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Bluebunch Wheatgrass Response to Spring Defoliation on Foothill Rangeland

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Abstract

Spring elk grazing may reduce forage availability for wildlife or livestock in summer and may harm forage resources on foothill rangeland. We quantified bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] A. Love) response to spring defoliation on foothill rangeland in southwestern Montana. Two experiments were conducted simultaneously on a foothill grassland site and a foothill sagebrush steppe site. Bluebunch wheatgrass plants ($n = 800$) were selected and excluded from wild and domestic ungulates. Clipping treatments were applied in either early spring (mid- to late April) or late spring (mid- to late May), and plants were clipped to 1 of 3 residual heights (3, 6, or 9 cm) for 1, 2, or 3 successive years. Unclipped plants served as controls. Plant response was measured in late June and late July on both sites. April clipping for 3 successive years did not adversely affect bluebunch wheatgrass in June or July ($P > 0.05$) at either site. On foothill grassland, May defoliation to 3 cm for 2 consecutive years reduced leaf height ($P = 0.04$) in July. May defoliation for 3 successive years to 3 or 6 cm reduced plant yield ($P < 0.05$) and leaf height ($P < 0.05$) in June, and May defoliation for 3 successive years to 3 cm reduced leaf height ($P = 0.02$) in July. On foothill sagebrush steppe, 3 successive years of May defoliation to $\leq$9-cm stubble heights decreased leaf height in June ($P < 0.05$). We conclude that foothill rangelands where bluebunch wheatgrass receives moderate or light defoliation (6–9-cm residual stubble heights) in mid- to late May should be limited to no more than 2 successive years of mid- to late May grazing, whereas sites that receive heavy to severe defoliation ($\leq$3-cm residual stubble heights) in mid- to late May should not be grazed for 2 successive years during mid- to late May.

Resumen

El apacentamiento del alce en primavera puede reducir la disponibilidad de forraje en verano para la fauna silvestre o el ganado y dañar los recursos forrajeros de los pastizales de piedemonte. Cuantificamos la respuesta del "Bluebunch wheatgrass" (*Pseudoroegneria spicata* [Pursh] A. Love) a la defoliación en primavera en un pastizal de piedemonte del sudoeste de Montana. Se condujeron dos experimentos en forma simultánea, uno en un sitio de pastizal de piedemonte y el otro en un sitio de estepa de "Sagebrush." Se seleccionaron plantas de "Bluebunch wheatgrass" ($n = 800$) y se excluyeron de los ungulados domésticos y silvestres. Los tratamientos de corte se aplicaron a inicios de primavera (mediados a fines de de abril) o a fines de primavera (mediados a fines de mayo), las plantas fueron cortadas a una de tres alturas (3, 6, o 9 cm) durante uno, dos o tres años consecutivos, las plantas sin corte se utilizaron como control. La respuesta de la planta se midió a fines de junio y julio en ambos sitios. El corte en abril por tres años consecutivos no afectó adversamente al "Bluebunch wheatgrass" ni en junio ni julio en ninguno de los sitios ($P > 0.05$). En el pastizal de piedemonte, la defoliación de mayo a 3 cm por dos años consecutivos redujo la altura de la hoja en julio ($P = 0.04$). La defoliación en mayo por tres años seguidos a 3 o 6 cm redujo el rendimiento de la planta ($P < 0.05$) y la altura de la hoja ($P < 0.05$) en junio y la defoliación en mayo por tres años consecutivos redujo la altura de la hoja ($P = 0.02$) en julio. En la estepa de "Sagebrush," tres años consecutivos de defoliación en mayo a una altura del rastrojo $\leq$ 9 cm disminuyó la altura de la hoja en junio ($P < 0.05$). Concluimos que los pastizales de piedemonte, donde el "Bluebunch wheatgrass" recibe una defoliación de ligera a moderada (6 a 9 cm de altura del rastrojo remanente) a mediados de mayo debe limitarse a no mas de dos años consecutivos de apacentamiento a mediados de mayo, mientras que sitios que reciben defoliaciones de moderado a fuerte ($\leq$ 3 cm de altura del rastrojo residual) a mediados o fines de mayo no deben ser apacentados por dos años seguidos de mediados a fines de mayo.

Key Words: clipping, defoliation response, elk, grazing management, herbivory, overcompensation

INTRODUCTION

Wild and domestic ungulates on rangelands often consume similar diets and utilize similar portions of the landscape. This is particularly true on Rocky Mountain foothill rangeland, where diets and feeding sites of elk (*Cervus elaphus nelsoni*) in spring overlap greatly with those of cattle (*Bos taurus*) in summer (Stevens 1966; Berg and Hudson 1982; Vavra et al. 1989; Ngugi et al. 1992; Torstenson et al. 2006). For example, elk in spring and cattle in summer exhibited 61% foraging niche overlap in a recent study on foothill rangeland in northwestern Wyoming (Torstenson et al. 2006). In that study, elk in spring and cattle in summer consumed graminoid-dominated diets (72% and 91% of their diets, respectively),

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which is similar to the results found in other studies on foothill and mountain rangeland in the northern Rocky Mountains (Stevens 1966; Miller and Kreuger 1976; McLean and Willms 1977; Skovlin and Vavra 1979; Kasworm et al. 1984; Ngugi et al. 1992).

Elk use of seasonal, foothill rangeland is heavily influenced by environmental factors. Elk move to areas of minimal snow depth in winter and spring by following receding snow lines to utilize accessible forage (Nelson and Leege 1982a; Skovlin 1982; Powell et al. 1986). Therefore, distribution of elk feeding sites in spring parallels snowmelt patterns. The proportion of the landscape that is free of snow coupled with the number of elk present determines the intensity of grazing on a site. Elk prefer southern to southwestern slopes because these slopes are the first to become free of snow (Nelson and Leege 1982a; Skovlin et al. 2002), which results in consistent annual spring utilization of forage by elk on exposed, southerly slopes at a time when elk diets are dominated by graminoids (Stevens 1966; Mackie 1970; Nelson and Leege 1982b; Ngugi et al. 1992; Torstenson et al. 2006). The same foothill rangeland sites grazed by elk in spring are also critical habitat for cattle grazing in summer. Use of foothill rangeland in summer by domestic ungulates is dictated by management decisions made by ranchers and resource managers and often needs to be adjusted in areas where wild ungulates occupy critical cattle summer range in spring.

Bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] A. Love) is a dominant forage plant throughout foothill rangeland of the northern Rocky Mountains (Mueggler and Stewart 1980). Grazing bluebunch wheatgrass on foothill rangeland in spring by elk may adversely affect bluebunch wheatgrass leaf height in summer (Payne 1959; McLean and Wikeem 1985), reproductive culm production (McLean and Wikeem 1985), and forage availability for cattle and other ungulates in summer (Blaisdell and Pechanec 1949; Wilson et al. 1966; Mantz 1993). Early season elk grazing may also delay livestock turnout dates onto summer range, increase annual feeding costs of livestock operations, lower summer grazing capacities for cattle and other ungulates, and decrease ungulate growth and reproductive success (Salter and Hudson 1980; Hobbs et al. 1996). Ultimately, excessive levels of grazing may threaten the sustainability of the forage resource. The magnitude of the effects of spring grazing depends on the timing, frequency, and intensity of use by ungulates, variations in weather and rate of snowmelt, and the degree of plant recovery before plants are grazed again. Past studies have focused largely on the response of bluebunch wheatgrass to defoliation the following summer, and very few studies have measured responses to spring grazing in the summer of the same year. We report a manipulative experiment designed to examine bluebunch wheatgrass response to spring defoliation on foothill rangeland in summer.

The objectives of this study were to 1) compare the effects of early versus late spring defoliation for a single year on plant yield, average leaf height, and inflorescence production of bluebunch wheatgrass in the summer on foothill rangeland and 2) compare the cumulative effects of early versus late spring defoliation for 1, 2, and 3 years on plant yield, average leaf height, and inflorescence production of bluebunch wheatgrass in the summer on foothill rangeland. We hypothesized that defoliation in May would be more deleterious than defoliation in April, and we hypothesized that bluebunch wheatgrass could sustain at least 2 consecutive years of heavy to severe defoliation in spring without causing significant reductions in plant yield, leaf height, or inflorescence production.

METHODS

Study Area

We conducted our study on 2 foothill rangeland sites in southwestern Montana, a foothill grassland site and a foothill sagebrush steppe site. These study sites represented the 2 vegetation types that provide the majority of spring forage for elk in the Rocky Mountain foothills of southwestern Montana. Sites had southerly exposures to match the aspect preferred for spring grazing by elk in the northern Rocky Mountains (Hudson et al. 1976; Willms et al. 1979). These 2 vegetation types also provide the majority of summer forage for domestic cattle grazing foothill rangeland in southwestern Montana. Both sites were located on private land that had historically received light to moderate elk grazing in spring and light to moderate cattle grazing in summer–autumn under a rotational grazing system.

The foothill grassland site was located in Granite County, Montana, approximately 8 km west of Philipsburg, Montana, within the foothills of the John Long Mountains. The study area averages 370 mm of annual precipitation, with 50% occurring as rain from April through July (WRCC 2007). Elevation of the study site is 1 645 m. Soils are classified as deep, Ustic Cryoboralls (Montagne et al. 1982). The site was a *Festuca scabrella/Agropyron spicatum* (MONT) habitat type (Mueggler and Stewart 1980). Vegetation was dominated by rough fescue (*Festuca scabrella* Torr.) and bluebunch wheatgrass, with Idaho fescue (*Festuca idahoensis* Elmer), prairie junegrass (*Koeleria macrantha* [Ledeb.] J.A. Schultes), arrowleaf balsamroot (*Balsamorhiza sagittata* [Pursh] Nutt.), and lupine (*Lupinus* spp. L.) also present.

The foothill sagebrush steppe site was located in Madison County, Montana, approximately 32 km southwest of Alder, Montana, within the foothills of the Ruby Mountains. The study area averages 340 mm of annual precipitation, with 53% occurring as rain from April through July (WRCC 2007). Elevation of the study site is 2 225 m. Soils are classified as shallow to deep, Ustic Cryoboralls (Montagne et al. 1982). The site was an *Artemisia tridentata/Agropyron spicatum* (MONT) habitat type (Mueggler and Stewart 1980). Vegetation was dominated by mountain big sagebrush (*Artemisia tridentata* Nutt. subsp. *vaseyana* [Rybd.] Beetle) and bluebunch wheatgrass, with Idaho fescue, prairie junegrass, Sandberg bluegrass (*Poa secunda* J. Presl), western yarrow (*Achillea millefolium* L. var. *occidentalis* DC.), and lupine also present.

Treatments

We conducted 2 experiments at each study site. Experiment 1 compared the effects of a single year of spring defoliation at 2 timings and 4 intensities on plant yield, leaf height, and inflorescence production of bluebunch wheatgrass plants in the summer. Individual bluebunch wheatgrass plants ($n = 160$/site) with stature and size representative of the corresponding site were tagged for identification and excluded from large animal grazing within a 0.13-ha, barbed-wire exclosure. The 1999 treatment plants were excluded in the autumn of 1998, and the 2001 treatment plants were excluded in the autumn of 2000.

Experiment 2 compared the effects of 1 year, 2 consecutive years, and 3 consecutive years of spring defoliation at 2 timings and 4 intensities on plant yield, leaf height, and inflorescence production of bluebunch wheatgrass plants in the summer. Individual bluebunch wheatgrass plants ($n = 240$/site) with stature and size representative of the corresponding site were tagged for identification and excluded from large animal grazing within a 0.27-ha, barbed-wire exclosure in the autumn of 1998. Gross and Knight (2000) documented that small-sized exclosures such as the ones we used strongly reduce the likelihood that elk and, presumably, other wild ungulates will cross a barbed-wire fence to enter a grassland exclosure. Average basal diameter of treatment plants was 7 cm on the foothill grassland site and 10 cm on the foothill sagebrush steppe site.

