

Response of Bluebunch Wheatgrass and Medusahead to Defoliation

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Abstract

Our objective was to determine the short-term response of bluebunch wheatgrass and medusahead to defoliation of wheatgrass designed to stimulate regrowth through tillering. We hypothesized that defoliating bluebunch wheatgrass by 20% at the 3 to 3.5 leaf stage followed by a 50% defoliation at peak standing crop would increase its tillering and biomass production. Consequently, we expected a reduction of the density and biomass of medusahead over that of bluebunch wheatgrass defoliated 50% at peak standing crop. Treatments included four initial medusahead densities (200, 333, 444, 600 plants · m⁻²) created by hand-pulling and three defoliation regimes factorially arranged (12 treatment combinations) in a randomized complete-block design and replicated four times at two sites. In 2006 and 2007, defoliation was accomplished by hand-clipping bluebunch wheatgrass 1) by 50% once at peak standing crop (late June); 2) by 20% at the 3 to 3.5 leaf stage, then again to 50% at peak standing crop (mid May, late June); or 3) plants were not clipped. Density was sampled in 2006 and 2007, and biomass was harvested only at Star Mountain (near Riverside, Oregon) in 2007 because Warm Springs (near Drewsey, Oregon) was burned by a wildfire before final 2007 data could be collected. In 2006, no treatments applied at either site detectably altered the number of tillers produced by bluebunch wheatgrass nor did they affect bluebunch wheatgrass density or biomass in 2007 at Star Mountain. Changes in medusahead density were not detected in 2006, but this annual invasive grass increased in density and biomass in 2007 at Star Mountain in plots receiving two defoliations. The relatively short growing period caused by summer drought and the relative intolerance of bluebunch wheatgrass to grazing make the twice-over grazing an unlikely practice for arid rangelands in the western United States. In fact, it could possibly increase the risk of annual grass invasion.

Resumen

Nuestro objetivo fue determinar la respuesta a corto plazo de bluebunch wheatgrass y medusahead a la defoliación de wheatgrass diseñado para estimular el rebrote a través de la producción de nuevos tallos. Nuestra hipótesis fue que la defoliación de 20% de wheatgrass a un estado vegetativo con 3 a 3.5 hojas seguido por 50% de defoliación al final de la época de crecimiento podría incrementar la producción de tallos y la producción de biomasa. Como resultado, esperábamos la reducción tanto en densidad como la biomasa de medusahead cuando bluebunch wheatgrass se defoliara un 50% al final de la época de crecimiento. Los tratamientos incluyeron cuatro densidades iniciales de medusahead (200, 333, 444, y 600 plantas · m⁻²). Estas densidades se establecieron sacando manualmente las plantas, así como tres regímenes de defoliación en un arreglo factorial (combinación 12 tratamientos) en un diseño de bloques al azar, con dos repeticiones en dos sitios. Durante el 2006 y 2007 la defoliación de wheatgrass se hizo manualmente: 1) 50% una sola vez al final de la época de crecimiento (finales de Junio); 2) 20% cuando el estado de crecimiento de las plantas era entre 3 y 3.5 hojas, después de nuevo una defoliación al final de la época de crecimiento (mediados de Mayo, finales de Junio); o 3) las plantas no se cortaron. La densidad fue muestreada durante 2006 y 2007, y la biomasa se colectó únicamente en el sitio Star Mountain durante 2007, debido a que en el sitio Warm Spring ocurrió un fuego sin control a finales del 2007 y no se colectaron datos de este sitio. Durante 2006, no se detectó ningún tratamiento aplicado a ambos sitios que alterara el número de tallos producidos por bluebunch wheatgrass, tampoco se afectó la densidad o la biomasa de bluebunch wheatgrass durante 2007 en el sitio de Star Mountain. No se registraron cambios en la densidad de medusahead en 2006, pero este pasto invasivo anual incrementó su densidad y biomasa en 2007 en la parcelas del sitio Star Mountain que se defoliaron. El periodo de crecimiento relativamente corto debido a la sequía del verano y la relativa intolerancia al pastoreo de bluebunch wheatgrass hace doblemente inexistente la práctica del sobrepastoreo para los pastizales áridos del Oeste de Estados Unidos. De hecho, podría ser posible que se incrementara el riego de la invasión de pastos anuales.

