

Defoliation increased above-ground productivity in a semi-arid grassland

MATTHEW R. LOESER, TIMOTHY E. CREWS, AND THOMAS D. SISK

Authors are Graduate Research Assistant, Department of Biological Sciences, Northern Arizona University, Box 5640, Flagstaff, Ariz. 86011-5640; Assistant Professor, Environmental Studies Program, Prescott College, 220 Grove Ave., Prescott, Ariz. 86301; and Associate Professor, Center for Environmental Sciences and Education, Northern Arizona University, Box 5694, Flagstaff, Ariz. 86011-5694. Senior author's current address: Center for Environmental Sciences and Education, Northern Arizona University, Box 5694, Flagstaff, Ariz. 86011-5694.

Abstract

In light of the continuing debate regarding overcompensation we studied the responses of above-ground biomass in a high-elevation, semi-arid grassland to defoliation, defoliation history, and livestock grazing. The above-ground annual net primary productivity (ANPP) was measured over 2 years in one-hundred twenty, 1-m² plots that were exposed to single- and multi-year defoliation and grazing treatments. Plant communities showed an average increase in ANPP of 31%–45% due to a single defoliation event. The most conservative estimate of average ANPP of defoliated subplots was 29.4 g m⁻² greater than the non-defoliated controls. A history of defoliation, due to clipping or grazing, lessened the magnitude of the compensatory response, but above-ground overcompensation of biomass was still observed, ranging on average from 17% to 26%. One dominant species, squirreltail grass [*Elymus elymoides* (Raf.) Swezeyi], accounted for nearly one-third of the community-level increases in ANPP. In contrast to above-ground patterns, below-ground root production of squirreltail did not increase in response to defoliation events. These results suggest that the above-ground production of high-elevation, semi-arid grasslands in the American Southwest may be temporarily increased through certain grazing events, and may help explain shifts in species dominance in grasslands exposed to long-term grazing by livestock.

Key Words: high-elevation grasslands, ANPP, overcompensation, clipping, root biomass, western wheatgrass, squirreltail

The hypothesis that certain plant species can respond to a defoliation event, such as grazing by an herbivore, in a manner that increases their reproductive fitness or productivity has recently attained greater acceptance in the scientific literature (Strauss and Agrawal 1999, Agrawal 2000). This response has been called "overcompensation" (Owen 1980, Owen and Wiegert 1976, 1981) to signify that production exceeds the level needed to

We gratefully acknowledge the assistance of S. Mezulis, L. Taylor, Z. Bayham, R. Rieder, G. Kendall, J. Chirco, J. White, T. Muñoz, and J. Battin in collecting these data. In addition we thank the Diablo Trust, Flying M Ranch, and the Peaks and Mormon Lake Districts of the Coconino National Forest for their participation in this collaborative research effort. This manuscript has benefited from the comments of two anonymous reviewers, the Sisk lab group, and specifically Brad McRae, Lisa Taylor, and Sharon Mezulis. This study has been supported through funding from Northern Arizona University, Merriam-Powell Center for Environmental Research, and the Ecological Restoration Institute.

Manuscript accepted 21 Feb. 04.

Resumen

A raíz del debate continuo respecto a la sobrecompensación estudiamos las respuestas de la biomasa aérea a la defoliación en una elevación alta de un pastizal semi-árido, al historial de defoliación y al apacentamiento por ganado. La productividad primaria neta anual aérea (ANPP) se midió en dos años en 120 parcelas de 1 m² que fueron expuestas a tratamientos de una sola defoliación y defoliaciones múltiples por año y tratamientos de apacentamiento. Las comunidades vegetales mostraron un incremento promedio en la ANPP del 31 al 45% debido a un solo evento de defoliación. La estimación más conservadora de la ANPP promedio de las subparcelas defoliadas fue 29.4 g m⁻² mayor que las parcelas control no defoliadas. Un historial de defoliación debido a cortes o apacentamiento redujo la magnitud de la respuesta compensatoria, pero la sobrecompensación de la biomasa aérea aun se observó, variando en promedio de 17% a 26%. Una de las especies dominantes, "Squirreltail grass" [*Elymus elymoides* (Raf.) Swezeyi], aportó casi un tercio del incremento a nivel comunidad de la ANPP. En contraste a los patrones de biomasa aérea, la producción de raíces del "Squirreltail" no se incrementó en respuesta de los eventos de defoliación. Estos resultados sugieren que la producción de biomasa aérea en elevaciones altas de los pastizales semiáridos del Suroeste de Americano puede ser temporalmente incrementada a través de ciertos eventos de apacentamiento y puede ayudar a explicar los cambios en la dominancia de especies en los pastizales expuestos a un largo plazo de apacentamiento por ganado.