In both experiments, all treatment plants were located a minimum of 1 m away from each other to eliminate confounding of treatment effects between individual plants. No shrubs were located within a 50-cm radius of each treatment plant in order to minimize confounding effects caused by neighboring shrub competition. Prior to spring treatment in both 1999 and 2001 in Experiment 1 and prior to the spring 1999 treatment in Experiment 2, leaf height and basal diameter were measured on each of the tagged bluebunch wheatgrass plants. In addition, percent basal cover of mature perennial grasses was ocularly estimated within a 0.50-cm radius of each tagged plant. Mature perennial grasses were defined as those plants with basal diameter $\geq$3 cm, measured at the longest distance across the base of the plant. Basal cover was estimated to account for potential confounding effects caused by neighboring plant competition (Mueggler 1972). Covariables used in the data analyses were initial leaf height and basal diameter of treatment plants and percent basal cover of surrounding mature perennial grasses.

Experiment 1. Hand-clipped treatments were applied to 80 bluebunch wheatgrass plants in the spring of 1999 and to another set of 80 plants in the spring of 2001 at each study site (total = 160 plants/site). Clipping treatments were applied at 2 timings in the spring: 1) early spring (mid- to late April, bluebunch wheatgrass at 3- to 4-leaf stage), or 2) late spring (mid- to late May, bluebunch wheatgrass at 5- to 6-leaf stage). Timing of treatments did not occur on the same calendar dates both years, but treatments were applied at the same phenological stages of bluebunch wheatgrass growth.

During both April and May, 4 intensities of clipping were applied: 1) 3-cm residual stubble height, 2) 6-cm residual stubble height, 3) 9-cm residual stubble height, or 4) an unclipped control. Each timing $\times$ intensity treatment combination was randomly assigned to 10 bluebunch wheatgrass plants per site (2 timings $\times$ 4 intensities $\times$ 10 plants = 80 plants $\cdot$ y^{-1} $\cdot$ $site^{-1}$).

Experiment 2. Hand-clipped treatments were applied to bluebunch wheatgrass plants in the spring of 1999, 2000, and 2001. Clipping treatments were applied at 2 timings in the spring: 1) early spring (mid- to late April, bluebunch wheatgrass at 3- to 4-leaf stage), or 2) late spring (mid- to late May, bluebunch wheatgrass at 5- to 6-leaf stage). The timings of defoliation in experiments 1 and 2 were chosen to represent the critical periods of grazing by elk on foothill rangeland in spring, as dictated by weather (snow melt on south-facing slopes) and forage availability (initiation of spring graminoid growth). Again, timing of treatments did not occur on the same calendar dates each year, but treatments were applied at the same phenological stages of bluebunch wheatgrass growth.

During both April and May, 4 intensities of clipping were applied: 1) 3-cm residual stubble height, 2) 6-cm residual stubble height, 3) 9-cm residual stubble height, or 4) an unclipped control. Each timing $\times$ intensity treatment combination was applied for 3 durations: 1) a single year (1999 only), 2) 2 consecutive years (1999 and 2000), or 3) 3 consecutive years (1999, 2000, and 2001). The intensities of defoliation in Experiments 1 and 2 represented the spectrum of elk grazing intensities observed by the authors on foothill rangeland sites in spring, as dictated by the rate of snowmelt and subsequent available forage, and densities of elk present. Each timing $\times$ intensity $\times$ duration treatment combination was randomly assigned to 10 bluebunch wheatgrass plants per site (2 timings $\times$ 4 intensities $\times$ 3 durations $\times$ 10 plants = 240 plants/site).

Measured Responses

Plant yield, average leaf height, and inflorescence production were measured in the summer of 1999 and 2001 for Experiment 1 and in the summer of 1999, 2000, and 2001 for Experiment 2. Responses were measured in both early summer (late June, bluebunch wheatgrass at boot stage) and late summer (late July, bluebunch wheatgrass at flowering stage) in both experiments at times when foothill rangeland is commonly utilized by cattle or other livestock.

Average leaf height of individual plants was measured in both June and July by measuring the average height of current year's leaves in their natural position (USDA–USDI 1996). The number of inflorescences produced per plant was counted only in July because, phenologically, the plants had not reached the flowering stage by June.

Plant yield was measured as grams of current year's standing crop per plant in June and July. In order to measure plant yield in July, plants could not be destructively sampled in June to attain a yield measurement. Plant yield was estimated in June by applying the average leaf height of each individual plant to a height–weight linear regression equation (Bonham 1989). Separate regression equations were developed for each site and each year by first measuring the average leaf heights of 75 individual bluebunch wheatgrass plants outside each exclosure that were representative of the treatment plants. Current year's growth of each plant was then clipped to ground level, oven-dried at 55°C for 48 hours, and weighed to the nearest 0.01 g. Plant yield was measured in July by clipping current year's growth of individual treatment plants to ground level and weighing the sample after oven-drying the forage at 55°C for 48 hours.

Statistical Analyses

Analysis of covariance was used to examine plant responses in Experiments 1 and 2. Data from the foothill grassland and

Table 1. Least squares means for yield (± standard error) of bluebunch wheatgrass plants in June and July after 1 year of April or May defoliation on foothill rangeland in southwestern Montana.