Key Words: competitive ability, grazing management, invasive plants, stimulation grazing, tillering

INTRODUCTION

Invasive plant species negatively affect rangeland throughout the western United States by displacing desirable species, altering ecological processes, reducing wildlife habitat, and decreasing productivity for livestock production (DiTomaso

2000; Masters and Sheley 2001). Throughout the Great Basin and surrounding ecosystems, medusahead (*Taeniatherum caput-medusae* [L.] Nevski subsp. *asperum* [Simonk] Melderis) is aggressively invading once productive grazing land (Miller et al. 1999). Within the sagebrush steppe, medusahead aggressively displaces perennial plants by preempting resources and promotes frequent fires that destroy the shrub portion of the plant community (Young 1992). Thus, in this ecosystem, fire facilitates the conversion of rangeland from a perennial-dominated to an annual-dominated system. Medusahead-

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dominated sites have 50% to 80% less grazing capacity than the original native plant community (Hironaka 1961). Grazing systems designed to favor desired species over medusahead have potential for assisting large-scale management of this invasive weed.

Timing, intensity, and frequency of defoliation affect the competitive interactions between invasive species and perennial grasses and, thus, influence the ability of perennial grass to persist and dominate plant communities (Maschinski and Whitman 1989; Briske 1991). On seasonally grazed rangeland, moderate defoliation and alternating grazing seasons constitute proper grazing management (Heitschmidt and Stuth 1991), even where invasive weeds are present (Sheley et al. 1997). Our prior study (Sheley et al. 2008) showed that periodic defoliation of crested wheatgrass (*Agropyron cristatum* [L.] Gaertn.) is required to maintain enough young, vigorous growth to successfully outcompete invading medusahead. At one site, defoliating crested wheatgrass in the summer or fall, regardless of intensity, stimulated enough aggressive growth to completely remove all medusahead that had established in the prior year (Sheley et al. 2008). Without other disturbances, moderate to heavy grazing intensity applied to crested wheatgrass and alternating the season of use should prevent medusahead invasion on clayey-loam soils.

Grazing management aimed at stimulating desired grass tillering has been proposed as a biologically effective strategy. Defoliation can stimulate tillering by reducing the influence of apical dominance, the physiological process by which the apical meristem and young leaves of a lead tiller exert hormonal regulation of axillary bud growth, which inhibits development of vegetative tillers (Briske 1991; Murphy and Briske 1992; Briske and Richards 1994; Briske and Richards 1995; Manske 1996). Stimulation of the tillering process in grass plants can result in increased plant density and greater quantity and quality of aboveground herbage production (Manske 2003).

Our objective was to determine the short-term response of bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] A. Löve subsp. *Spicata*) and medusahead to defoliation designed to stimulate tillering of wheatgrass. We hypothesized that defoliating bluebunch wheatgrass by 20% at the 3 to 3.5 leaf growth stage followed by a 50% defoliation at peak standing crop would increase its tillering and total biomass production. That stage coincides with the light defoliation of bluebunch wheatgrass described by Brewer et al. (2007), in which plants fully recovered by the end of the growing season. Consequently, we expected a reduction of the density and biomass of medusahead over that of bluebunch wheatgrass defoliated by 50% at peak standing crop.

MATERIALS AND METHODS

Study Sites

This study was conducted from 2005 to 2007 on two sites. Both sites were within the Wyoming big sage/bluebunch wheatgrass community types of eastern Oregon (Franklin and Dyrness 1988). Site 1 was located near Riverside, Oregon, on Star Mountain (lat 43°28'44.539"N, long 118°08'12.075"W), and site 2 was located about 14 km north of Warm Springs Reservoir (lat 43°44'2.794"N, long 118°22'33.057"W) near

Drewsey, Oregon. This habitat, especially with clay soils, is susceptible to invasion by medusahead (Miller et al. 1999). These sites had a 50:50 mixture of bluebunch wheatgrass and medusahead cover.

