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Defoliation effects on reproductive biomass: Importance of scale and timing

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Abstract

Community-level (per unit area) and individual tiller reproductive biomass inside and outside of long-term exclosures on the northern winter range of Yellowstone National Park, USA were compared. Grazed areas had twice the number of reproductive tillers m^{-2} (186 compared to 88 tillers m^{-2}), and greater total reproductive biomass m^{-2} than ungrazed plots (13 compared to 7 g m^{-2}). In contrast, seed number tiller^{-1} was greater for grasses in exclosures. Because of these offsetting responses, seed production (no. m^{-2}) was unaffected by herbivores. On an area basis, grazed grasses allocated proportionally more biomass to reproduction (reproductive biomass/aboveground biomass) than ungrazed grasses. We propose that altered plant demography and morphology following defoliation explain how grazers might increase the allocation of biomass to reproduction in Yellowstone grasslands.

To understand these results in light of ecological and agronomic studies, we reviewed literature from 118 sources that reported the effects of defoliation on the production of reproductive biomass. The review suggested that the results of herbivory or defoliation on plant reproductive biomass depended on the scale of measurement (community vs. plant). In addition, timing of grazing or defoliation emerged as a key factor that determined whether sexual reproduction was inhibited. Like the early season grazing that is typical of Yellowstone's northern winter range, studies often showed that early season defoliation stimulated production of community-level reproductive biomass. Our results rectify disagreements in the literature that ultimately derive from differences in either timing of defoliation or measurement scale.

Resumen

Se comparó la biomasa de tallos reproductivos a nivel individual y de comunidad (por unidad de área)dentro y fuera de exclusiones de largo plazo localizadas en un pastizal de invierno del norte del Parque Nacional Yellowstone, E.U.A. Las áreas apacentadas tuvieron el doble de hijuelos reproductivos m^{-2} (186 contra 88 hijuelos m^{-2}) y una mayor biomasa reproductiva m^{-2} que las parcelas sin apacentar (13 versus 7 g^{-2}). En contraste, el número de semillas por hijuelo^{-1} fue mayor en los zacates dentro de la exclusión. Debido a estas respuestas compensatorias, la producción de semilla (número m^{-2}) no fue afectada por los herbívoros. En términos de área, los zacates apacentados destinaron proporcionalmente más biomasa a la reproducción (biomasa reproductiva/biomasa aérea) que los zacates sin apacentar. Proponemos que la demografía y morfología vegetal alterada después del apacentamiento explica como los apacentadores pueden incrementar la asignación de biomasa a la reproducción en los pastizales del Yellowstone. Para entender estos resultados a la luz de estudios ecológicos y agronómicos revisamos literatura de 118 fuentes que reportaron los efectos de la defoliación en la producción de biomasas reproductiva. La revisión sugiere que los resultados de la herviboría o defoliación en la biomasa reproductiva de la planta depende de la escala de medición (comunidad vs. planta). Además, la época de apacentamiento o defoliación surgió como un factor clave que determinó si la reproducción sexual fue inhibida. Como el apacentamiento a inicios de la estación es típico en los pastizales invernales del norte de Yellowstone, los estudios a menudo mostraron que la defoliación temprana estimulo la producción de biomasa reproductiva a nivel de comunidad. Nuestros resultados rectifican desacuerdos de la literatura que finalmente se derivan de diferencias tanto en el tiempo de defoliación o en la escala de medida.

Key Words: grassland, ungulate, grazing, clipping, seed production and yield, Yellowstone National Park, literature review

Seed production can influence the structure, composition, and function of grassland ecosystems. Recruitment from seed facilitates colonization after disturbance, offsets mortality of individual plants in a community, and maintains genetic variability of populations, allowing them to adapt to environmental change. There are 2 disparate views of how large herbivores influence grassland seed production. To plant ecologists studying the effect of herbivory on fitness at the individual plant level, grazing should reduce carbon allocation to seed production. This generality seems to be well supported; defoliation reduces biomass of flowers, fruits, seeds, and reproductive tillers of individuals (for examples see Jameson 1963, Crawley 1983, Belsky 1986a, Maschinski and Whitham 1989, Whitham et al. 1991), with a few exceptions (Paige and Whitham 1987, Lennartsson et al. 1998). This viewpoint is reinforced by observations that grazing ecotypes of several grass species allocate less biomass to seed pro-

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duction than conspecific nongrazing ecotypes (Stapledon 1928, Kemp 1937, Hickey 1961, Detling and Painter 1983, Jaramillo and Detling 1988, Painter et al. 1993, Smith 1998).

In contrast, agricultural managers of seed crops, interested in seed yield per unit area, find that the response of grassland seed production to herbivory depends on the timing and intensity of defoliation. Several studies suggest that grazing does not decrease seed yield (Roberts 1958, 1965, Bean et al. 1979, Watson and Watson 1982, Hebblewaite and Clemence 1983, Winter and Thompson 1987, Conlan et al. 1994) and in many cases increases it (Sprague 1954, Day et al. 1968, Steiner and Grabe 1986, Sharrow and Motazedian 1987, Miller et al. 1993, Conlan et al. 1994, Young et al. 1996). In some studies, grazing or clipping increased the number of reproductive tillers per unit area (Herron 1976, Brown 1980), however this was not always followed by a corresponding increase in seed yield. Thus, the effect of defoliation on production of reproductive biomass is viewed differently by plant ecologists and agricultural managers. Plant ecologists tend to expect inhibition and agricultural researchers report neutral or even positive effects.

Approximately 2,000 elk (*Cervus elaphus* L.), 300–700 bison (*Bison bison* L.), and 600 pronghorn (*Antilocarpa americana* Ord.) graze the northern winter range of Yellowstone National Park from November–April each year (Singer and Mack 1993). Ungulates increase rates of plant production and nutrient cycling in Yellowstone grasslands (Frank et al. 1998, Frank and Groffman 1998). Moreover, comparisons of grasslands inside and outside long-term exclosures indicate that grazers have not significantly influenced grassland species composition (Houston 1982, Coughenour 1991, Singer 1995). Our objective was to determine how migratory native grazers influence seed production on the northern winter range of Yellowstone National Park.

Materials and Methods

Site Description

We sampled the effects of grazing on aboveground reproductive tiller numbers per plot, seed numbers per tiller and per plot, and allocation to reproductive versus vegetative biomass at the plot level. Field data were collected on the northern winter range of Yellowstone National Park, USA (44°55' to 45°10' N and 110°10' to 110°50' W), from July 1999–Sep. 1999. Long-term effects of excluding ungulates on community level patterns of reproductive biomass allocation in grasses was studied by sampling grassland plots inside and outside of 5 exclosures erected between 1958 and 1962. Soils of the northern winter range are largely derived from andesitic and sedimentary glacial till that was deposited during the Pleistocene (Keefer 1987). The climate in the northern winter range is cool and dry; 15 year 95% confidence intervals for mean annual precipitation and temperature from 2 weather stations range from 33.7–38.6 cm (mean = 36.1 cm) and 4.6–5.3° C (mean = 4.9° C) at Mammoth (44°59'N/110°42'W) to 39.2–45.5 cm (mean = 42.3 cm) and 1.7 – 2.4° C (mean = 2.1° C) at Tower (44°55'N/110°25'W) (NOAA 2001). Neither mean annual precipitation nor annual temperature in the year of our study was significantly different from the 15-year average at either weather station; 1999 annual precipitation and temperature was 34.8 and 43.2 cm, and 5.2 and 1.8° C, at Mammoth and Tower, respectively (Table 1).

Two treatments, fenced for ~40 years and unfenced, were replicated across the 5 sites. At each site, 2 paired grassland plots, 1 inside and 1 outside exclosures, approximately 100 m^2 (usually 10 x 10 m) each, were chosen to minimize variation in slope, aspect, and water drainage. Dominant native grass species at the sites were *Festuca idahoensis* Elmer, *Koeleria macrantha* (Ledeb.) Schult., *Poa secunda* Presl., *Pseudoroegneria spicata* (Pursh) A. Love, and *Hesperostipa comata* (Trin. & Rupr.) Barkworth. The non-native species *Agropyron cristatum* (L.) Gaertn. was dominant at 1 of the sites, but was equally abundant inside and outside of the exclosure. Less common grasses were *Eremopyrum triticeum* (Gaertn.) Nevski, *Bromus* sp., *Danthonia* sp., *Achnatherum hymenoides* (Roemer & Schult.) Barkworth, *Elymus elymoides* (Raf.) Swezey, and *Nassella viridula* (Trin.) Barkworth. Common genera of forbs and shrubs were *Artemisia, Achillea, Antennaria, Chrysothamnus, Cirsium, Crepis, Erigeron, Lupinus, Potentilla, Taraxacum,* and *Trifolium.* The 3 most common grazers at the sites were elk, bison, and pronghorn. Descriptions of the 5 grassland sites, 2 at Stephen's Creek, 2 at Blacktail Plateau, and 1 at Junction Butte, are described in detail elsewhere (Houston 1982).