Response measured	Clipping height	Year 1999 April	1999 May	2001 April	2001 May
		(g·plant^{-1})			
Foothill grassland					
June	3 cm	1.9 ± 0.3a[1]A[2]	1.4 ± 0.3aA	0.6 ± 0.3aA	0.2 ± 0.2aA
	6 cm	1.4 ± 0.3aA	1.4 ± 0.3aA	1.1 ± 0.2aAB	0.4 ± 0.2aA
	9 cm	3.5 ± 0.3aB	3.1 ± 0.3aB	1.2 ± 0.3aAB	1.4 ± 0.3aAB
	Control	1.7 ± 0.2aA	1.7 ± 0.2aA	1.8 ± 0.3aB	1.8 ± 0.3aB
July	3 cm	1.9 ± 0.8aA	1.6 ± 0.8aA	2.0 ± 0.8aA	1.1 ± 0.7aA
	6 cm	1.9 ± 0.8aA	1.3 ± 0.8aA	2.1 ± 0.7aA	0.9 ± 0.7aA
	9 cm	9.2 ± 1.0aB	6.5 ± 0.9aB	2.9 ± 0.7aA	2.2 ± 0.7aA
	Control	1.8 ± 0.7aA	1.8 ± 0.7aA	2.5 ± 0.8aA	2.5 ± 0.8aA
Foothill sagebrush steppe					
June	3 cm	1.1 ± 0.3a[1]A[2]	1.0 ± 0.3aA	2.2 ± 0.3aA	1.2 ± 0.3aA
	6 cm	2.0 ± 0.3aA	1.7 ± 0.3aA	2.2 ± 0.3aA	1.7 ± 0.3aA
	9 cm	1.1 ± 0.3aA	1.0 ± 0.3aA	2.4 ± 0.3aA	2.3 ± 0.3aAB
	Control	1.5 ± 0.3aA	1.5 ± 0.3aA	3.2 ± 0.3aA	3.2 ± 0.3aB
July	3 cm	0.3 ± 2.7aA	3.5 ± 2.5aA	7.9 ± 3.0aA	4.6 ± 2.5aA
	6 cm	9.4 ± 2.5aA	10.9 ± 2.6aA	7.1 ± 2.8aA	5.9 ± 2.4aA
	9 cm	6.7 ± 2.6aA	7.2 ± 2.9aA	8.0 ± 2.5aA	6.7 ± 2.5aA
	Control	8.5 ± 2.7aA	8.5 ± 2.7aA	7.1 ± 2.8aA	7.1 ± 2.8aA

[1]Means in the same row within years with the same lowercase letter are not different ($P > 0.05$).
[2]Means in the same column within vegetation types and measurement periods (June or July) with the same uppercase letter are not different ($P > 0.05$).

foothill sagebrush steppe site were analyzed separately. Analyses were conducted using least squares means in the GLM procedure of SAS (SAS 2004). Multiple means comparisons of least squares means were made using the Tukey–Kramer method (SAS 2004). Differences were considered significant at $P \leq 0.05$.

Individual plants were the experimental units. For each response variable, covariables were initial leaf height and initial basal diameter of each treatment plant and percent basal cover of mature perennial grasses within a 50-cm radius of treatment plants. All covariates and interactions were retained in the model throughout the analyses.

Experiment 1. Experimental design was completely randomized, and treatments were in a 2 × 4 × 2 factorial arrangement. Factors included 2 timings and 4 intensities of clipping and 2 years. The statistical model for experiment 1 included year, timing, intensity, year × timing interaction, year × intensity interaction, timing × intensity interaction, and year × timing × intensity interaction. On each study site, treatments in experiment 1 were replicated in time (i.e., 2 years) and space (i.e., 10 plants per timing × intensity × year combination).

Experiment 2. Experimental design was completely randomized. Treatments were in a 2 × 4 × 3 factorial arrangement, and factors included 2 timings, 4 intensities, and 3 durations of clipping. The statistical model for experiment 2 included duration, timing, intensity, duration × timing interaction, duration × intensity interaction, timing × intensity interaction, and duration × timing × intensity interaction. On each study site, treatments in experiment 2 were replicated in space (i.e., 10 plants per timing × intensity × duration combination) but not time (i.e., treatments were applied in only 1 3-year period).

RESULTS

The 30-year average precipitation in April and May combined was 94 mm at the foothill grassland site and 84 mm at the foothill sagebrush steppe site (WRCC 2007). Among the 3 study years, April–May was the driest in 2001 at both study sites, with only 43% and 65% of the 30-year average falling in 2001 at the foothill grassland site and the foothill sagebrush steppe site, respectively. April–May precipitation was 52% and 110% of the 30-year average at the foothill grassland site in 1999 and 2000, respectively, and was 125% and 123% of the 30-year average at the foothill sagebrush steppe site in 1999 and 2000, respectively.

Plant Yield

Foothill Grassland Site. One year of clipping to 9 cm in April or May generally increased plant yield of bluebunch wheatgrass in both June and July ($P \leq 0.01$; Tables 1 and 2). Conversely, 1 year of clipping to 3 or 6 cm in April or May generally did not affect plant yield in either June or July ($P > 0.05$). The exceptions to these results occurred in 2001. Clipping to 3 cm in April or May 2001 reduced bluebunch wheatgrass yield in June 67% and 89%, respectively ($P = 0.02$ and $P < 0.01$), and clipping to 6 cm in May 2001 reduced plant yield in June 78% ($P < 0.01$) compared with unclipped plants (Table 1).

Table 2. Least squares means for yield (± standard error) of bluebunch wheatgrass plants in June and July after 1, 2, or 3 years of April or May defoliation on foothill rangeland in southwestern Montana.

