permanent willow belt transects (Table 41). Furthermore, only eight male aments were found in an additional 1.13 ha of willow-dominated habitat which I searched adjacent to the four exclosures on Yellowstone's northern range. In contrast, Salix bebbiana, S. boothii, S. lutea and S. geyeriana produced an average, respectively, of 1445, 583, 694 and 1346 female aments per m^2 of canopy-coverage inside exclosures (Table 42).

For all willow species inside exclosures, male aments were 2.7 times more abundant per m^2 of canopy-coverage than female aments. The number of seeds per m^2 of female willow canopy-coverage ranged from a low of around 109,000 for S. geyeriana to over 583,000 for S. lutea and averaged nearly 307,000. Willows protected for three growing seasons increased in height (S. Chadde, pers. commun. 1989) but produced less than two male or female aments per m^2 (Table 43). It will apparently take several years for those plants to reach their full reproductive potential.

Female willows were more common than male plants inside exclosures and on average outnumbered males 1.7 to 1 (Table 44). When the mean sex ratio is combined with species canopy-coverage (Table 29-31) and species seed production values (Table 42), an estimate of the total number of

Table 41. Number of aments produced by willows on permanent belt transects and adjacent areas outside Yellowstone exclosures.

	Permanent belt transects		Adjacent areas	
Exclosure	Area(m^2)	Number of aments	Area(m^2)	Number of aments
Mammoth*	46.5	0	3000	0
Junction Butte	34.8	0	800	0
Lamar-West	**	**	3500	0
Lamar-East	46.5	0	4500	8***
Mean number of aments per m^2		0		0.00068

* There were also no male or female aments on river birch plants in this belt transect.

** There is no permanent willow belt transect outside this exclosure; see Chapter 2.

*** Male <u>Salix bebbiana</u> protected from browsing by dead stems.

Table 42. Mean number of aments, fruits, and seeds produced by willows inside Yellowstone exclosures.

Species-exclosure	Mean (SEM) aments per m^2 of canopy-coverage		Mean (SEM) matured fruit per female ament (n=60)	Mean (SEM) seeds per fruit (n=10)	Mean number of seeds per m^2 of canopy-coverage
	Male	Female			
Salix bebbiana					
Mammoth	1878 (102)	1006 (320)	31.6 (1.2)	5.1 (0.2)	162,127
Junction Butte	1219 (539)	1631 (594)	23.7 (1.2)	6.1 (0.4)	235,794
Lamar-West	4083 (827)	1482 (216)	46.5 (1.5)	5.8 (0.5)	399,695
Lamar-East	3080 (0)	1660 (213)	47.8 (1.4)	6.5 (0.3)	515,854
Subtotals	2565 (636)	1445 (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	1860 (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	1860 (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	1340 (0)	612 (130)	---- ----	---- ----	-------
Lamar-West	---- ----	980 (0)	69.2 (3.4)	10.9 (0.6)	739,194
Subtotals	1340 (0)	694 (147)	73.8 (4.6)	11.4 (0.4)	583,876

Table 42. (continued)

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	4300 (0)	1846 (666)	29.0 (0.9)	5.9 (0.4)	315,850
Lamar-East	3560 (0)	1260 (502)	16.4 (0.6)	4.4 (0.3)	90,922
Subtotals	3930 (370)	1346 (267)	17.6 (3.9)	4.6 (0.5)	108,972
Total	2665* (620)	1001* (241)			306,988

* $t = 3.98$, $p < .01$

Table 43. 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 (Chadde et al. 1988).

	Number of aments per m^2 for total enclosed area			
Location/mini-exclosure	Salix bebbiana		Salix lutea	
	Female	Male	Female	Male
Mammoth				
M-North	0.0	1.0	0.0	0.0
M-South	0.0	0.0	2.8	0.4
Junction Butte				
M-West	0.5	0.0	1.4	2.9
M-East	0.0	1.1	0.5	0.2
Mean	0.13	0.53	1.18	0.88

Table 44. Sex of willow plants inside Yellowstone exclosures.

Exclosure and species	Number of plants: Male	Number of plants: Female	Ratio of 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

seeds produced on inside and outside willow belt transects can be calculated. Thus, approximately 5,857,000 seeds were produced on the willow transect inside the Junction Butte exclosure and zero outside; Lamar-East 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

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 (2.5m) produced an abundance of male or female aments while no aments were produced on that portion of the plant exposed to browsing (Table 45). Individual river birch (Table 46) and chokecherry (Table 47) plants exhibited a similar pattern. Repeated ungulate browsing has virtually eliminated willow seed and berry production on the northern range and other winter ranges within the Greater Yellowstone Ecosystem.