Sampling Methods

Within a plot, aboveground biomass, species richness, and the number of reproductive tillers on grasses were sub-sampled at 4 random locations. Aboveground grass biomass was estimated by clipping all live grass within one, 50 x 50 cm quadrat at each of the 4 sub-sampling locations to ground level. Samples were then dried at 70° C for at least 2 days and weighed. Total aboveground live biomass and species composition were estimated by counting the number of vegetation contacts from 50 randomly located pins passed through a 50 cm high frame at a 53° angle within each of the 4 sub-sampling locations. The number of pin contacts was used to estimate total aboveground biomass inside and outside exclosures using previously established regression equations for the herbaceous vegetation of Yellowstone (Frank and McNaughton 1990).

Grass reproductive tiller density was estimated by counting reproductive tillers within three, 50 x 50 cm quadrats placed randomly within each of the 4 sub-sampling locations. From 1 of the 3 quadrats, all reproductive tillers were collected and dried for at least 2 days at 70° C. Tillers were sorted by species, and then separated into stem and inflorescence. After drying,

Table 1. Mean annual precipitation and temperature from 2 weather stations on the northern winter range of Yellowstone National Park, Wyo., USA. Data are from 1999 (the year of our study) and the mean for the previous 15 years.

			Precipitation			Temperature	
Weather Station	Location	1999	15 yr. mean	95% confidence interval for mean	15 yr. 1999	95% confidence mean	interval for mean
		(cm)			(°C)		
Mammoth	44°59'N/110°42'W	34.8	36.1	33.7 – 38.6	5.2	4.9	4.6 – 5.3
Tower	44°55'N/110°25'W	43.2	42.3	39.2 – 45.5	1.8	2.1	1.7 – 2.4

stem and inflorescence mass was weighed and lengths were measured. As an index of seed number, we estimated the number of reproductive florets per tiller for grass each species. When the number of tillers in a sub-sample for a given species was > 10, a random sample of 10 seed heads was selected and the florets were counted. The mean number of florets per tiller for the 10 seed heads was then multiplied by the number of tillers of each species to derive species-specific estimates of floret number per sub-sample. When sub-samples contained $\leq$ 10 seed heads of a species, all florets were counted.

Grass Demography

As part of a separate study on spatial heterogeneity of Yellowstone grasslands, baseline data on grass density and size were collected at 1 exclosure from Steven's Creek and Blacktail. Data were also collected at Lamar, at which grass reproductive biomass was not measured, but is similar in grazing, precipitation, and species composition to Junction Butte. A grid of 80 evenly spaced points (8 x 10) was established inside and outside of each of the 3 exclosures. At each point, the distance to the center of the nearest grass and the basal lengths of 2 perpendicular axes of the nearest individual were measured. Plant density (D, plants m^{-2}) was estimated by the nearest individual method, $D = 1/(k*L)^2$, where the method correction factor k = 2 and L is the average distance (in m) to the nearest plant for each grid (Cottam and Curtis 1956). Plant size was estimated by calculating elliptical basal area (cm^2) from the lengths of the 2 axes for each individual.

Data analysis

Tiller density is reported per unit area (no. m^{-2}), while floret number and tiller biomass components (inflorescence, stem, and total) are reported per unit area (no. m^{-2} and grams m^{-2}) and per tiller (no. $tiller^{-1}$ and grams $tiller^{-1}$). Data presented per plot represent the mean community response to a treatment. Data per tiller were averaged by tiller within a sub-sample and then averaged within a plot to calculate a tiller-based mean. Data per plot are summed within a sub-sample and then averaged within a plot to calculate a plot mean. Finally, to determine the effects of excluding grazers on community level patterns of biomass allocation, we compared reproductive biomass per unit of aboveground biomass (the ratio inflorescence biomass:plot aboveground biomass) between treatments with a Wilcoxon matched pair test.

Grazer effects were determined with paired t-tests, with sites as replicates, when differences between paired treatment means were normally distributed (determined with a Shapiro – Wilks' W test; $P > 0.05$). When differences were not normally distributed, data were analyzed with a Wilcoxon matched pair test. Because of small sample sizes, all P-values < 0.10 were considered significant. All statistical analyses were performed in Statistica release 5 (1998).

Literature Review

We summarized published literature that reported effects of grazing, clipping, or seed removal on seed yields or plant reproductive biomass. The primary literature was searched with online databases such as Agricola and Cambridge Scientific Abstracts, using keywords such as "defoliation", "grazing", "clipping", "reproduction", "seeds", etc. Our main objective was to compile data sets that allowed quantitative assessment of how plant tissue removal influenced plant reproductive biomass at 2 scales, whole plots and individual plants, from as ecologically diverse sources as possible. Therefore, studies of all natural defoliators or seed predators (insects, birds, etc.) were included. Moreover, we included studies that reported grazer effects on soil seed banks and studies where populations of plants with different grazing histories were compared. Studies were hierarchically grouped by the spatial scale of measurement (individual plant or whole plot), by broad functional group (graminoids or non-graminoids), by the method of defoliation (clipping or grazing), and by identity of defoliator (insect or ungulate). Within each category, we listed all plant species for which data were presented and assessed the effects of defoliation on reproductive biomass as reported by the authors. Results were reported as positive (+), negative (–), or no difference (0) among defoliation and control treatments. Studies in which the timing of defoliation relative to anthesis was manipulated commonly had early, intermediate, or late defoliation treatments. Biomass removal well before the initiation of flowering (i.e. before internode elongation for grasses) was classified as early, several weeks prior to flowering was classified as intermediate (i.e. boot stage for grasses), and at or later than the initiation of flowering was classified as late. Defoliation was categorized as intermediate when information on the timing of defoliation relative to flowering was not provided. Results from studies that include the effects of the severity of defoliation are also reported.

Results

Yellowstone National Park Study

Grazing did not affect species richness ($t_4 = 0.848$; $P = 0.44$). The mean (± SE) percentage similarity of species composition inside and outside of exclosures was 70.5% (± 1.3) and ranged from 67.0 to 74.4% across the 5 sites. Total aboveground biomass was unaffected by grazers ($t_4 = 1.185$, $P = 0.30$; Table 2), as was aboveground grass biomass ($t_4 = 1.269$, $P = 0.273$; Table 2). However, grazing resulted in a nearly doubling of the number of reproductive grass tillers per plot ($t_4 = 3.542$, $P = 0.024$; Table 2). Likewise, grazed plots had greater total reproductive tiller biomass per area ($Z_4 = 2.023$; $P = 0.043$), which was caused by both greater total inflorescence ($Z_4 = 2.023$; $P = 0.043$) and total stem weights ($t_4 = 2.210$; $P = 0.091$). However, on a per tiller basis, neither reproductive tiller mass ($t_4 = 1.624$; $P = 0.180$) nor the inflorescence mass ($t_4 = 1.190$; $P = 0.300$) differed between grazed and ungrazed plots (Table 2). Thus, increased reproductive tiller mass per plot in grazed areas was caused by an increase in reproductive tiller number, rather than by greater individual tiller mass.

On a per tiller basis, florets were more numerous on tillers that were excluded from grazers ($Z_4 = 1.753$; $P = 0.078$). However, the total number of florets per plot was unaffected by grazing ($t_4 = 1.392$, $P = 0.236$), as a result of the greater number of reproductive tillers per area in grazed plots. Reproductive tiller length was greater in ungrazed areas ($Z_4 = 2.023$; $P = 0.043$); this was attributed to differences in both stem length ($Z_4 = 2.023$; $P = 0.043$) and inflorescence length ($t_4 = 2.949$; $P = 0.042$).