Response measured	Clipping height	April 1 year	April 2 years	April 3 years	May 1 year	May 2 years	May 3 years
		(g·plant^{-1})					
Foothill grassland							
June	3 cm	1.7 ± 0.3a[1]A[2]	0.9 ± 0.3aA	0.8 ± 0.3aA	1.3 ± 0.3aA	0.3 ± 0.3aA	0.4 ± 0.3aA
	6 cm	1.3 ± 0.3abA	0.9 ± 0.3aA	2.5 ± 0.3bB	1.4 ± 0.3aA	0.8 ± 0.3aA	0.4 ± 0.3aA
	9 cm	3.4 ± 0.3aB	0.9 ± 0.3bA	1.5 ± 0.3bAB	3.0 ± 0.3aB	0.8 ± 0.3bA	0.7 ± 0.3bAB
	Control	1.7 ± 0.3aA	1.0 ± 0.3aA	1.9 ± 0.3aAB	1.7 ± 0.3aAB	1.0 ± 0.3aA	1.9 ± 0.3aB
July	3 cm	2.5 ± 0.8aA	2.2 ± 0.8aA	2.5 ± 0.9aA	2.2 ± 0.9aA	−0.2 ± 0.9aA	0.0 ± 0.9aA
	6 cm	2.8 ± 0.8aA	2.0 ± 0.8aA	3.8 ± 0.9aA	2.4 ± 0.9aA	1.8 ± 0.8aA	0.5 ± 0.9aA
	9 cm	10.6 ± 0.9aB	2.0 ± 0.8bA	3.0 ± 0.8bA	7.6 ± 0.9aB	0.8 ± 0.8bA	2.1 ± 0.8bA
	Control	2.4 ± 0.9aA	1.6 ± 0.8aA	1.5 ± 0.8aA	2.4 ± 0.9aA	1.6 ± 0.8aA	1.5 ± 0.8aA
Foothill sagebrush steppe							
June	3 cm	1.2 ± 0.5a[1]A[2]	2.5 ± 0.5aA	2.4 ± 0.5aA	1.4 ± 0.5aA	1.2 ± 0.5aA	0.9 ± 0.5aA
	6 cm	2.4 ± 0.5aA	3.1 ± 0.5aA	2.1 ± 0.5aA	1.9 ± 0.5aA	1.3 ± 0.5aA	1.5 ± 0.5aA
	9 cm	1.5 ± 0.5aA	2.2 ± 0.5aA	2.6 ± 0.5aA	0.9 ± 0.5aA	3.0 ± 0.5aA	1.3 ± 0.5aA
	Control	1.7 ± 0.5aA	3.1 ± 0.6aA	3.2 ± 0.5aA	1.7 ± 0.5aA	3.1 ± 0.6aA	3.2 ± 0.5aA
July	3 cm	3.8 ± 2.2aA	8.1 ± 2.3aA	7.5 ± 2.2aA	5.2 ± 2.2aA	2.7 ± 2.2aA	3.9 ± 2.2aA
	6 cm	10.6 ± 2.3aA	5.3 ± 2.2aA	5.9 ± 2.3aA	14.7 ± 2.2aA	2.9 ± 2.4aA	4.3 ± 2.3aA
	9 cm	8.2 ± 2.6aA	8.3 ± 2.3aA	4.9 ± 2.3aA	12.7 ± 2.3aA	6.0 ± 2.2aA	3.9 ± 2.2aA
	Control	11.0 ± 2.2aA	4.2 ± 2.9aA	1.3 ± 2.3aA	11.0 ± 2.2aA	4.2 ± 2.9aA	1.3 ± 2.3aA

[1]Means in the same row within timings of defoliation (April or May) with the same lowercase letter are not different ($P > 0.05$).
[2]Means in the same column within vegetation types and response measurement periods (June or July) with the same uppercase letter are not different ($P > 0.05$).

Two consecutive years of clipping to any height in April or May did not affect plant yield in either June or July ($P > 0.05$; Table 2). Similarly, 3 years of April clipping or 3 years of May clipping to 9 cm did not affect plant yield in either June or July ($P > 0.05$). Three consecutive years of May clipping to 3 or 6 cm did not affect plant yield in July ($P > 0.05$) but reduced plant yield in June 79% ($P = 0.04$ and $P = 0.04$, respectively) compared with unclipped plants.

Foothill Sagebrush Steppe Site. Plant yield of bluebunch wheatgrass in June or July was largely unaffected by 1 year of clipping in either April or May ($P > 0.05$; Tables 1 and 2), except when clipping in May 2001 to 3 and 6 cm decreased June yield 62% and 47%, respectively, compared with unclipped plants ($P > 0.01$ and $P = 0.01$, respectively; Table 1). Two or 3 consecutive years of clipping in either April or May did not affect plant yield in June or July ($P > 0.05$; Table 2).

Leaf Height

Foothill Grassland Site. One year of clipping in April or May generally did not adversely affect leaf height of bluebunch wheatgrass plants in June or July ($P > 0.05$; Tables 3 and 4). The most notable exceptions were in 2001, when clipping to 3 cm in April ($P = 0.01$) and clipping to 3 or 6 cm in May 2001 ($P = 0.01$ and $P < 0.01$, respectively) reduced June leaf height 40%, 80%, and 49%, respectively, compared with unclipped plants (Table 3). Similarly, clipping to 3 or 6 cm in May 2001 ($P = 0.01$ and $P < 0.01$, respectively) reduced July leaf height 57% and 33%, respectively, compared with no clipping.

Clipping to any height for 2 consecutive years in April did not affect leaf height in June or July ($P > 0.05$), and 2 years of clipping in May did not affect leaf height in July ($P > 0.05$; Table 4). However, 2 years of clipping to 3 cm in May reduced leaf height in June 41% ($P = 0.04$).

Three consecutive years of clipping in April did not affect June or July leaf height ($P > 0.05$; Table 4). May clipping to 3 or 6 cm for 3 years, however, reduced June leaf height 59% and 50%, respectively ($P < 0.01$ and $P < 0.01$, respectively), and May clipping to 3 cm for 3 years reduced leaf height in July 46% ($P = 0.02$).

Foothill Sagebrush Steppe Site. Leaf height of bluebunch wheatgrass plants was largely unaffected by 1 year of April or May clipping ($P > 0.05$; Tables 3 and 4), except in 2001, when May clipping to 3 cm reduced June leaf height 41% and July leaf height 34%. Clipping to 6 cm in May 2001 reduced June leaf height 28% compared with unclipped plants (Table 3).

Two consecutive years of either April or May clipping did not affect bluebunch wheatgrass leaf height in June or July ($P > 0.05$; Table 4). Similarly, 3 consecutive years of April clipping did not affect leaf height in June or July ($P > 0.05$), and 3 years of May clipping did not affect July leaf height ($P > 0.05$). However, 3 years of May clipping to 3, 6, or 9 cm decreased June leaf height 48%, 26%, and 30%, respectively, compared with unclipped plants ($P < 0.01$, $P = 0.05$, and $P < 0.01$, respectively).

Table 3. Least squares means for leaf height (± standard error) of bluebunch wheatgrass plants in June and July after 1 year of April or May defoliation on foothill rangeland in southwestern Montana.