Balsamroot

Ungulates apparently are having a similar effect on at least one forb. Balsamroot in Eagle Creek produced 155 times more flowers per plant than did plants in the park (Table 48). Observations indicate that elk and other ungulates in the park ate the flower heads as they developed.

DISCUSSION

Mechanisms Which Limit Seed Production

Winter browsing limits berry and willow seed production in at least three ways. First, browsing removes flower buds which developed the previous fall (Garrison 1953:315-316, Jameson 1963, Childers 1975:128, Mosseler and Papadopol 1989:2569). When the plants begin

Table 45. Number of aments produced above and below the browse height (2.5m) on individual willows in Yellowstone National Park near Geode Creek.

Species-plant	Plant size (m^2) canopy-coverage	Number of stems above browse height	Number of aments per plant	
			Below browse height	Above browse height
Salix lutea				
A - female	12	5	0	1680
B - female	2	1	0	78
C - female	2	2	0	170
D - male	3	9	0	1140
Salix geyeriana				
E - female	4	2	0	160
F - female	1	3	0	1351
G - female	3	5	0	600
Salix boothii				
H - female	2	2	0	182
Mean			0*	670*

* $t = 2.80$, $p < .02$

Table 46. Number of aments produced above and below the browse height (2.5m) on individual river birch plants near Yellowstone's Mammoth exclosure.

Plant	Plant size (m^2) canopy-coverage	Number of stems above browse height	Number of aments on plant			
			Below browse height		Above browse height	
			Female	Male	Female	Male
A	4	1	0	18*	16	280
B	16	2	0	0	0	39
C	12	2	0	0	951	1291
D	12	1	0	3*	272	784
Mean			0	5	310	598

*Protected from browsing by dead stems.

Table 47. Number of berries produced above and below browse height (2.5m) on individual chokecherry plants in Yellowstone National Park.

Plant	Plant size (m^2) canopy-coverage	Number of stems above browse height	Number of berries on plant	
			Below browse height	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*

*$t = 3.88$, $p < .01$

Table 48. Effect of ungulate grazing on flowers of balsamroot.

Area-sample site	Number of plants	Percent of plants with at least one flower	Mean number of flowers per plant
High ungulate use			
Yellowstone Park			
A	150	3%	0.03
B	150	3%	0.04
C	150	5%	0.10
D	150	5%	0.05
E	150	4%	0.04
F	150	4%	0.05
G	150	6%	0.09
H	150	3%	0.09
I	150	8%	0.15
Total	1,350	4%	0.07
Low ungulate use			
Eagle Creek			
1	150	89%	13.29
2	150	88%	6.19
3	150	84%	6.79
4	150	92%	12.86
5	150	93%	9.88
6	150	82%	12.07
7	150	89%	17.47
8	150	86%	13.73
9	150	86%	5.48
Total	1,350	88%	10.86*

* $t = 7.49$, $p < .01$

growth the following spring, few flowering buds remain. 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, the plants cannot flower the following spring and berries or seeds are not produced. From 1970 to 1978, ungulates on Yellowstone's northern range, on average consumed 91% of the current year's willow stem growth (Houston 1982:149). Willow utilization has not decreased in recent years (F. Singer, pers. commun. 1988; S. Chadde, pers. commun. 1989). Winter browsing also removes virtually all of the previous summer's growth on serviceberry, chokecherry, and other deciduous shrubs throughout much of the Greater Yellowstone Ecosystem.

Second, as Harper (1977:Chap. 21) noted, plants allocate resources between vegetal growth and reproduction. Plants which allocate resources to herbivore-induced vegetative growth are unlikely to produce many seeds or berries (Garrison 1953:316, Hemmer 1975). Further, woody plants pass through a juvenile or vegetative phase during which they cannot be induced to flower (Zimmerman 1972, Krugman et al. 1974). On Yellowstone's northern range, repeatedly browsed willows often exhibit juvenile characteristics (D. Despain, pers. commun. 1988).

Finally, since there is a positive correlation between the size of individual plants and the size of the fruit crop (Herrera 1984:390, Peters et al. 1988), grazing-induced size limitation also reduces the number of berries produced. Inside Yellowstone exclosures, a positive correlation exists between the size of individual plants and the number of berries produced (Table 49). Since plants outside exclosures are significantly smaller (Table 39), this factor also works to limit berry production. These three mechanisms apparently operate to curtail berry and seed production when plants are exposed to frequent ungulate browsing.

While I only measured seed production in willows, there is a

Table 49. Effect of plant size on berry production inside Yellowstone area exclosures.