Defoliated plants allocated significantly more biomass to reproduction per unit of standing biomass than did plants in ungrazed plots ($Z_4 = 2.03$, $P = 0.043$, Table 2). Whether or not grazers also increased the ratio of reproductive to aboveground biomass after accounting for foliage removed by herbivores early in the growing season cannot be determined from this study, nor has it been addressed in any study of which we are aware.

Few significant differences exist between grazed and ungrazed dominant native plants when data are analyzed on a species-specific basis (Table 3). Only *P. spicata* had significantly more reproduc-

Table 2. Mean ± 1 S.E. values for vegetation characteristics on a per area and per tiller basis for grazed and ungrazed plots in Yellowstone National Park. Associated P-values from statistical analyses (either paired t-test or Wilcoxon matched pair test) tested for effects of grazing. Total reproductive biomass = stem + inflorescence.

Variable	Ungrazed mean ± SE	Grazed mean ± SE	P-value
	Plot means		
Total aboveground live biomass (g m^{-2})	71.2 ± 8.6	64.6 ± 7	0.30
Aboveground live grass biomass (g m^{-2})	34.8 ± 5.5	28.8 ± 4	0.27
Reproductive tiller density (no. m^{-2})	87.8 ± 16.2	186.4 ± 31.3	**0.02***
Inflorescence biomass per plot (g m^{-2})	1.5 ± 0.5	3.4 ± 1.4	**0.04***
Reproductive stem biomass per plot (g m^{-2})	5.4 ± 1.3	9.2 ± 2.7	**0.09**
Total reproductive biomass per plot (g m^{-2})	6.8 ± 1.8	12.6 ± 4.1	**0.04***
Number florets per plot (no. m^{-2})	2,944 ± 485	4,348 ± 954	0.24
Reproductive : aboveground biomass ratio	0.26 ± 0.12	0.53 ± 0.25	**0.04***
	Tiller means		
Inflorescence biomass per tiller (g $tiller^{-1}$)	0.02 ± 0.01	0.02 ± 0.01	0.30
Reproductive stem biomass per tiller (g $tiller^{-1}$)	0.07 ± 0.02	0.05 ± 0.01	0.17
Total reproductive biomass per tiller (g $tiller^{-1}$)	0.10 ± 0.03	0.07 ± 0.02	0.18
Number florets per tiller (no. $tiller^{-1}$)	41.9 ± 7.7	24.1 ± 4.8	**0.08**
Reproductive tiller stem length (mm)	257.1 ± 8.8	207.7 ± 13.5	**0.04***
Reproductive tiller inflorescence length (mm)	54.1 ± 4.5	42.5 ± 3.7	**0.04***

*Treatment means significantly different at $P < 0.05$
Bold type indicates treatment means significantly at $P < 0.10$

tive tillers per plot (t_4= 3.553, P = 0.038) and greater ratio of tillers to aboveground biomass (t_4= 2.740, P = 0.071) in grazed compared to ungrazed plots. Likewise, estimates for reproductive tiller mass and length are statistically greater only for *K. macrantha* (t_4= 5.772, P = 0.010). Thus, even though mean estimates of reproduction are not different for grazed and ungrazed dominant grasses, the effect of defoliation on reproductive biomass clearly emerges when plant responses are analyzed at the community level (Table 2).

Basal areas of grasses were smaller in grazed compared with ungrazed plots, suggesting that previous grazing reduced plant size (inside mean = 7.1 cm^2, outside mean = 3.7 cm^2, t_2 = 7.07; P = .02, from a paired t-test for a difference in $\log_e$ transformed mean basal area, Table 4). Grass tiller densities were greater in grazed than ungrazed plots at all 3 sites measured (inside mean = 56.6 tillers m^{-2}, outside mean = 110.3 tillers m^{-2}, Table 4).

Literature Review

We identified 118 articles that reported the effects of defoliation on reproductive biomass of 115 plant species from 88 genera (Appendix 1). Taxonomic references and authorities in Appendix 1 follow directly from the original studies; authori-

Table 3. Mean aboveground biomass and tiller characteristics of 4 dominant grass species inside (UG) and outside (G) herbivore exclosures at 5 sites in Yellowstone National Park. P = P-value from a paired t-test. Sample sizes are reported in parentheses next to species names.

	Species											
	Festuca Idahoensis (3)			*Koeleria macrantha* (4)			*Poa secunda* (5)			*Psudoregnaria spicata* (4)		
	UG	G	P	UG	G	P	UG	G	P	UG	G	P
Aboveground live biomass (g m^{-2})	31.2	20.5	0.29	9.1	14.3	0.36	1.7	2	0.51	14.3	20.2	0.14
Reproductive tiller density (no. m^{-2})	57.4	72.8	0.37	22.7	53.3	0.14	6.8	9.2	0.55	15.4	45.8	**0.04***
Tillers per gram biomass (no. m^{-2} g^{-1})	1.8	3.8	0.15	3.4	3.9	0.82	3.9	4.3	0.83	0.9	2.3	**0.07**
Total reproductive biomass per tiller (g $tiller^{-1}$)	0.04	0.02	0.24	0.06	0.04	**0.09**	0.03	0.04	0.21	0.13	0.09	0.31
Total reproductive tiller length (mm)	340.5	267.4	0.15	250.4	209	**0.01***	219.1	240.9	0.53	386.9	302.4	0.20
Number florets per tiller (no. $tiller^{-1}$)	8.7	9.1	0.77	79.1	74.4	0.45	25.7	24.1	0.76	4.9	5.2	0.37

*Treatment means significantly different at $P < 0.05$
Bold type indicates treatment means significantly at $P < 0.10$

Table 4. Grass sizes and densities for grasses measured inside and outside of 3 Yellowstone National Park exclosures. Values represent means from data collected from the nearest individuals to each point in an 8 x 10 grid.

Site	Ungrazed mean ± SE	Grazed mean ± SE
	------ Plant basal area (cm^2) ------	
Lamar	3.1	1.9
Blacktail	6.8	3.1
Steven's Creek	11.2	6.2
	------ Plant density (no. m^{-2}) -----	
Lamar	59.6	184.7
Blacktail	83.2	113
Steven's Creek	26.9	33.3

ties are not presented if not provided in the original paper. Investigations examined individual plant traits (n = 73), whole plot effects (n = 50), or both (n = 3). Whole plot studies included data for 39 plant species, 30 of which were grasses or sedges. Graminoids were disproportionately represented in whole plot studies because of their agronomic importance and the tendency for crop biomass to be measured per unit area. Likewise, 5 of the remaining 10 forbs were crop or forage species. The 84 species included in studies of individual plants were more evenly distributed between graminoids (n = 36) and forbs (n = 48).

Where data were collected at the plot level, the previous studies showed that early defoliation stimulated reproductive biomass in 33%, had no effect in 56%, and reduced it in 11% of the cases. For plot-level studies, intermediately timed defoliation stimulated reproductive biomass in 11% of the cases, had no effect in 36%, and decreased reproductive biomass in 52% of the 85 cases. For late defoliation treatments measured at the whole plot, reproductive biomass was stimulated in only 8% of the cases, was unaffected in 21%, and reduced in 71% of the 71 cases. In all, over half the studies that measured the effects of defoliation on reproductive biomass per unit area reported either no effect (37%) or a stimulatory effect (16%) of defoliation (Table 5). This was the case for both graminoids and non-graminoid species, but a lower percentage of non-graminoids increased reproductive biomass after defoliation (11 compared to 18%; Table 5). For whole-plot studies, similar percentages of negative effects from defoliation were reported for graminoids (47%) and non-graminoids (45%).

For individual plants, of the 19 studies that included an early defoliation treatment, 16% reported an increase in reproductive biomass, 42% reported no effect, and 42% reported a negative effect. For both studies in which the timing of seed removal was controlled, early removal increased seed production. For the 122 individual plant studies with a single defoliation of intermediate timing, reproductive biomass increased in 10%, was unaffected in 39%, and decreased in 51% cases. In the 29 individual plant studies that included a late defoliation treatment, reproductive biomass was not stimulated in any case, but was unaffected in 17%, and negatively affected in 83%. Compared to whole-plot studies, a greater percentage of individual plant studies reported negative effects of defoliation (55 compared to 47%). Graminoids and non-graminoids from individual plant studies contributed roughly equally to this result; 55 and 56% of the graminoid and non-graminoid studies, respectively, reported a decrease subsequent to defoliation.