Soils at Star Mountain are a Risley clayey soil (fine, montmorillonitic, mesic Xeric Haplargids). Soils at Warm Springs are a Poall-Waspo complex. Poall soils are fine montmorillonitic, mesic Xeric Paleargids. Waspo soils are montmorillonitic, mesic, Aridic Haploxererts. Both sites are about 1 050 m in elevation and are nearly level.

Environmental conditions were monitored daily at a weather station within 6 km of both sites within the same community type (Fig. 1). Precipitation for the first year (2005) of the study was 250 mm, with most of the precipitation falling in October through December. In the second year (2006), precipitation was 315 mm with large amounts in both the spring and fall. During January 2007 to July of 2007, the area received 110 mm of precipitation.

Experimental Design and Procedures

Treatments included four medusahead densities and three defoliation regimes factorially arranged (12 treatment combinations) in a randomized complete-block design and replicated four times at each site. In June 2005, medusahead was removed by hand pulling plants at ground level to densities of 200, 333, 466, or 600 plants · m⁻²) because these densities are commonly found in medusahead-infested rangeland, and density can control competitive interactions. In 2005, all 2 × 2 m plots were defoliated to 50% by weight in late June (peak standing crop) to ensure that prior plant removal was similar across all plots. In 2006 and 2007, defoliation was accomplished by hand-clipping bluebunch wheatgrass 1) by 50% once at peak standing crop (late-June); 2) by 20% at the 3 to 3.5 (mid May) leaf stage, then again to 50% at peak standing crop (late-June); or 3) the plants were not clipped at all. Plants were initiating culm elongation at this time. All material was dried at 60°C for 48 hr and weighed.

Sampling

Density was sampled in mid-July 2006 and 2007 by counting the number of medusahead plants and bluebunch wheatgrass tillers in three randomly located 2 × 5 dm frames in each plot. We considered a tiller to be successive phytomers differentiated from a single apical meristem (Etter 1951; Hyder 1972; Briske 1986; Briske 1991). The Warm Springs site was burned by a wildfire before 2007 data could be collected. On 11 July 2007, aboveground biomass of bluebunch wheatgrass and medusahead was harvested from each frame at Star Mountain, dried at 60°C for 48 hr, and weighed.

Data Analysis

The treatments (removed biomass) and response variables (tiller density and final biomass at Star Mountain) were analyzed with least-squares means analysis of variance (AN-OVA). To provide an indication of the amount of biomass removed, ANOVA was conducted between the 50% defoliation in 2005 and the 50% defoliation treatment in 2006 (2007 data were not included because Warm Springs burned prior to clipping that year). We also compared the biomass removed