merely compensate for the defoliation event. Although numerous cautionary notes and objections have been raised following early evidence for overcompensation (Belsky 1986, Bartolome 1993, Painter and Belsky 1993, Patten 1993) the debate no longer revolves around whether overcompensation exists, but rather, under what circumstances it occurs, the magnitude of the response, and how this information should be applied to guide management of plants and herbivores. Within this ongoing ecological discussion, the understanding of community-level productivity responses in western rangelands has lagged, largely because of a lack of experimentation. Nonetheless, grazing advocates have advanced the idea of overcompensation as a fundamental principle to guide rangeland management in the Southwest where grazing is among the most contentious public lands management issues (Fleischner 1994, Curtin 2002).

The "herbivore optimization hypothesis" (McNaughton 1979, Dyer et al. 1982) suggests that grassland communities may show

overall increases in productivity because of grazing, but the ecological literature regarding community-level productivity of semi-arid grasslands includes positive, negative, and neutral results. Frank et al. (2002) found herbivory stimulated above-ground annual net primary productivity (ANPP) by 21% in the grasslands of Yellowstone National Park, U.S.A. In the same study, grazing increased net below-ground productivity by 35% and total root production was 7 times greater than above-ground shoot production (Frank et al. 2002). In a shortgrass prairie, lightly grazed areas produced 20% more above-ground biomass than exclosures, but this pattern was nearly reversed when both treatments were irrigated (Varnamkhasti et al. 1995). In a global review of grazing studies, Milchunas and Lauenroth (1993) found a trend of reduced above-ground production with grazing and suggested that the results at any given locality were strongly influenced by moisture availability and evolutionary history of grazing. The arid rangelands west of the Continental Divide typically did not support herds of large mammalian herbivores during the past 11,000 years (Mack and Thompson 1982). Nevertheless, large herbivores are believed to have been present in much of this region prior to 11,000 years before present (Van Devender 1995) and could have substantially influenced the evolution of species that are now common in grasslands west of the Rockies.

To explore whether high-elevation, semi-arid grasslands in the American Southwest show signs of overcompensation or other traits suggesting tolerance of grazing despite the relatively short history (100–200 years) of frequent livestock grazing, we asked the following questions: 1) Does community ANPP show compensatory responses to defoliation? 2) If a single defoliation event affects ANPP, does the recent history (< 10 yrs) of defoliation mediate effects on ANPP? 3) Do the dominant species of this grassland respond similarly to defoliation? and 4) Does root productivity parallel trends in ANPP?

Materials and Methods

Study site – The study site was located in a high-elevation, semi-arid grassland approximately 32 km southeast of Flagstaff in north-central Arizona (34° 59' 03" N 111° 26' 30" W) at an elevation of 2,160 m. This study site occupies Upper Great Basin grassland (Brown 1994), and lies at an ecotone that includes Ponderosa

pine (*Pinus ponderosa* P.& C. Lawson) and one-seed juniper [*Juniperus monosperma* (Engelm.) Sarg.]. The herbaceous plant community is dominated by the perennial grasses, western wheatgrass [*Pascopyrum smithii* (Rydb.) A. Löve] and squirreltail [*Elymus elymoides* (Raf.) Swezey], and the subshrub, prairie sage-wort (*Artemisia frigida* Willd.). Average annual precipitation is estimated to be 500 ± 100 mm, with approximately 60% of this amount falling as snow in October through April. Summer rains from July to September account for the majority of the remaining precipitation. Annual precipitation for the duration of this study, years 2000 and 2001, was approximately 25% below the 50-year mean. July is the warmest month of the year with a mean monthly maximum temperature of 27° C, and January is the coldest month with a mean minimum temperature of –9° C.

In 1997 three, 1-ha livestock exclosures were erected in a 325-ha pasture that had been grazed by cattle in varying densities dating back to at least the late 1800's. Each exclosure was paired with a 1-ha exclosure that annually received a very high impact grazing treatment with an average stocking density of 200 cow-calf pairs ha⁻¹ for 8 hours per year. Grazing events generally occurred between June and September. This very high impact treatment was originally designed as part of another long-term research project studying the ecological effects of different grazing intensities (Sisk et al. 1999).