To compare the effects of defoliation on reproductive biomass of cool-season with warm-season grasses, graminoid studies that reported the effects of clipping or grazing were grouped according to photosynthetic pathway (C_3 or C_4). The percentage of studies reporting positive, negative, and no effects were determined for whole-plot studies, individual plant studies, and the 2 combined (Table 6). When timing treatments and study scales were combined, defoliation reduced reproductive biomass of C_4 grasses in more cases than for C_3 grasses (67% compared to 47%). Reproductive biomass of C_4 grasses was rarely stimulated by defoliation (2%

Table 5. Results from 118 studies that measured the effect of defoliation on vegetation reproductive biomass or number of reproductive structures. Table values represent the percentage of n studies that report positive (+), no (0), or negative (–) effects of defoliation on the production of reproductive biomass or number or reproductive structures. Studies are separated by early, intermediate, and late defoliation treatments and grouped hierarchically by study scale (whole-plot or individual plant), vegetation type (graminoids or non-graminoids), and type of defoliation (see text). Totals in the last column are the combined results of early, intermediate, and late treatments. See Appendix 1 for the studies used to generate table values.

	Timing															
	Early				Intermediate				Late				Total			
	n	–	0	+	n	–	0	+	n	–	0	+	n	–	0	+
								(%)								
Whole-plot	64	11	56	33	88	52	36	11	73	71	21	8	225	47	37	16
Graminoids	47	11	49	40	69	51	38	12	54	74	19	7	170	47	35	18
Grazing	12	17	50	33	15	67	20	13	14	57	29	14	41	49	32	20
Cutting	35	9	49	43	54	46	43	11	40	80	15	5	129	47	36	18
Non-graminoids	17	12	76	12	19	58	32	11	19	63	26	11	55	45	44	11
Grazing	5	40	60	0	7	43	29	29	7	29	43	29	19	37	42	21
Cutting	12	0	83	17	12	67	33	0	12	83	17	0	36	50	44	6
Individual plant	19	42	42	16	122	51	39	10	29	83	17	0	170	55	36	9
Graminoids	13	46	31	23	62	45	50	5	22	86	14	0	97	55	39	6
Grazing					6	0	83	17					6	0	83	17
Clipping	11	55	36	9	41	56	41	2	20	90	10	0	72	65	32	3
Transplants					13	38	62	0					13	38	62	0
Seed removal	2	0	0	100	2	50	0	50	2	50	50	0	6	33	17	50
Non-graminoids	6	33	67	0	60	57	28	15	7	71	29	0	73	56	32	12
Insects	1	0	100	0	16	69	19	13	1	100	0	0	18	67	22	11
Grazers					12	25	50	25					12	25	50	25
Clipping	5	40	60	0	32	63	25	13	6	67	33	0	43	60	30	9

Table 6. Results from 38 whole-plot and 27 individual plant studies that measured the effect of grazing or clipping (transplants and seed removals are not included) on reproductive biomass for C_3 and C_4 graminiods. Table values represent the percentage of n studies that report positive (+), no (0), or negative (–) effects of defoliation on the production of reproductive biomass or number or reproductive structures. Studies are separated by early, intermediate, and late defoliation treatments. All studies represent the result of whole-plot and individual plant studies combined. Totals in the last column are percentages for the sum of early, intermediate, and late treatments. See Appendix 1 for the studies used to generate table values.

	Timing															
	Early				Intermediate				Late				Total			
	n	–	0	+	n	–	0	+	n	–	0	+	n	–	0	+
	(%)															
C_3 grasses																
All studies	50	14	48	38	77	49	40	10	54	74	19	7	181	47	36	17
Whole-plot	46	11	50	39	56	54	34	13	48	71	21	8	150	46	35	19
Individual plant	4	50	25	2	21	38	57	5	6	100	0	0	31	52	42	6
C_4 grasses																
All studies	8	50	38	13	35	60	40	0	15	93	7	0	58	67	31	2
Whole-plot	1	0	0	100	11	45	55	0	4	100	0	0	16	56	38	6
Individual plant	7	57	43	0	24	67	33	0	11	91	9	0	42	71	29	0

of the cases), while a moderate percentage of studies reported some stimulatory effect for C_3 grasses (17% of the cases). For both study scales, the results of summing early, intermediate, and late defoliation treatments produced similar trends; C_4 grasses respond more negatively to defoliation than do C_3 grasses. Individual plant studies of C_4 grasses reported more negative responses (71%) compared to C_3 grasses (52%), and out of 42 cases no stimulatory effects were reported for the C_4 species. Likewise, at the whole-plot scale, 19% of C_3 studies reported an increase in reproductive biomass subsequent to defoliation, while stimulatory effects were reported in only 6% of the C_4 studies. This was a result of the strong negative response of C_4 grasses to intermediate and late defoliation treatments, which was reported in 60% and 93% of the studies respectively (Table 6).

In general, stimulation of reproductive biomass in individual plant studies was usually associated with morphological changes such as increased number of branches or basal rosettes leading to greater flower and fruit production without an associated decrease in seed number, weight, or viability. Stimulatory effects of defoliation were not reported in any of the studies that compared the response of grasses with variable grazing history. Historically grazed grass populations had equal or lower reproductive to vegetative biomass ratios than conspecifics from historically ungrazed sites.

Discussion

Early season grazing on the northern winter range of Yellowstone Park more than doubled the number of reproductive tillers per unit area across sites, despite similar aboveground biomass and vegetation cover inside and outside of exclosures at peak biomass. Correspondingly, the inflorescence mass per unit area was over twice as great in grazed compared with ungrazed plots. Stimulation of community level reproductive biomass by grazing is consistent with reports from agricultural systems. However, our results from Yellowstone are inconsistent with findings from other natural grassland systems (McNaughton 1979, O'Connor and Pickett 1992), where grazers directly consumed seed heads and reduce seed production. In the northern winter range of Yellowstone, migratory herds of elk and bison graze newly emerging vegetation early in the growing season, usually in April and May, then move off the sites. The seasonal pattern of grazing in Yellowstone's northern winter range matches management strategies developed to reduce removal of reproductive meristematic tissue and increase seed yield in agricultural systems (Young et al. 1996).

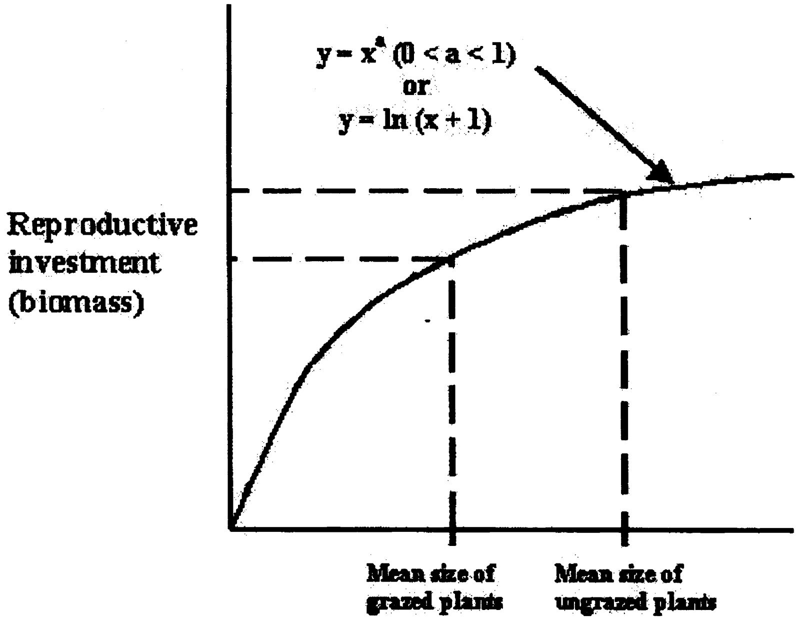

Fig. 1. The proposed function between mean plant size and investment in reproductive biomass for grasses in Yellowstone National Park. The saturating curve, along with evidence that mean plant size is smaller and density greater in grazed Yellowstone grassland, may explain the greater proportional reproductive biomass m^{-2} identified in our grazed plots.