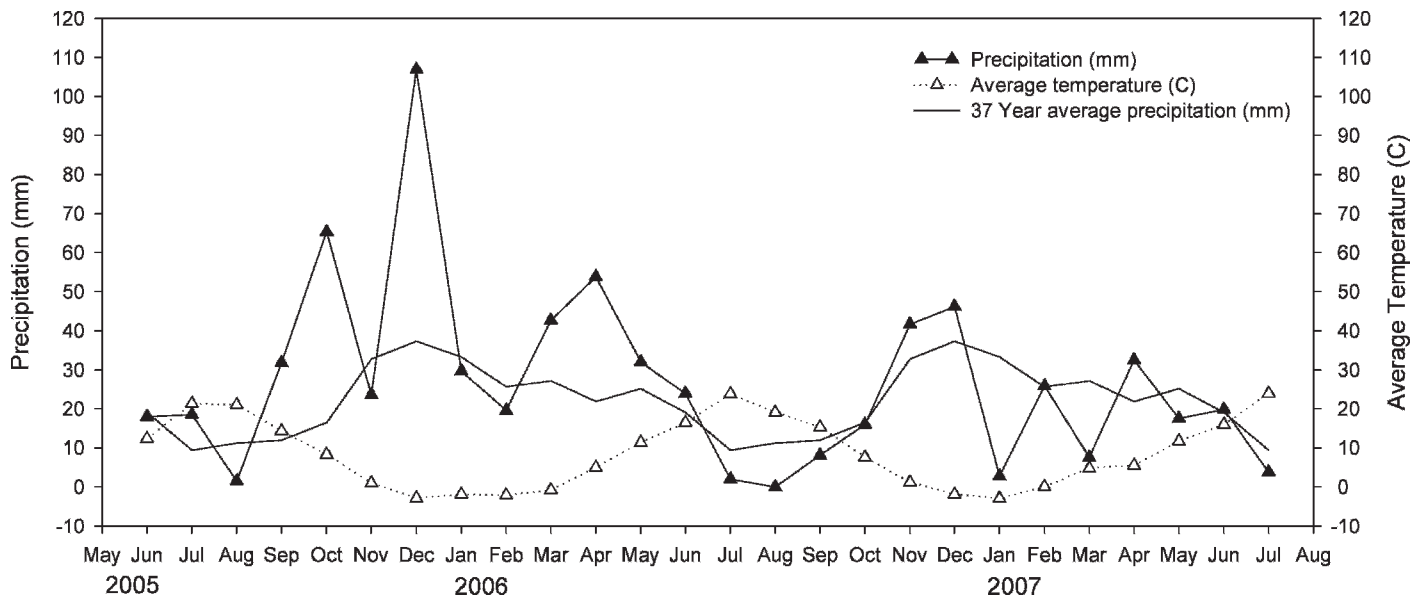


Figure 1. Monthly precipitation (mm), average monthly temperature ($^{\circ}\text{C}$), and 37-yr average monthly precipitation (mm) at a weather station near both study sites (monitored daily).

between the 50% and the 20% plus 50% defoliation treatments in 2006 (both sites) and 2007 (Star Mountain only). For biomass removal and density data, ANOVA was conducted as a split-plot using Proc Mixed software (SAS 2004). The ANOVA model analyzed density between sites in 2006 and between years (2006 versus 2007) at Star Mountain only because plots at Warm Springs were burned by a wildfire in the spring 2007. In these models, *rep* (site or year) was used as the error term for site or year depending on the comparison. Initial medusahead density by defoliation regime by *rep* (site or year) was used as the error term for testing the effects of initial medusahead density and defoliation regime on final medusahead and bluebunch density within site. Because biomass was only collected in 2007 at Star Mountain, year and site were not included in the ANOVA model for biomass. Means and standard errors are presented. In addition, Honestly Significant Differences (HSD) are provided for comparing multiple means. Data presented are averaged over factors that were not significant or did not interact.

RESULTS

Biomass Removed

The amount of biomass removed was lower in 2006 than in 2005 at Warm Springs, where the plants were annually defoliated at peak standing crop to 50% (Fig. 2). Presumably, lower biomass was the result of prior years standing dead material because biomass in 2005 probably included some of the prior year's material. Conversely, the amount of biomass removed from the plots at Star Mountain increased from $19 \text{ g} \cdot \text{m}^{-2}$ in 2005 to $26 \text{ g} \cdot \text{m}^{-2}$ in 2006 ($P < 0.05$). At Warm Springs, the amount of biomass removed was similar between defoliation regimes across years (Fig. 3). The biomass removed, at Star Mountain, at plots that were twice (20% and 50%)

defoliated, was about one-half of that at plots where only a single 50% defoliation occurred.

Bluebunch Wheatgrass

In 2006, no treatments applied at either site altered the number of tillers produced by bluebunch wheatgrass ($P > 0.15$). Across treatments, bluebunch wheatgrass produced $227 \text{ tillers} \cdot \text{m}^{-2} \pm 24.0 \text{ SE}$ in 2006 and only about $60 \text{ tillers} \cdot \text{m}^{-2} \pm 23.6 \text{ SE}$ in 2007 ($P < 0.0001$) at Star Mountain (Table 1). No effects of initial medusahead density or defoliation regime on bluebunch wheatgrass biomass were detected in 2007 ($P = > 0.10$). Across treatments, bluebunch wheatgrass yielded about $9 \text{ g} \cdot \text{m}^{-2}$.