In 2000, 3 years after release from livestock grazing pressures, 8 experimental plots, each approximately 16 m², were randomly located within each of 3 exclosures (n = 24). Eight additional plots were located in each exclosure (n = 24). Plot locations were random, but each plot conformed to the following criteria: 1) at least 2 m from a fence-line to minimize edge effects; 2) at least 2 m from the canopy of a tree to minimize tree litterfall effects; 3) at least 2 m from other study plots; and 4) located within the half of the exclosure closest to road access, for compatibility with other ongoing studies.

In the livestock exclosures, each 16-m² experimental plot included four, 1-m² subplots arranged diagonally from one another (Fig. 1). The diagonal positioning of subplots allowed researchers access to all sides of a subplot without disturbing adjacent subplots. In May of 2000 one subplot was defoliated to a height of 2.5 cm (subplot A, Fig. 1) and subplots A and B (Fig. 1) were harvested at the end of the 2000 growing season.

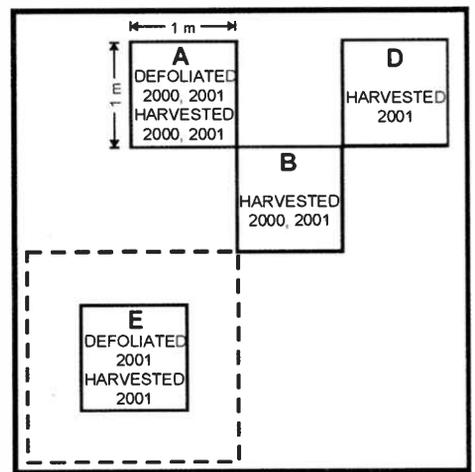


Fig. 1. Arrangement of sub-plots within each experimental plot placed in livestock exclosures. Subplot A was defoliated early in the 2000 and 2001 growing seasons; subplots A and B were harvested at the end of the growing seasons of 2000 and 2001. Subplot E was defoliated early in the 2001 growing season; subplots D and E were harvested at the end of the 2001 growing season. Plots located within the grazing exclosures (not shown) consisted of a single 1 m² subplot defoliated early in the 2000 and 2001 growing seasons and harvested at the end of each growing season.

The defoliation treatment was repeated in 2001 on subplot A and end-of-season harvests were made on subplots A and B. Two additional subplots were added (subplots D and E, Fig. 1) in 2001. The E subplots were defoliated to the same height as subplot A, but a 0.5-m perimeter was clipped around the entire E subplot. This minimized potential effects caused by a partial defoliation of plants that straddled the subplot edge. Although a buffer was not clipped around control subplots (subplots B and D, Fig. 1), we found no statistically significant effect of the buffer on ANPP (M.R. Loeser, unpublished data) and disregard it for the remainder of the discussion. Plant material was sorted by species into live or dead material, dried in an oven at 65° C for at least 48 hours, and weighed.

The B and D subplots represented non-defoliated controls. All above-ground growth in subplot B represented 2001 ANPP because its biomass was harvested at the end of the 2000 growing season. A second control (subplot D, Fig. 1) was implemented to address speculation that end-of-season biomass harvests lessened ANPP. Production in D subplot was more challenging to measure because end-of-season biomass collections tend to underestimate ANPP due to early senescence of plant parts. To compensate for this possi-

ble bias, we collected dead biomass from E subplots early in the growing season, calculated the average dry weight (13.2 g m^{-2}), and subtracted this from the total year-end biomass harvest (live + dead) of subplot D. The remainder for each subplot D was considered the ANPP for 2001.

We chose clipping as a surrogate for ungulate herbivory, and therefore some caution should be used in applying results from this study to grazing animals. The extent of the clipping in this study generally exceeded 80% of above-ground biomass (M. Loeser, pers. obs.) to represent the upper limits of biomass removal rather than an average grazing event. Furthermore, Reardon et al. (1972) suggested that animal saliva can stimulate shoot production in addition to the effects of clipping. For the purposes of this study, we argue that limitations of clipping are minor in contrast to the logistical benefits of controlling defoliation timing, location and extent.