Grazer mediated changes in plant species composition, implicated in other seed production or seed bank studies (Jones 1968, Kinucan and Smeins 1992, O'Connor and Pickett 1992, Willms and Quinton 1995), are not likely to explain the results from Yellowstone grasslands. First, species similarity measures between treatments were high. In addition, species found in different proportions inside and outside of exclosures at 1 site were often found at inverse proportions at another site; this lowered percentage similarity between treatments but also argues strongly against differences in reproductive biomass across exclosures resulting from an artifact of species compositional differences. Finally, prior studies have found no differences in species composition between communities inside and outside of the Yellowstone exclosures (Houston 1982, Coughenour 1991, Singer 1995, Stolgren et al. 1999, Augustine and Frank 2001).

The increase in reproductive tiller density by grazers is consistent with the phenomenon of herbivory increasing vegetative tillering in a number of grasses (Jewiss 1972, Detling and Painter 1983, Belsky 1986b). However, reductions in floret number per tiller in grazed plots suggests that defoliation may have an inhibitory effect per plant, but a stimulatory effect when plants are measured per unit area. A potential explanation might be the general relationship between reproductive output and plant size and the effects of grazers on reducing plant size and increasing plant density. In addition to this study, large herbivores reduced bunchgrass basal size in several grasslands (Hickey 1961, Butler and Briske 1988, Pfeiffer and Hartnett 1995). Thus, if a positive saturating function of reproductive investment on plant size exists for Yellowstone grasses (Fig. 1), such as has been described for plants elsewhere (Crawley 1983), smaller plants that result from grazing might invest relatively more in reproductive growth. In addition to influencing plant size, 2 lines of evidence suggest that plant density differed between grazed and ungrazed plots. First, grass tiller density was greater in grazed plots for the 3 sites measured. Second, that biomass was not statistically different inside and outside exclosures, but grazed plants were smaller, further suggests plant density was greater in grazed plots. Therefore, the stimulation of reproductive biomass observed in plots in our study may be the result of grazers promoting more dense populations of smaller individuals that allocated proportionally more to reproduction than ungrazed grasses.

Thus, the stimulation of reproductive biomass subsequent to defoliation may result from 2 different mechanisms, which may be identifiable at different scales. 1) Reproductive biomass per individual is increased because plants allocate more biomass to reproduction after defoliation; this mechanism could be identified in studies of individual plants. 2) Reproductive biomass per individual is reduced or unaffected, but since plants are smaller and more dense per unit area, community-level reproductive biomass is greater subsequent to defoliation; this mechanism could be identified in whole-plot studies. Both mechanisms will be influenced by the phenological stage of vegetation at the time of defoliation, but the latter less so because a community-level stimulatory effect can result even if reproduction per individual is decreased. In addition, precipitation, and more importantly soil water, will influence phenological stage and the capacity for regrowth after grazing.

The literature clearly demonstrates that the timing of grazing is of critical importance to the production of reproductive biomass in many of the studies that we reviewed. The grazing of leaf material before internode expansion does not result in the removal of apical meristems and thus regrowth can ensue if soil water is adequate, whereas grazing after internode elongation may remove terminal meristems of developing floral buds (Jewiss 1972). Thus, timing and intensity of grazing in natural systems determines the outcome of grazing on reproductive tiller number and seed yield (Young et al. 1996, O'Connor and Pickett 1992). Hebblethwaite and Clemence (1983) reported that if grazing of perennial ryegrass (*Lolium perenne* L.) ceased before spiklet initiation, seed yield was not affected; if grazing continued after the initiation of spiklets, seed yield was greatly depressed. Similar results have been reported for tall fescue (*Festuca arundinacea* Schreb.) (Watson and Watson 1982), spring oats (*Avena* sp.) (Morris and Gardner 1958, Gardner and Wiggins 1960) and wheat (*Triticum aestivum* L.) (Finnell 1929, Aldrich 1959, Winter and Thompson 1987).

In addition to the importance of phenological stage controlling the response of plants to grazing, environmental factors may interact with timing of herbivory. Microclimatic conditions conducive for regrowth often vary over the growing season. For example, in western U.S. rangelands, where soil water typically declines throughout the growing season, plants may not be able to recover if grazed late in the season when precipitation has little influence on regowth (Sneva 1977). Thus, phenology and growth conditions probably both play roles in the allocation to reproductive tissue by grazed plants.

Whether or not smaller, denser plants, that allocate relatively more to reproduction, explain increases in reproductive biomass in the previous studies is not known. Herbivory increases plant density in some natural communities (i.e. Crawley 1983), yet the generality of this response has not emerged from the literature. Alternatively, defoliation may increase reproductive biomass per plant, without an associated change in plant density. For example, Young et al. (1996) reported that grazing stimulated reproductive tiller production per unit area with no difference in plant density between grazed and control plots, suggesting that it was the phenological stage at the time of defoliation that was more important than density in their study. Additionally, results from agricultural studies usually reflect short-term grazing treatments rather than the longer time periods that may be necessary to produce differences in plant density. Thus, in studies that measure the influence of short-term defoliation, on the scale of seasons, the phenological stage of vegetation is likely more important than population level effects such as plant density. The results from studies that measured reproductive biomass at either of 2 scales, whole-plot and individual plant level, are complex but seem to suggest whole plot studies report stimulatory effects more often than individual studies. This suggests population level effects that lead to greater reproductive biomass per area, such as increased densities of smaller individuals with higher fecundity, might be implicated in at least some cases. Another possibility is that plant defoliation is less severe in whole-plot studies than in individual plant studies. Most of the individual plant studies reviewed were clipped as opposed to grazed, and previous research suggests that clipping to simulate grazing results in more severe defoliation than does actual grazing (Hart and Balla 1982).

Our review of the literature suggests that, in terms of sexually reproductive biomass, C_4 plants exhibit a more negative response to defoliation than do C_3 plants. This finding is intriguing because, in general, C_4 plants are more grazing tolerant than their C_3 counterparts (Heckathorn et al. 1999). It is not known why C_4 plants are more grazing tolerant than C_3 plants, or why defoliation suppresses sexually reproductive tissues during regrowth, however, physiological differences and different environmental conditions may be responsible. For example, C_4 plants have higher water and nutrient use efficiencies and maximum rates of photosynthesis, which may favor reallocation of biomass for vegetative versus sexual reproduction (Heckathorn et al. 1999). On the other hand, C_3 and C_4 plants vary in their distribution across rainfall and temperature gradients (e.g. Epstein et al. 1997 for the U.S. Great Plains). Growth conditions of C_4 may, on average, favor greater allocation to leaves and roots after defoliation and less to sexual reproduction. However, the relative importance of physiology and environment in producing different responses of C_3 and C_4 grasses to defoliation requires specific testing.

Our study was designed to address both community level and individual plant level effect of grazing on seed production of grasslands in Yellowstone National Park. We found that early season grazing leads to greater numbers of reproductive tillers per unit area and did not decrease seed yield per unit area. We suggest that grazing in Yellowstone's Northern winter range maintains populations of smaller, denser grasses that, if grazed early, produce (per unit area) more reproductive tillers, equal numbers of seed, and more reproductive biomass than where grazers are absent. These results, together with our literature review, suggest that the timing and organizational scale (individual versus community) of the plant trait measured may differentially influence interpretation of how herbivory influences seed production. Thus, grazing may reduce individual plant fitness, but need not reduce the reproductive capacity of plant communities. However, to answer this, one must assess whether or not grazing affects seed viability in addition to numerical production as was done in our study. There is evidence that defoliation history does not influence seed viability (Orodho et al. 1998), but whether seeds produced by grazed and ungrazed Yellowstone grasses exhibit similar viability is not known. We suggest that early spring defoliation in Yellowstone National Park's northern winter range has played a role in the persistence of grazed plant communities by maintaining community level seed production. Future studies that emphasize the individual versus per unit area effects of grazing on reproductive output may aid in understanding community organization and the sustainability of grazed ecosystems.