Response measured	Clipping height	Year 1999 April	1999 May	2001 April	2001 May
		(cm)			
Foothill grassland					
June	3 cm	21.6 ± 1.3a[1]A[2]	17.9 ± 1.2aA	12.1 ± 1.2aA	4.0 ± 1.2bA
	6 cm	17.7 ± 1.2aA	18.5 ± 1.2aA	16.4 ± 1.1aAB	10.2 ± 1.2bB
	9 cm	28.4 ± 1.5aB	28.1 ± 1.5aB	16.8 ± 1.2aAB	15.7 ± 1.2aC
	Control	20.3 ± 1.2aA	20.3 ± 1.2aA	20.1 ± 1.3aB	20.1 ± 1.3aC
July	3 cm	20.9 ± 1.4aA	14.3 ± 1.4bA	18.5 ± 1.4aA	9.4 ± 1.3bA
	6 cm	17.7 ± 1.4aA	19.4 ± 1.4aAB	18.7 ± 1.3aA	14.5 ± 1.3aAB
	9 cm	22.0 ± 1.7aA	22.7 ± 1.6aB	20.1 ± 1.4aA	18.3 ± 1.4aBC
	Control	19.2 ± 1.3aA	19.2 ± 1.3aAB	21.7 ± 1.5aA	21.7 ± 1.5aC
Foothill sagebrush steppe					
June	3 cm	20.3 ± 1.3a[1]A[2]	19.0 ± 1.2aA	21.3 ± 1.4aA	14.4 ± 1.2bA
	6 cm	23.7 ± 1.2aA	22.6 ± 1.3aA	21.1 ± 1.3aA	17.7 ± 1.2aAB
	9 cm	21.3 ± 1.3aA	18.6 ± 1.4aA	21.3 ± 1.2aA	21.4 ± 1.2aBC
	Control	22.6 ± 1.3aA	22.6 ± 1.3aA	24.5 ± 1.3aA	24.5 ± 1.3aC
July	3 cm	20.7 ± 1.5aA	19.4 ± 1.4aA	23.0 ± 1.7aA	17.3 ± 1.4aA
	6 cm	28.6 ± 1.4aB	28.2 ± 1.5aB	22.5 ± 1.5aA	20.2 ± 1.4aAB
	9 cm	25.0 ± 1.5aAB	22.2 ± 1.6aAB	22.6 ± 1.4aA	23.5 ± 1.4aAB
	Control	25.5 ± 1.5aAB	25.5 ± 1.5aAB	26.4 ± 1.5aA	26.4 ± 1.5aB

[1]Means in the same row within years with the same lowercase letter are not different ($P > 0.05$).
[2]Means in the same column within vegetation types and measurement periods (June or July) with the same uppercase letter are not different ($P > 0.05$).

Table 4. Least squares means for leaf height (± standard error) of bluebunch wheatgrass plants in June and July after 1, 2, or 3 years of April or May defoliation on foothill rangeland in southwestern Montana.

Response measured	Clipping height	Month April 1 year	April 2 years	April 3 years	May 1 year	May 2 years	May 3 years
		(cm)					
Foothill grassland							
June	3 cm	20.9 ± 1.4a[1]A[2]B	17.4 ± 1.3abA	13.5 ± 1.3bA	17.0 ± 1.4aA	10.7 ± 1.4abA	7.7 ± 1.4bA
	6 cm	16.9 ± 1.3aA	17.4 ± 1.3aA	21.0 ± 1.4aB	17.6 ± 1.3aA	15.3 ± 1.3abAB	9.3 ± 1.4bA
	9 cm	27.3 ± 1.4aB	16.7 ± 1.3bA	16.2 ± 1.3bAB	27.2 ± 1.3aB	17.2 ± 1.3bAB	2.3 ± 1.3bAB
	Control	19.9 ± 1.4aAB	18.2 ± 1.3aA	18.7 ± 1.4aAB	19.9 ± 1.4aAB	18.2 ± 1.3aB	18.7 ± 1.4aB
July	3 cm	21.7 ± 1.4aA	19.4 ± 1.5aA	14.7 ± 1.4aA	14.9 ± 1.5aA	10.7 ± 1.5aA	10.0 ± 1.6aA
	6 cm	18.1 ± 1.4aA	19.1 ± 1.5aA	22.3 ± 1.5aB	19.4 ± 1.4aAB	14.5 ± 1.5abA	11.5 ± 1.5bAB
	9 cm	22.4 ± 1.5aA	18.4 ± 1.4aA	16.2 ± 1.4aAB	23.7 ± 1.5aB	16.6 ± 1.4abA	13.3 ± 1.4bAB
	Control	19.3 ± 1.5aA	16.0 ± 1.4aA	18.6 ± 1.5aAB	19.3 ± 1.5aAB	16.0 ± 1.4aA	18.6 ± 1.5aB
Foothill sagebrush steppe							
June	3 cm	22.0 ± 1.1a[1]A[2]	23.1 ± 1.2aA	21.1 ± 1.1aA	20.5 ± 1.1aA	20.3 ± 1.1aA	12.3 ± 1.1bA
	6 cm	25.0 ± 1.2aA	23.4 ± 1.2aA	20.6 ± 1.2aA	24.3 ± 1.1aA	19.5 ± 1.1abA	17.3 ± 1.2bA
	9 cm	23.3 ± 1.2aA	22.9 ± 1.1aA	22.2 ± 1.2aA	20.1 ± 1.2abA	22.7 ± 1.1aA	16.4 ± 1.1bA
	Control	24.1 ± 1.2aA	25.4 ± 1.5aA	23.5 ± 1.2aA	24.1 ± 1.2aA	25.4 ± 1.5aA	23.5 ± 1.2aB
July	3 cm	22.6 ± 1.3aA	23.5 ± 1.3aA	23.8 ± 1.3aA	21.3 ± 1.3aA	19.3 ± 1.3aA	16.3 ± 1.3aA
	6 cm	30.6 ± 1.3aB	22.9 ± 1.3bA	22.4 ± 1.3bA	30.1 ± 1.3aB	19.7 ± 1.3bA	19.3 ± 1.3bA
	9 cm	26.6 ± 1.3aAB	21.4 ± 1.3aA	22.8 ± 1.3aA	24.2 ± 1.3aAB	22.3 ± 1.3aA	22.2 ± 1.3aA
	Control	27.4 ± 1.3aAB	24.0 ± 1.7aA	24.5 ± 1.3aA	27.4 ± 1.3aAB	24.0 ± 1.7aA	24.5 ± 1.3aA

[1]Means in the same row within timings of defoliation (April or May) with the same lowercase letter are not different ($P > 0.05$).
[2]Means in the same column within vegetation types and response measurement periods (June or July) with the same uppercase letter are not different ($P > 0.05$).