ANPP response to defoliation – Comparisons of 2001 ANPP were made between single-year defoliated subplots (subplot E, Fig. 1), 2 consecutive years of defoliation (subplot A, Fig. 1) and non-defoliated controls (subplots B and D, Fig. 1). The primary control was subplot B, which provided a more conservative, direct measure of non-defoliated ANPP due to the end-of-season harvest in 2000. To test for statistical differences in ANPP, we used a partly-nested analysis of variance (ANOVA) examining treatment and enclosure as main factors, the interaction of main factors, and plots nested within enclosures. A post hoc test was applied if the model was significant (Sokal and Rohlf 1995). This analysis and all subsequent analyses were completed with the JMP software (SAS 2001).

To more closely simulate the effects of livestock grazing, twenty-four, 1-m^2 plots (no figure shown) located in the cattle-grazed enclosures received early-season defoliations on the same schedule as the A subplots in the livestock enclosures. In 2000, livestock grazed the enclosures within 7 days after the clipping to minimize the loss of grazeable biomass, while other impacts of grazing (e.g. trampling, urination, and defecation) remained. In 2001, livestock grazed after the harvests were complete. Defoliated subplots in the grazed enclosures were compared with non-defoliated controls (subplot B, Fig. 1). These data were analyzed with a one-way ANOVA blocked by the enclosure-exclosure pairs. One outlier was removed from the defoliated treatment because its ANPP was greater than 2 standard deviations above the mean, and due to the blocked

design one non-defoliated control was removed at random.

ANPP responses of dominant species – The extent of ground covered by just a few species exceeded 50% of the ground cover. To explore the importance of the contribution of individual species to overall ANPP responses, we separated biomass collections of single-year defoliated subplots (subplot E, Fig. 1) and non-defoliated subplots (subplot B, Fig. 1) into the 3 dominant species (western wheatgrass, squirreltail, and prairie sagewort) and an Other group (all remaining species). Within each category the effects of defoliation on ANPP were analyzed with a t-test.

Root productivity of squirreltail – Root production of a randomly selected squirreltail plant in both defoliated (subplot E, Fig. 1) and non-defoliated treatments (subplot D, Fig. 1) was measured in June 2001 by placing in-growth root cores (Fahey et al. 1999) at the base of each selected plant. In-growth root cores were mesh bags (5-cm wide, 10-cm deep with 0.2-cm^2 holes) filled with root-free soil and placed in a similarly sized hole at the base of a squirreltail plant. After summer rains ended in 2001 mesh bags were collected and taken back to the laboratory. Organic debris were sieved from each mesh bag and one-quarter of the total was randomly subsampled for careful dissection. Roots were isolated, dried at 65°C for at least 48 hours, and weighed. These data were \log_{10} transformed to normalize their distribution and comparisons between the defoliated and non-defoliated treatments were analyzed with paired t-tests.

ANPP response to defoliation – ANPP of this high-elevation, semi-arid grassland was increased by 27% even when defoliation occurred in 2 consecutive years (Fig. 2, $F = 7.159$, $df = 2$, $P = 0.002$). No other factors were significant in the ANOVA model. The average ANPP of the subplots defoliated for 2 consecutive years (subplot A, Fig. 1) was 120.8 g m^{-2} while the average ANPP of the non-defoliated control (subplot B, Fig. 1) was 95.2 g m^{-2} . Moreover, a single year of defoliation (subplot E, Fig. 1) increased aboveground biomass by 31% compared with the non-defoliated control (subplot B, Fig. 1) and by 45% when compared with the secondary non-defoliated control (subplot D, Fig. 1). These results suggest plant community tolerance to grazing and were corroborated by subplots located in grazing enclosures that had been exposed to annual livestock grazing for more than 100 years. Defoliated subplots in grazing enclosures had an average ANPP of 113.9 g m^{-2} , which represented 20% more aboveground biomass than the non-defoliated control (Fig. 3, $F = 8.293$, $df = 1$, $P = 0.006$).