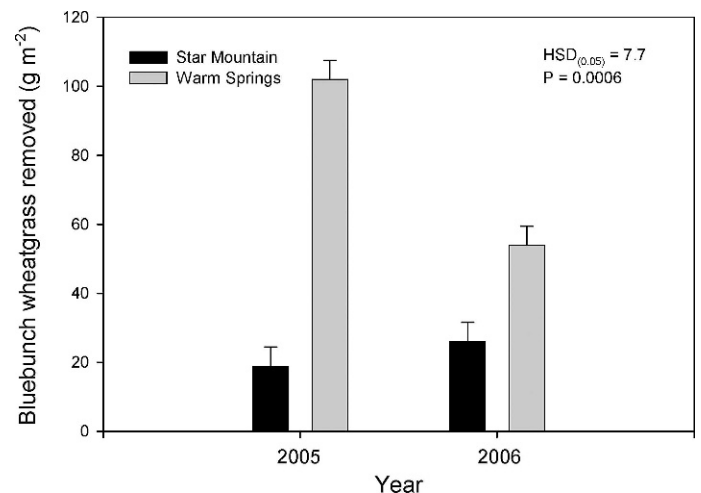


Figure 2. Effect of year on bluebunch wheatgrass biomass removed at the two sites. Error bars are plus or minus the standard error of the mean (SEM). HSD indicates Honestly Significant Difference.

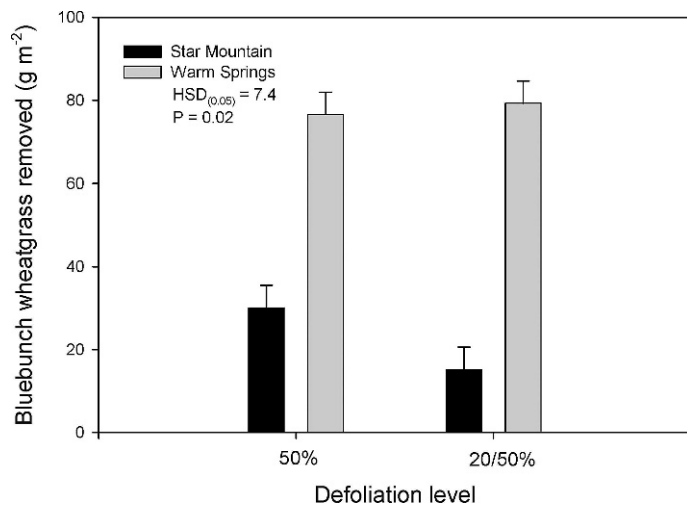


Figure 3. Effect of year on bluebunch wheatgrass biomass defoliation regime (50% peak standing crop or 20% at the 3–3.5 leaf stage and again at 50% at peak standing crop) in 2006 at Warm Springs (near Drewsey, Oregon) and across 2006 and 2007 at Star Mountain (near Riverside, Oregon) on biomass removed. Error bars are plus or minus the standard error of the mean (SEM). HSD indicates Honestly Significant Difference.

Medusahead

There were no effects of either treatment detected on medusahead density at either site in 2006 ($P \geq 0.07$). Mean density of medusahead across treatments and sites was 643 ($SE=101$) plants $\cdot m^{-2}$ that year. At Star Mountain, medusahead density ($P = 0.056$) and biomass ($P = 0.066$) depended upon the bluebunch wheatgrass defoliation regime, but the P value was slightly > 0.05 for both parameters (Figs. 4a and 4b). No defoliation and a single defoliation of 50% at peak standing crop produced about 500 plants $\cdot m^{-2}$ of medusahead, whereas a 20% defoliation at the 3 to 3.5 leaf stage followed by a 50% defoliation at peak standing crop yielded about 650 medusahead plants $\cdot m^{-2}$. No defoliation produced about 20 g $\cdot m^{-2}$ of medusahead, and 50% defoliation or 20% plus 50% defoliation of bluebunch wheatgrass increased medusahead biomass to 27 g $\cdot m^{-2}$ and 32 g $\cdot m^{-2}$, respectively (Fig. 4b).