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Appendix 1. Defoliation impacts on the production of reproductive biomass, from 118 published sources, reported as positive (+), negative (–), or no effect (0). Results are separated by the timing of defoliation (early, intermediate, or late) when possible. Study species are grouped hierarchically by study scale (whole plot or individual plant), vegetation type (graminods, non-graminoids, or seed bank study), method of defoliation (cutting, grazing, transplant of previously grazed species, or removal of flowers or seeds), and identity of herbivore (ungulate or insect). References and notes are identified with superscripts. Study types are field (F), laboratory (L), and garden (G), which includes planted agricultural fields.

Species	Plant Functional Type	Study Type	Timing			Citation
			Early	Intermediate	Late	
Whole-plot studies						
Graminiods						
Grazing						
Agropyron spicatum (Prush) Scribn. & Smith	C_3 grass	F		–		Hanson and Stoddart 1941
Andropogon greenwayi Napp.	C_4 grass	F		–		Belsky 1986c
Avena sp[1]	C_3 grass	G	0		0 (+)	Sprauge1954
Avena sp.[2]	C_3 grass	G		–		Washko 1947
Festuca idahoensis Elmer	C_3 grass	F		0		Olson et al. 1997
Hordeum sp.[2]	C_3 grass	G		–		Washko 1947
Lolium sp.[3]	C_3 grass	G		– (+)		Brown 1980
Lolium multiflorum Lam.[4]	C_3 grass	G	+ (0)	+ (0)	+ (0)	Young et al. 1996
Lolium multiflorum Lam.	C_3 grass	G	–			Herron 1976
Lolium perenne L.	C_3 grass	G	0	0		Hebblethwaite and Clemence 1983
Lolium perenne L.[5]	C_3 grass	G	0		0 (–)	Roberts 1958
Phleum sp.[5]	C_3 grass	G	0		– (0)	Roberts 1958
Secale sp.[1]	C_3 grass	G	+		– (–)	Sprauge 1954
Secale sp.[2]	C_3 grass	G		–		Washko 1947
Triticum aestivum L.[6]	C_3 grass	G	–	–	–	Pumphrey 1970
Triticum aestivum L.	C_3 grass	G	+			Sharrow and Motazedian 1987
Triticum aestivum L.[1]	C_3 grass	G	+		– (–)	Sprauge 1954
Triticum aestivum L.[2]	C_3 grass	G	–			Washko 1947
Triticum aestivum L.[7]	C_3 grass	G	0	–	–	Winter and Thompson 1987
Triticum dicoccoides	C_3 grass	G		0 (+)	– (–)	Noy-Meir and Briske 2002
Unspecified grasses	C4 grass	F		–		McNaughton 1979
Cutting						
Agropyron spicatum (Prush) Scribn. & Smith	C_3 grass	F	–	–	–	Blaisdell and Pechanec 1949

Species	Plant Functional Type	Study Type	Timing			Citation
			Early	Intermediate	Late	
Agropyron trachycaulum	C_3 grass	F	0	+	0	Mueggler 1967
Andropogon gayanus Kunth.	C_4 grass	F	+			Andrade and Thomas 1981
Andropogon gerardi Vit.	C_4 grass	G		0		Neiland and Curtis 1956
Andropogon scoparius Michx.	C_4 grass	G		0		Neiland and Curtis 1956
Avena sp.[10]	C_3 grass	G	0 (0)	– (0)	– (–)	Morris and Gardner 1958
Avena sp.[11]	C_3 grass	G		– (–)		Thakur and Shands 1954
Avena sp.	C_3 grass	G			–	Gardner and Wiggans 1960
Bouteloua curtipendula Michx.	C_4 grass	G		0		Neiland and Curtis 1956
Bromus marginatus	C_3 grass	F	+	+	+	Mueggler 1967
Bromus mollis[12]	C_3 grass	G	+	0	–	Laude et al. 1957
Bromus ruben[12]	C_3 grass	G	+	0	–	Laude et al. 1957
Dactylis glomerata	C_3 grass	G	0	–	–	Roberts 1965
Elymus canadensis L.	C_3 grass	G		0		Neiland and Curtis 1956
Festuca arundinacea Schreb.[13]	C_3 grass	F	+ (0)			Kroth et al. 1977
Festuca arundinacea Schreb.[14]	C_3 grass	G	0	0 (–)	–	Watson and Watson 1982
Festuca elatior	C_3 grass	G	0	–	–	Roberts 1965
Festuca idahoensis Elmer	C_3 grass	F	–	–	–	Mueggler 1967
Hordeum sp.[15]	C_3 grass	G	+	–	–	Hubbard and Harper 1949
Hordeum sp.[11]	C_3 grass	G		– (–)		Thakur and Shands 1954
Hordeum murinum L.	C_3 grass	F	0	–	–	El-Shatnawi et al. 1999
Hordeum vulgare L. emend Lam.	C_3 gras	G	+	0		Day et al. 1968
Lolium multiflorum Lam.[16]	C_3 grass	G	0	– (0)	–	Bean et al. 1979
Lolium perenne L.	C_3 gras	G	0	–	–	Hebblethwaite and Clemence 1983
Lolium perenne L.	C_3 grass	G	0	–	–	Roberts 1965
Panicum virgatum L.	C_4 grass	G		0		Neiland and Curtis 1956
Panicum virgatum L.[17]	C_4 grass	G		–	–	George et al. 1990
Panicum virgatum L.[18]	C_4 grass	G		0 (–)	– (–)	Brejda et al. 1994
Pennisetum hybrid[19]	C_4 grass	G		0	–	Diz et al. 1995
Phleum sp.	C_3 grass	G	0	–	–	Roberts 1965
Poa pratensis L.[20]	C_3 grass	G		0 (0)	0 (0)	Ahlgren 1938
Poa pratensis L.	C_3 grass	G	+ (+)	0 (+)	0 (0)	Evans 1975
Secale sp.[15]	C_3 grass	G	+	–	–	Hubbard and Harper 1949
Secale sp.[10]	C_3 grass	G	+ (+)	0 (+)	– (0)	Morris and Gardner 1958
Sorghastrum nutans (L.) Nash	C_4 grass	G		–		Neiland and Curtis 1956
Triticum aestivum L.[21]	C_3 grass	G	+	0	–	Cutler et al. 1949
Triticum aestivum L.[15]	C_3 grass	G	+	–	–	Hubbard and Harper 1949
Triticum aestivum L.[10]	C_3 grass	G	0 (0)	– (0)	– (–)	Morris and Gardner 1958
Triticum aestivum L.[10]	C_3 grass	G		0 (0)		Thakur and Shands 1954
Triticum aestivum L.[7]	C_3 grass	G	–	–	–	Pumphrey 1970
Triticum aestivum L.[22]	C_3 grass	G	+ (0)	0 (+)	– (+)	Miller et al. 1993
Triticosecale hybrid[22]	C_3 grass	G	0 (0)	– (–)	– (–)	Miller et al. 1993
Non-graminiods						
Grazing						
Medicago murex Zodiac	leguminous forb	G	0	–	0	Conlan et al. 1994
Ornitopus compressus L.	leguminous forb	G	–	–	–	Conlan et al. 1994
Trifolium subterraneum L.[23]	leguminous forb	G		+	0 (+)	Steiner and Grabe 1986
Trifolium subterraneum L.[24]	leguminous forb	G	0	+	+	Conlan et al. 1994
Trifolium subterraneum L.[24]	leguminous forb	G	0	0	0	Conlan et al. 1994
Trifolium subterraneum L.[24]	leguminous forb	G	–	–	–	Conlan et al. 1994
Trillium sp.	perennial forb	F		–		Augustine and Frelich 1998
Cutting						
Aster integrifolius	perennial forb	F	0	–	–	Mueggler 1967
Balsamorhiza sagitta[9] (Prush) Nutt.	perennial forb	F	0	–	–	Blaisdell and Pechanec 1949
Glycine max (L.) Merr.[25]	leguminous forb	G		0 (–)	– (–)	Begum and Eden 1965
Glycine max (L.) Merr.[26]	leguminous forb	G	+ (+)		0 (–)	Pickle and Caviness 1984
Glycine max (L.) Merr.[26]	leguminous forb	G	0 (0)	0 (–)		Teigen and Vorst 1975
Glycine max (L.) Merr.	leguminous forb	G	0	–	–	Thomas et al. 1974
Potentilla gracilis	perennial forb	F	0	–	–	Mueggler 1967
Ricinus communis L.[27]	ann. or per. forb	G	0 (0)	0 (0)	0 (–)	Kittock and Williams 1967
Trifolium subterraneum L.	leguminous forb	G	0	–	–	Collins et al. 1983
Trifolium incarnatum L.	leguminous forb	G	0	–	–	Knight and Hollowell 1962