Table 5. Least squares means for inflorescence production (± standard error) of bluebunch wheatgrass plants in July after 1 year of April or May defoliation on foothill rangeland in southwestern Montana.

	Year			
	1999		2001	
Clipping height	April	May	April	May
	(No.·plant^{-1})			
Foothill grassland				
3 cm	1.2 ± 1.6a[1]A[2]	1.2 ± 1.6aAB	3.3 ± 1.7aA	1.2 ± 1.6aA
6 cm	−1.0 ± 1.6aA	−2.0 ± 1.6aA	1.8 ± 1.5aA	−0.1 ± 1.6aA
9 cm	12.5 ± 2.0aB	7.7 ± 2.0aB	2.4 ± 1.6aA	2.4 ± 1.6aA
Control	0.8 ± 1.5aA	0.8 ± 1.5aAB	1.9 ± 1.8aA	1.9 ± 1.8aA
Foothill sagebrush steppe				
3 cm	1.1 ± 3.1a[1]A[2]	2.4 ± 2.9aA	5.2 ± 3.4aA	1.6 ± 2.9aA
6 cm	6.3 ± 2.9aA	5.9 ± 3.0aA	4.3 ± 3.2aA	3.0 ± 2.8aA
9 cm	0.2 ± 3.0aA	2.0 ± 3.3aA	7.1 ± 2.9aA	6.3 ± 2.9aA
Control	9.8 ± 3.1aA	9.8 ± 3.1aA	12.0 ± 3.2aA	12.0 ± 3.2aA

[1]Means in the same row within years with the same lowercase letter are not different ($P > 0.05$).
[2]Means in the same column within vegetation types with the same uppercase letter are not different ($P > 0.05$).

Inflorescence Production

Foothill Grassland Site. Inflorescence production per plant of bluebunch wheatgrass was not adversely affected by 1 year of clipping in either April or May ($P > 0.05$; Tables 5 and 6). In fact, inflorescence production increased 146% in response to clipping to 9 cm in April 1999 ($P < 0.01$; Table 5) compared with unclipped plants. Two or 3 consecutive years of clipping did not affect inflorescence production per plant ($P > 0.05$; Table 6).

Foothill Sagebrush Steppe Site. Inflorescence production per plant was unaffected ($P > 0.05$) by 1, 2, or 3 years of clipping in April or May (Tables 5 and 6).

DISCUSSION

We hypothesized that defoliation in April would have less deleterious effects than defoliation in May. Our results confirmed that bluebunch wheatgrass plants on both the foothill grassland and the foothill sagebrush steppe sites were not adversely affected by April defoliation, even when defoliation occurred for 2 or 3 consecutive years. These results compare favorably with Hobbs et al. (1996), who studied effects of spring elk grazing on foothill rangeland in northern Colorado. When grazing by elk ended in mid-April, perennial grass yield recovered by early May. In our study, April clipping at any intensity likely did not remove active intercalary or apical meristems because of their location at or near ground level early in the spring (Dahl and Hyder 1977; Briske and Richards 1995). Richards and Caldwell (1985) also found that clipping bluebunch wheatgrass in late April (5–7-cm stubble height) did not remove active apical or intercalary meristems. We believe that the apical meristems remained intact when bluebunch wheatgrass plants in our study were clipped to 9 cm in May because no tillering was observed in June or July on those plants. When Richards and Caldwell (1985) clipped bluebunch wheatgrass lower than 9 cm (5–7-cm stubble height)

Table 6. Least squares means for inflorescence production (± standard error) of bluebunch wheatgrass plants in July after 1, 2, or 3 years of April or May defoliation on foothill rangeland in southwestern Montana.

	Month					
	April			May		
Clipping height	1 year	2 years	3 years	1 year	2 years	3 years
	(No.·plant^{-1})					
Foothill grassland						
3 cm	1.8 ± 1.6a[1]A[2]	−0.4 ± 1.6aA	−0.2 ± 1.6aA	2.2 ± 1.7aAB	−2.3 ± 1.7aA	−0.3 ± 1.8aA
6 cm	0.4 ± 1.6aA	1.6 ± 1.6abA	9.3 ± 1.7bB	−0.2 ± 1.6aA	1.9 ± 1.6aA	−0.5 ± 1.7aA
9 cm	14.7 ± 1.7aB	1.6 ± 1.6bA	0.0 ± 1.6bA	8.9 ± 1.6aB	−0.1 ± 1.6bA	−0.3 ± 1.6bA
Control	1.5 ± 1.7aA	1.4 ± 1.6aA	3.0 ± 1.7aAB	1.5 ± 1.7aAB	1.4 ± 1.6aA	3.0 ± 1.7aA
Foothill sagebrush steppe						
3 cm	3.3 ± 2.9a[1]A[2]	8.2 ± 3.0aA	14.4 ± 2.8aA	3.3 ± 2.8aA	2.3 ± 2.9aA	2.2 ± 2.9aA
6 cm	5.4 ± 2.9aA	0.0 ± 4.2aA	10.8 ± 3.0aA	7.5 ± 2.8aA	0.0 ± 3.8aA	4.5 ± 2.9aA
9 cm	4.2 ± 3.0aA	0.0 ± 3.8aA	7.2 ± 3.0aA	2.9 ± 3.0aA	0.0 ± 3.9aA	11.0 ± 2.9aA
Control	11.1 ± 2.9aA	7.9 ± 3.8aA	13.0 ± 2.9aA	11.1 ± 2.9aA	7.9 ± 3.8aA	13.0 ± 2.9aA

[1]Means in the same row within timings of defoliation (April or May) with the same lowercase letter are not different ($P > 0.05$).
[2]Means in the same column within vegetation types and with the same uppercase letter are not different ($P > 0.05$).

in mid-May, tillering occurred after removal of active apical meristems and after activation of basal, axillary meristems. Plants clipped to 9 cm in May in our study also had sufficient residual leaf area and growing days to recover and regrow by early and late summer.