Species and size class*	n	Mean (SEM) 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 (373.4)
> 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); see Chapter 2 above.

direct correlation between chokecherry, buffaloberry, and serviceberry fruits and seed production. Since chokecherry fruits are a one-seeded drupe and buffaloberry produce drupelike ovoid fruits (achenes enveloped in a fleshy perianth), fruit and seed production are equivalent in these species (Schopmeyer 1974). Serviceberry fruits each contain from four to ten small seeds (Schopmeyer 1974, Robinson 1986).

Despite a consistent yearly bloom in most fruiting shrubs, fruit production is highly variable (Schopmeyer 1974, Kendall 1986, Weaver et al. 1990). "In any given locality, heavy crop years are often interspersed by years in which few fruit can be found" (St. Pierre 1989). Thus, I would expect seed production to vary inside the exclosures, but since the shrubs' current annual growth is consumed year after year outside the exclosures, few if any seeds could ever be produced by those plants. Hence, even though I measured seed production only in 1 year, the pattern of virtually no seed production outside the exclosures, but seed production within, most likely reflects what happens every year. Observations on willows and fruiting shrubs at these exclosures in other years and at other exclosures not included in this study support this conclusion (Kay unpub. photos).

Comparison With Other Studies

Moose herbivory on the perennial herb _Aralia nudicaulis_ significantly altered population structure by reducing the total number of flowering shoots and decreasing fruit production (Edwards 1985). On Washington State's Mount St. Helens, both seed production and seedling recruitment of _Aster ledophyllus_ "within elk exclosures were significantly greater than for uncaged plants . . . Elk reduced the viable seed crop by 22% and seedling recruitment by 76% as compared to control plants" (Wood and Anderson 1990:193). They concluded that elk herbivory was an important factor limiting _Aster ledophyllus's_ ability to colonize the Mount St. Helen blast zone. However, Scarlet galia

(Ipomopsis aggregata) grazed early in the season by elk and mule deer in Arizona enjoyed a 3.1-fold increase in seed production and a 2.4-fold increase in relative fitness over ungrazed plants (Paige and Whitham 1987).

Katsma and Rusch (1980) reported that simulated deer browsing in winter reduced apple production the following year. Ungulate browsing caused a 61-86% reproductive depression in Rosa canina (Herrera 1984). Allison (1987) concluded that winter browsing by white-tailed deer affected Canada yew (Taxus canadensis) sexual reproduction by reducing male strobili production and seed production. Browsing reduced pollen production to such an extent that sexual reproduction in this wind-pollinated species may have been pollen limited. 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, et al. 1990:162).

To the best of my knowledge, no published studies have reported the nearly complete elimination of seed production I encountered. Even studies of small mammals, birds, and insects have seldom documented the level of seed loss I observed in Yellowstone. For instance, Elmquist et al. (1987) reported that stem girdling by mice reduced willow seed production a maximum of 94% while Sork (1987) reported 97% predation on seeds beneath Dipteryx panamensis trees on Barro Colorado Island. Smith (1987) found an average 75% of the seeds used in his experiments were consumed by predators. In other experiments, predation by mice and beetles reduced the seed pods of Carex pilulifera by approximately 21% and 65%, respectively (Kjellsson 1985). Jensen (1982) reported that rodents consumed an estimated 1-3% of beech (Fagus sylvatica) endosperm production in mast years while between mast years, that figure rose to 30-100%. Mice consumed 75% of Avena fatua seed, 44% of Hordeum leporinum seed, and 37% of Bromus diandrus seed (Borchert and Jain 1978) while seed predation on Guazuma ulmifolia by beetles ranged from 2 to

75% depending on site conditions (Janzen 1975). However, in Yellowstone Park, ungulate browsing reduced berry and willow seed production by more than 99%.

Based on photographic evidence (see Chapter 8 below), few willows on Yellowstone's northern range appear to have produced seeds for the last 50 or so years. Similarly, serviceberry and chokecherry plants have likely produced few berries since the early 1900s (see below). While other studies have suggested a link between seed loss and reduced plant populations (Louda 1983), under the present conditions in Yellowstone, it is not possible to separate seed predation effects from other aspects of ungulate browsing such as herbage removal and trampling.

"Natural Regulation"

I suggest that the virtual elimination of willow seed production by ungulates also indicates that herbivores and vegetation are not in equilibrium as proposed by the Park Service's "natural regulation" paradigm (see Chapter 1 above). Once the existing willows die of old age, disease, insects or other causes, they cannot be replaced by new plants produced from local seed. Under these conditions, willows would eventually disappear. Willows commonly colonize new habitats by producing vast numbers of wind-dispersed seeds. During a 3 year study to classify wetland communities on the northern range, Chadde et al. (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 long-lived perennials (Duggan 1985, Anderson 1989, Borchert et al. 1989). Anderson (1989:314) 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. In the species he studied, seed banks were adequately maintained despite seed predation rates approaching 95%.