Species	Plant Functional Type	Study Type	Timing			Citation
			Early	Intermediate	Late	
Seed banks						
Grazing						
Grasses and forbs^{28}		F		0		Kinucan and Smeins 1992
Grasses and forbs^{28}		F		+		Willms and Quinton 1995
Individual Plant Studies						
Graminiods						
Grazing						
Andropogon gerardii Vit.	C_4 grass	F		0		Vinton and Hartnett 1992
Festuca idahoensis Elmer	C_3 grass	F		0		Olson et al. 1997
Lolium multiflorum Lam.	C_3 grass	G		+		Herron 1976
Oryzopsis hymenoides (Roem. & Schult.) Ricker	C_3 grass	F		0		Trlica and Orodho 1989
Oryzopsis hymenoides (Roem. & Schult.) Ricker	C_3 grass	F		0		Orodho et al. 1998
Panicum virgatum L.	C_4 grass	F		0		Vinton and Hartnett 1992
Clipping or Defoliation						
Agropyron desertorum (Fisch. Ex Link) Schult.	C_3 grass	F		–		Caldwell et al. 1981
Agropyron spicatum (Prush) Scribn. & Smith	C_3 grass	F		–		Caldwell et al. 1981
Agropyron spicatum (Prush) Scribn. & Smith	C_3 grass	F	–		–	Mueggler 1972
Agropyron spicatum (Prush) Scribn. & Smith	C_3 grass	F	0		–	Mueggler 1975
Agropyron spicatum (Prush) Scribn. & Smith	C_3 grass	F	–	–		McLean and Wikeem 1985
Andropogon gerardii Vit.	C_4 grass	L		–		Hartnett 1989
Andropogon gerardii Vit.	C_4 grass	L		–		Heckathorn and Delucia 1996
Andropogon semiberbis (Nees) Kunth.	C_4 gras	G		–		Silva and Raventos 1999
Aristida armata^{29}	C_4 grass	L			–	Brown 1985
Asrebla lappacea^{29}	C_4 grass	L			–	Brown 1985
Bouteloua curtipendula Michx.	C_4 grass	F	0	–	–	Sims et al. 1971
Bromis inermis Leyss	C_3 grass	F	0	0	–	Harrison and Romo 1994
Cenchrus ciliaris^{29}	C_4 grass	L			–	Brown 1985
Cynodon dactylon	C4 grass	L	0			Van Auken 1994
Digitaria ammophila^{29}	C_4 grass	L			–	Brown 1985
Elymus lanceolatus^{30}	C_3 grass	F		–		Jones and Nielson 1993
Elymus lanceolatus^{30}	C_3 grass	F		– (0)		Jones and Nielson 1993
Elymus lanceolatus^{30}	C_3 grass	F		– (0)		Jones and Nielson 1993
Elymus lanceolatus^{30}	C_3 grass			0		Jones and Nielson 1993
Elymus lanceolatus^{30}	C_3 grass			0		Jones and Nielson 1993
Eriophorum vaginatum L.^{31}	C_3 sedge	F	+	0	–	Archer and Tieszen 1983
Eulalia trispicata^{32}	C_4 grass	L	– (–)	– (0)	– (–)	Pemadasa and Amarasinghe 1982
Festuca idahoensis Elmer	C_3 grass	F		0	–	Mueggler 1975
Heteropogon contortus^{33} (L.) P. Beauv. ex Roem. & Schult.	C_4 grass	L		0 (0)		Goergen and Daehler 2001
Kyllinga nervosa Steud.	C_4 sedge	L		–		McNaughton et al. 1983
Kyllinga nervosa Stued.	C_4 sedge	L		–		Ruess et al. 1983
Luzula arcuata^{34} Swartz ssp. *confusa* (Lindeb.) Blytt	C_3 sedge	L		0 (–)		Brathen et al. 2000
Panicum virgatum (L.) var. Caddo	C_4 grass	F	0	–	–	Sims et al. 1971
Panicum virgatum L.	C_4 grass	L		–		Hartnett 1989
Panicum virgatum L.^{35}	C_4 grass	L		+		Hartnett 1989
Pennisetum polystachyon^{32}	C_4 grass	L	– (0)	– (0)	– (0)	Pemadasa and Amarasinghe 1982
Pennisetum setaceum^{33} (Forssk.) Chiov	C_4 grass	L		0 (–)		Goergen and Daehler 2001
Schizachyrium scoparium^{36} (Michx.) Nash	C_4 grass	G		–		Wallace 1987
Schizachyrium scoparium (Michx.) Nash	C_4 grass	L		–		Heckathorn and Delucia 1996
Spartina pectina Link	C_4 grass	L		–		Heckathorn and Delucia 1996
Themeda triandra	C_4 grass	F	–		–	Tainton and Booysen 1965

Species	Plant Functional Type	Study Type	Timing			Citation
			Early	Intermediate	Late	
Thyridolepis mitchelliana[29]	C_4 grass	L			–	Brown 1985
Triticum aestivum L	C_3 grass	G	–		–	Simmons et al. 1982
Triticum dicoccoides[37]	C_3 grass	G		0 (0)	– (0)	Noy-Meir and Briske 2002
Trachypogon plumosus (Humb. & Bonpl.) Nees	C_4 grass	G		–		Silva and Raventos 1999
Transplants with Different Grazing Histories						
Agropyron smithii Rydb.	C_3 gras	L		–		Painter et al. 1989
Andropogon gerardii Vit.	C_4 grass	L		0		Painter et al. 1993
Bouteloua curtipendula var. *caespitosa* Gould & Kapadia	C_4 grass	L		–		Smith et al. 2000
Bouteloua gracilis (H. B. K.) Griffiths	C_4 grass	L		–		Jaramillo and Detling 1988
Bouteloua gracilis (H. B. K.) Griffiths	C_4 grass	L		–		Painter et al. 1989
Bouteloua gracilis (H. B. K.) Griffiths	C_4 grass	L		0		Painter et al. 1993
Danthonia linkii Kunth.	C_3 grass	L		0		Scott and Whaley 1984
Danthonia racemosa R. Br.	C_3 grass	L		0		Scott and Whaley 1984
Danthonia richardsonii Cashmore	C_3 grass	L		0		Scott and Whaley 1984
Oryzopsis hymenoides (Roem. & Schult.) Ricker	C_3 grass	F		0		Trlica and Orodho 1989
Oryzopsis hymenoides[38] (Roem. & Schult.) Ricker	C_3 grass	F		0 (–)		Orodho et al. 1998
Schizachyrium scoparium Michx.	C_4 grass	L		0		Painter et al. 1993
Seed Removal						
Triticum aestivum L.	C_3 grass	G	+		0	Simmons et al. 1982
Zea mays L.	C_4 grass	G		+		Dyer 1975
Zea mays L.[39]	C_4 grass	G	+	–	–	Woronecki et al. 1980
Non-graminiods						
Natural Defoliation						
Insects						
Allium porrum L.[39]	biennial forb	G	0	+	–	Boscher 1979
Aristolochia reticulata	perennial forb	F		–		Rausher and Feeny 1980
Cardamine cordifolia	perennial forb	F		–		Louda 1984
Chelone sp.	perennial forb	F		–		Stamp 1984
Jurinea mollis Ascherson[40]	perennial forb	F		+		Inouye 1982
Mirabilis hirsuta (Prush) MacM.	perennial forb	F		–		Kinsman and Platt 1984
Pastinaca sativa L.[41]	biennial forb	F		0 (–)		Hendrix 1979
Quercus robar L.	tree	F		–		Crawley 1985
Rhus glabra L.	perennial shrub	F		–		Strauss 1991
Rosa nutkana Presl.	perennial shrub	F		–		Myers 1981
Rumex crispus L.	perennial forb	F		0		Bentley et al. 1980
Rumex obtusifolius L.	perennial forb	F		–		Bentley et al. 1980
Salix lasiolepis	perennial shrub	G		–		Sacchi et al. 1988
Solidago altissima L[42]	perennial forb	L		– (0)		Meyer and Root 1993
Grazers or Browsers						
Baptista braceata[43] Muhl. ex Ell. var. glabrescens (Larisey) Isley	leguminous forb	F		0 (0)		Damhoureyeh and Hartnett 1997
Echium plantagineum L.	annual forb	F		–		Smyth et al. 1997
Jurinea mollis Ascherson	perennial forb	F		–		Inouye 1982
Pteronia empetrifolia D. C.	perennial shrub	F		–		Milton 1995
Rhus glabra L.[44]	perennial shrub	F		+		Strauss 1991
Salvia azurea Lam.[43]	perennial forb	F		0 (0)		Damhoureyeh and Hartnett 1997
Solidago missouriensis Nutt.[43]	perennial forb	F		+ (0)		Damhoureyeh and Hartnett 1997
Veronia baldwinii Torr.[43]	perennial forb	F		0 (+)		Damhoureyeh and Hartnett 1997
Clipping or Defoliation						
Acacia farnesiana L.	tree	F		–		Rockwood 1973
Albutilon theophrasti Medic.[45]	annual forb	L		0 (–)		Lee and Bazzaz 1980
Anthyllis vulneraria L.[46]	leguminous forb	L		0 (–)		Bastrenta and Belhassen 1992
Aralia nudicaulis L.	perennial forb	F		–		Edwards 1985