Table 1. P values from the ANOVA on the effect of initial medusahead density, defoliation regime, and year (2006, 2007) on bluebunch wheatgrass tiller density at Star Mountain (near Riverside, Oregon).

Source	df	P value
Rep ¹	3	0.141
Medusahead density	3	0.662
Defoliation	2	0.993
Medusahead density \times defoliation	6	0.056
Yr	1	< 0.001
Medusahead density \times yr	3	0.948
Defoliation \times yr	2	0.889
Medusahead density \times defoliation \times yr	6	0.294

¹Rep (site or year) was used as the error term for site or year depending on the comparison.

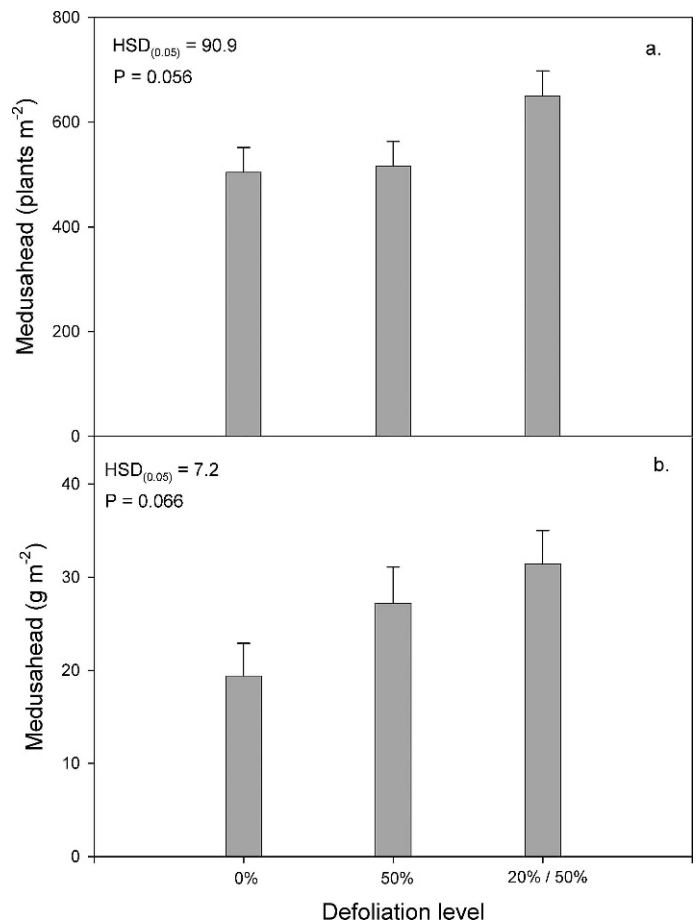


Figure 4. Effect of defoliation regime (50% peak standing crop or 20% at the 3–3.5 leaf stage and again at 50% at peak standing crop) on medusahead **a**, density and **b**, biomass in 2007 at Star Mountain. Error bars are plus or minus the standard error of the mean (SEM). HSD indicates Honestly Significant Difference.

DISCUSSION

Stimulation of the tillering process in grass plants can increase plant density and the quantity and quality of aboveground biomass production. In the Northern Great Plains, grazing that stimulated the defoliation resistance mechanisms in western wheatgrass increased tiller density (Gorder et al. 2004) and biomass production (Manske 2003). Conversely, we rejected our hypothesis that defoliating bluebunch wheatgrass by 20% at the 3 to 3.5 leaf stage followed by 50% defoliation at peak standing crop would increase its tillering and biomass production (Fig. 3). In fact, more of our data suggest that the tendency was toward less tillering, rather than more, with the early season, low-intensity defoliation.