In foothill grassland and sagebrush steppe habitats, growth rate of aboveground plant biomass peaks in late May (Sims and Singh 1978), and because soils in these habitats are typically frozen from November through March, herbaceous plant growth on these foothill rangeland sites depends primarily on precipitation received during April and May. During our 3-year study, the foothill grassland site received 68% of normal April–May precipitation, based on the 30-year average, and the foothill sagebrush steppe site received 104% of normal April–May precipitation. These precipitation patterns explain why bluebunch wheatgrass plants on the foothill grassland site exhibited more adverse effects to spring clipping than those seen on the foothill sagebrush steppe site.

In both April and May 1999, clipping plants a single time to 9 cm on the foothill grassland site had a stimulatory effect on plant yield and inflorescence production of bluebunch wheatgrass plants. This occurred despite a 48% precipitation deficit in April–May compared with the 30-year average (WRCC 2007). We attribute this result to the interactive effects of self-shading and residual leaf area (McNaughton 1992; Wegener and Odasz 1997). Clipping to 9 cm removed standing dead vegetation, enabling current year's leaves of clipped plants to receive more light than unclipped plants, which promoted more efficient photosynthetic activity. Clipping to ≤ 6 cm, however, apparently removed so much current year's leaf area that plant growth was unable to benefit from the increased availability of light. Increased plant yield in response to defoliation (i.e., overcompensation) has been documented elsewhere on semiarid rangeland of North America, including shortgrass prairie in north-central Colorado (Williamson et al. 1989; Varnamkhasti et al. 1995) and mountain grasslands in north-central Arizona (Loeser et al. 2004) and northern Wyoming (Frank et al. 2002). Plant yield in the summer of 1999, however, was not increased on our foothill sagebrush steppe site in response to 9-cm clipping in April or May 1999. Shading from the sagebrush plants may have prevented overcompensation by bluebunch wheatgrass (McNaughton 1983). Mountain big sagebrush also is known to effectively compete with bluebunch wheatgrass for soil moisture (Thorgeirsson 1985) and nutrients (Caldwell et al. 1985).

As we hypothesized, May defoliation imposed greater damage to bluebunch wheatgrass plants than April defoliation and those effects became more prominent after 3 consecutive years of defoliation. In general, a single year of May defoliation did not adversely affect bluebunch wheatgrass plants in either experiment. The exception to this was in 2001, when April–May precipitation was 43% and 65% of the 30-year average on the foothill grassland site and the foothill sagebrush steppe site, respectively. On both sites, bluebunch wheatgrass plants defoliated to ≤ 6 cm in April or May 2001 had reduced plant yield and leaf height in June and July. The removal of active meristematic tissue, especially in May (Richards and Caldwell 1985), and unfavorable soil moisture conditions likely slowed the recovery of defoliated bluebunch wheatgrass plants.

Two successive years of May defoliation had relatively little effect on bluebunch wheatgrass plants in our study. The only notable effect was a reduction in leaf height in June on the foothill grassland site when bluebunch wheatgrass plants were clipped to 3 cm in May. In this case, the apical meristem was likely removed in May, and recovery depended on growth initiation from axillary buds (Richards and Caldwell 1985). Tiller initiation following defoliation occurs within 2 to 3 weeks of defoliation (Olson and Richards 1988), but only 1 month elapsed between the clipping treatment in May and when responses were measured in June. Therefore, the plants had insufficient time for the leaves of new tillers to grow tall enough to be comparable to the leaves of unclipped plants.

After 3 consecutive years of May defoliation, bluebunch wheatgrass plants on both the foothill grassland and the sagebrush steppe sites began to show signs of reduced sustainability. Payne (1959), Vogel and Van Dyne (1966), and Wilson et al. (1966) observed similar results after 3 consecutive years of defoliation on bluebunch wheatgrass. Removal of the apical meristem by clipping to 3 or 6 cm in May for 3 successive years reduced recovery rate (Briske and Richards 1995) and induced greater stress on plants than clipping in April or clipping to 9 cm in May. Plant response after 3 consecutive years of clipping at all levels may have been exacerbated by selective defoliation because treatment plants and neighboring plants were enclosed within an ungulate-proof fence. Clipping resulted in selective defoliation of treatment plants for 3 years, while neighboring plants were not defoliated. Treatment plants may have been harmed more so than if the neighboring plants also had been clipped (Hulme 1996).

MANAGEMENT IMPLICATIONS

Our results indicate that in foothill grassland or foothill sagebrush steppe habitats where early spring (mid- to late April) grazing occurs, livestock or wildlife grazing management (e.g., turnout date or stocking rate) in June or July does not need to be adjusted. However, we recommend that on foothill rangelands where bluebunch wheatgrass receives moderate or light defoliation (6–9-cm residual stubble heights) in late spring (mid- to late May), grazing should be limited to no more than 2 successive years of mid- to late May grazing. Sites that receive heavy to severe defoliation ($\leq$ 3-cm residual stubble heights) in mid- to late May should not be grazed in 2 successive years during mid- to late May. Rangeland managers, wildlife biologists, and ranchers should carefully monitor bluebunch wheatgrass stubble height immediately after ungulate grazing in May on foothill rangeland to indicate when grazing management adjustments are needed to maintain the sustainable production of bluebunch wheatgrass. Grazing management options include encouraging wildlife or livestock to use sites in April instead of May, discouraging wildlife or livestock use until later in summer after bluebunch wheatgrass has set seed, or reducing grazing intensity in May.

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