Species	Plant Functional Type	Study Type	Timing Early	 Intermediate	 Late	Citation
Aristolochia reticulata Nutt.	perennial forb	L		0		Fowler and Rausher 1985
Astrocaryum mexicanum[47] Liebm.	understory palm	F		– (+)		Mendoza et al. 1987
Bauhinia ungulata L.	tree	F		–		Rockwood 1973
Brassica napus L.[48]	annual forb	L			0 (–)	Pechan and Morgan 1985
Catalpa speciosa (Warder ex Barney) Engelm.	tree	F		–		Stephenson 1980
Cochlospermum vitifolium (Willd.) Spreng.	tree	F		–		Rockwood 1973
Crescentia alata H. B. K.	tree	F		–		Rockwood 1973
Desmanthus virgatus[49]	leguminous shrub	L	–			Muir and Pitman 1991
Desmodium heterocarpon[49]	leguminous shrub	L	–			Muir and Pitman 1991
Epilobium angustifolium L.[50]	perennial forb	L	0		– (–)	Michaud 1991
Erythroxylum havanense[55]	proleptic shrub	F		0 (–)		Dominguez and Dirzo 1994
Gentianella campestris (L.) Borner	biennial forb	F	0	+	0	Lennartsson et al. 1998
Gliricidia sepium (Jacq.) Steud.	tree	F		–		Rockwood 1973
Indigofera spinosa Forsk.[51]	leguminous shrub	F		– (–)		Keya 1997
Ipomopsis aggregata (Prush) V. Grant	perennial forb	F		+		Paige and Whitham 1987
Ipomopsis arizonica (Greene) Wherry	perennial forb	F	0		–	Maschinski and Whitham 1989
Melampyrum pratense L.[52]	annual forb	F		– (–)		Lehtila and Syrjanen 1995
Melampyrum sylvaticum L.[52]	annual forb	F		+ (–)		Lehtila and Syrjanen 1995
Piper arieianum C. DC.	perennial shrub	F		–		Marquis 1984
Rubus chamaemorus L.[53]	annual forb	F		0 (–)		Agren 1989
Saponaria officinalis L.[54]	perennial forb	F		0 (–)		Lokker and Cavers 1995
Spondias purpurea L.	tree	F		–		Rockwood 1973
Triglochin palustris L.	perennial forb	F		0		Mulder and Ruess 1998
Trillium grandiflorum Michx.	perennial forb	F		0		Lubbers and Lechowicz 1989
Vicia sativa L.	leguminous forb	G		–		Koptur et al. 1996
Flower and Seed Removal						
Melampyrum pratense L.	annual forb	F		0		Lehtila and Syrjanen 1995
Melampyrum sylvaticum L.	annual forb	F		–		Lehtila and Syrjanen 1995

1 – Autumn (early) and spring (late) grazing; spring after fall in parentheses
2 – Spring grazing to March 15 + fall grazing into November
3 – Results for number of fertile tillers in parentheses
4 – Results are for number of fertile tillers with second year in parentheses; no effect of grazing on seed production in either year
5 – Winter (early) and spring (late) grazing; spring after winter in parentheses
6 – Early treatment similar in timing to intermediate treatment in other studies
7 – Severe grazing in all treatments
8 – Results are for plot level biomass, effect on plot level ratio of reproductive:total biomass shown in parentheses; see reference for taxonomic reference.
9 – Severe clipping; fall clipping had no effect
10 – 2x fertilization results shown in parentheses
11 – Early (May) and intermediate (June) clippings are late in comparison to other studies; 2x fertilization in parentheses
12 – Weight of spiklet decreased with clipping date
13 – Increased at 1 site, no effect at another; results are for no N addition
14 – No effect on panicle m^{-2}; spikes panicle^{-1} shown in parentheses
15 – Results shown for moderate intensity; severe cutting decreased seed production in all treatments
16 – Effect on tiller number in parentheses
17 – Their first defoliation treatment (May 30) was intermediate in relation to other defoliation treatments
18 – No effect of intermediate treatment (late may) on reproductive tiller density in year 1, negative effects in year 2 because tiller elongation had begun; seed yields shown in parentheses
19 – Intermediate treatment cut in June and August, late treatment cut in June, August and September
20 – No significant differences, but the author interpreted the continuous increase in total seed biomass of clipped plants as trend towards increased production. Results of fertilization shown in parentheses
21 – Results shown for normal year; all results were negative for drought year
22 – Year 2 in parentheses
23 – Extended grazing in parentheses, includes intermediate and late grazing
24 – Different varieties: T.s. subterraneum cv. Karridale, var. brachycalycinum cv. Clare, var. yanninicum cv. Trikkala
25 – No early treatment applied; parentheses show results of severe defoliation
26 – Results are for 1/4 defoliation; results for 1/2 defoliation are shown in parentheses
27 – Results are for 1/2 defoliation; 3/4 defoliation shown in parentheses; complete defoliation reduced reproductive biomass in all treatments
28 – Associated with species compositional changes
29 – All species had begun to flower when defoliation was initiated
30 – Different hybrids of *Elymus lanceolatus* ssp. *wawawaaiensis* (Scribner & Gould) J.R. Carlson & D. R. Dewey and E. l. ssp. *lanceolatus* (Scribner & J. G. Smith) Gould
31 – Results for different frequency treatments; only fall recovery defoliation increased flowering
32 – Experiment conducted on seedlings; data are for intermediate densities, low density reported in parentheses
33 – Results are for seed production, effect on time to flower reported in parentheses
34 – Data are for flowers plant^{-1} in second season when cut to 6 cm, data for plants cut to 3 cm in parentheses
35 – Grown from ramets rather than seeds

36 – Result is for entire reproductive tiller (stem + flowers); clipped plants did not flower
37 – Effects for survival of reproductive plants after clipping, results for spikelet number per reproductive plant shown in parentheses; see paper for nomenclature
38 – Results of clipping shown in parentheses
39 – Results are for low, moderate, and high intensity treatments
40 – Increased the number of basal rosettes
41 – Results depended on size; results for small plants shown in parentheses
42 – Beetles reduced seed production but aphids (in parentheses) had no effect
43 – Results are for grazing by cattle; results for bison grazing shown in parentheses
44 – Increase in the number of stems capable of reproducing
45 – Results were density dependent; high density treatment shown in parentheses
46 – Results of proportion of plants flowering shown in parentheses
47 – Results of the removal of old portions of leaves shown in parentheses
48 – Defoliation at anthesis; no effect on seed number, negative result on seed pod weight shown in parentheses
49 – Autumn defoliation; controls produced very little reproductive biomass so results are difficult to interpret
50 – Continuous defoliation decreased reproductive biomass
51 – 3 intensities and 2 frequencies all reduced pod output; effects of irrigating shown in parentheses
52 – Results are for clipping branches; results of defoliation given in parentheses
53 – No effects on seed number; effects on seed mass and complete defoliation shown in parentheses
54 – Effects on flower removal shown in parentheses
55 – Result is for 25% defoliation; effects of 100% defoliation shown in parentheses.