I did not measure soil seed banks, but since willow seeds are short-lived and are not stored in seed banks (Brinkman 1974, Densmore and Zasada 1983), this cannot be an important consideration in willow ecology. Serviceberry, chokecherry, and buffaloberry seeds are stored in soil seed banks (Schopmeyer 1974), but since virtually no seeds are being produced outside exclosures, those seed banks can only decrease over time until they eventually disappear. Moreover, even if seedlings become established outside the exclosures, the level of ungulate browsing which exists in Yellowstone 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, virtually none of those plants has been successfully recruited into the sexually reproducing populations over the last 80 or so years because repeated ungulate browsing has prevented them from growing taller than 1m (Chadde et al. 1988, Kay unpub. photos). As discussed in Chapter 6 (above), willows which 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.[1]

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[1]During the mid-1970s, a few tall willows were still alive above and below this gravel bar (Kay unpub. photos). Those plants probably produced the seeds which became established on the gravel bar. Since that time, continued ungulate browsing in combination with insects and pathogens (Houston 1982) have eliminated those tall willows (Kay unpub. photos).

Without abundant seed crops, willows also 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 be a 100-300 year event (Davis and Mutch 1989; Romme and Despain 1989a, 1989b; Schullery 1989a, 1989b). Hence, those fires were able to burn a limited number of 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 et al. 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 which had abundant soil moisture especially after snowmelt in 1989, ideal conditions for germination and seedling establishment of willow (Brinkman 1974).

Aspen has similar but even more demanding seed-bed requirements than willows. It needs bare mineral soil and high surface soil moisture throughout germination and the first growing season (McDonough 1979, 1985). Aspen's requirements are so demanding that few aspen seedlings have ever been reported in the Intermountain West (Kay 1990). Yet during 1989, millions of aspen seedlings grew on Yellowstone's northern range at densities up to 11.5×10^6 per ha in the severely burned riparian areas described above (Kay 1990). I observed only one willow seedling growing in those same areas. My data indicate there were practically no willow seeds available on Yellowstone's northern range to colonize this newly created habitat. Reduction in seed production decreases the probability of plants colonizing new sites (Allison 1987).

As has been shown, some serviceberry and chokecherry plants persist on the northern range, but nearly all are less than 0.3m tall (Houston 1982:419) and produce almost no fruit. Under the "natural regulation" paradigm, conditions which exist today are thought to reflect the pristine condition of the park prior to European influence and by inference, other Intermountain ungulate wintering areas. Gruell (1979:67, 1980a:8) concluded that a "suppressed growth form from persistent browsing was the historical norm" for serviceberry and other shrubs in Jackson Hole, implying berries were always rare.

However, in 1835, Reverend Samuel Parker (1967:85-86) 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 km north of Yellowstone Park (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). Moreover, reports that Native Americans frequently gathered large quantities of berries, especially serviceberries and chokecherries, are found in all ethnohistoric sources and most historic journals (Kay unpub. data). These early accounts suggest that the present lack of berries was not the condition prevailing in presettlement times.

Resource-limited ungulate populations and large quantities of berries are mutually exclusive on most western ranges. Moreover, even moderate numbers of ungulates will curtail berry production because those plants provide highly preferred forage, especially in winter (Nelson and Leege 1982). I suggest that without seed production, plants cannot be in long-term equilibrium with their ungulate herbivores.

CONCLUSIONS

1. Deciduous shrubs protected from ungulates exhibited significantly greater growth and canopy-coverage than unprotected plants.

2. Ungulate browsing virtually eliminated berry production in areas frequented by wintering elk in the Greater Yellowstone ecosystem. Plants inside exclosures produced up to 20,000 times more berries than unprotected plants.

3. Ungulate browsing also eliminated nearly all willow seed production on Yellowstone's northern range. Protected female willows, on average, produced nearly 307,000 seeds per m^2 of canopy-coverage while unprotected willows produced none.

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

5. Willows protected from browsing for 3 years produced less than two male or female aments per m^2 compared to 2,665 and 1,001, respectively, for plants protected for approximately 30 years. Based on repeat photographs of inside exclosure plots (see Chapter 6 above), it apparently takes 15 years or longer for heavily browsed willows to regain their reproductive potential.

6. No published studies have reported the level of seed loss encountered in Yellowstone.

7. Based on historic photographs (see Chapter 8 below) and journals, berries and willow seeds were common throughout this area prior to creation of Yellowstone National Park. The present lack of berries was not the condition prevailing in pre-European times.

8. Resource-limited ungulate populations and large quantities of berries are mutually exclusive on most western ranges.

9. Without adequate seed production, plant populations cannot be in long-term equilibrium with their environment or herbivores. Once existing plants die of old age, disease, insects, or other causes they cannot be replaced by new plants produced from seed.