Defoliation initiates tillering by reducing the influence of apical dominance, the physiological process by which the apical meristem and young leaves of a lead tiller exert hormonal regulation of axillary bud growth, which inhibits development of vegetative tillers (Briske 1991; Murphy and Briske 1992; Briske and Richards 1994; Briske and Richards 1995; Manske 1996). In grasses, leaf replacement after defoliation occurs most rapidly from intercalary meristems, followed by newly developed leaf primordia, and least rapidly from newly initiated

axillary buds (Cook and Stoddart 1958; Hyder 1972; Briske 1986). When the apical meristem is removed by grazing, leaf replacement originates from axillary buds, which require the greatest time interval following defoliation (Briske 1986). In contrast to the Great Plains, sagebrush-steppe plant communities in the Intermountain West have a very limited growing season because peak precipitation occurs in winter and spring, and there is limited precipitation in the summer (Fig. 1). We believe that the lack of soil moisture in June inhibited bluebunch wheatgrass growth before tillers grew from axillary buds, enough to recover from the early spring, low-intensity defoliation.

Grazing resistant grasses, such as crested wheatgrass, exhibit a greater capacity to reallocate carbon to reestablish photosynthetic tissues while temporarily decreasing allocation belowground compared to grazing intolerant species (Caldwell et al. 1981; Richards 1984). Investing in new photosynthetic tissue rapidly provides the new leaf area with the capability to enhance growth rates. Conversely, bluebunch wheatgrass expends newly assimilated carbon toward root growth immediately after defoliation (Caldwell et al. 1981). The latter strategy may constrain tiller production in this species.

We hypothesized that an increase in bluebunch wheatgrass tiller and biomass production would exert competitive pressure against medusahead and, thus, lower this weed's density and biomass. The density of seeded medusahead did not influence bluebunch wheatgrass either year. Most annual grasses possess a high degree of plasticity and low densities may have simply fostered larger plants with greater resource acquisition and growth (Sheley and Larson 1997). In 2006, we did not detect any response of medusahead to treatments. In 2007, medusahead density and biomass actually increased in the plots with the two-time defoliation at Star Mountain. Sheley et al. (1997) found that bluebunch wheatgrass populations that did not fully recover their biomass after severe defoliation were more susceptible to invasion by diffuse knapweed (*Centaurea diffusa* L.). Because severe defoliation can cause root mortality in bluebunch wheatgrass, we speculate that bluebunch wheatgrass root growth was decreased under the early, low-intensity defoliation, which, in turn, made it less competitive with medusahead for soil resources (Richards 1984). Grazing can increase the competitiveness of perennial grasses with medusahead, where decadent grasses limit their ability to acquire resources (Sheley et al. 2008). Maximizing the ability of perennial grasses to usurp resources in late spring and early summer appears critical to their ability to resist invasion. In this study, the lower biomass production (Fig. 3) of bluebunch wheatgrass in the 20% plus 50% defoliation at Star Mountain suggests reduced competitive ability and probably helps explain the higher medusahead density and biomass (Figs. 4a and 4b).

MANAGEMENT IMPLICATIONS

In the Great Plains region, ability to remove apical dominance and stimulate grass tillering and production has potential to guide the development of grazing systems that enhance overall forage production. However, our study suggests that on native rangeland in the Intermountain West, grazing 20% at the 3 to 3.5 leafy stage before 50% use in early summer does not favor bluebunch wheatgrass and tends to reduce its growth. The

relatively short growing period caused by summer drought and the relative intolerance of bluebunch wheatgrass to grazing reduce the utility of twice overgrazing, an unlikely practice for arid rangelands in the western United States. However, other defoliation regimes could illicit a more favorable response, such as those applied earlier or later in the phenological development of the grass. The grazing regime tested in this study could possibly increase annual grass invasion. In abnormally wet years, with high May and June precipitation, or with species that are more grazing tolerant (e.g., crested wheatgrass), designing grazing to increase tillering and biomass production may be possible.

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