The results of this study corroborate other studies (Fahnestock and Detling 1999, Eneboe et al. 2002) that show positive responses of ANPP to defoliation, and many mechanisms have been hypothesized to explain increases in an individual plant's ANPP (see McNaughton 1979, Turner et al. 1993, and Frank et al. 2002). Defoliation may have direct effects on

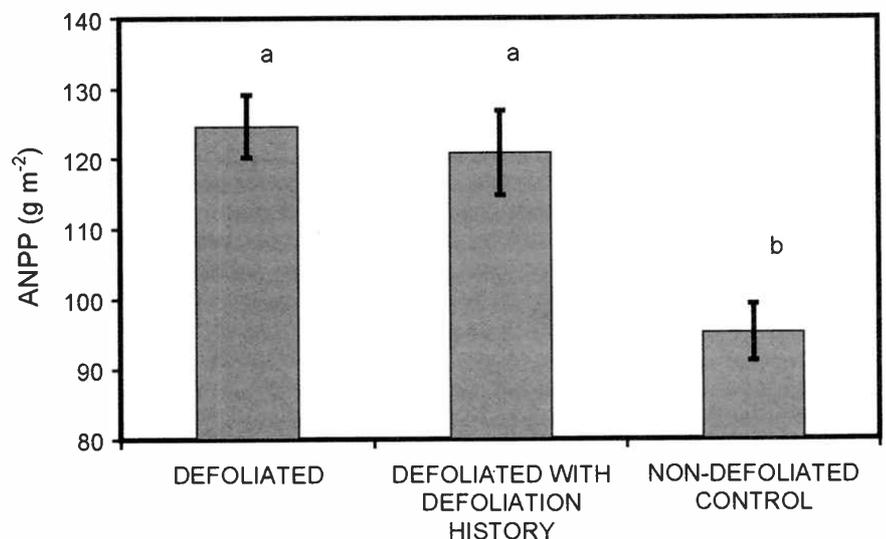


Fig. 2. A comparison of ANPP in defoliated (subplot E), defoliated with recent history of defoliation (subplot A) and non-defoliated (subplot B) treatments. Single-year defoliated subplots had 31% higher average ANPP than adjacent non-defoliated subplots, and second-year defoliated subplots had 27% higher average ANPP ($F = 7.159$, $df = 2$, $p = 0.002$). Different letters denote statistical significance.

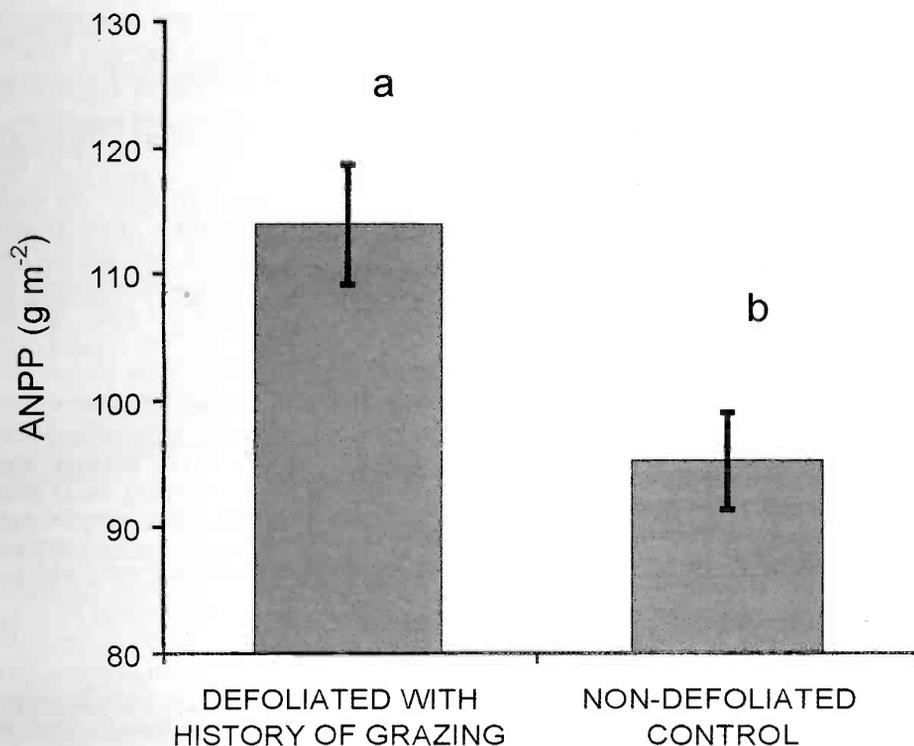


Fig. 3. A comparison of non-defoliated (subplot B) and defoliated treatments where the defoliated plots had more than a 100-year history of livestock grazing. Clipping in plots with ongoing livestock grazing yielded 20% higher ANPP on average, than the non-defoliated controls ($F = 8.293$, $df = 1$, $p = 0.006$).

individual plant productivity by increasing photosynthetic rates or growth of photosynthetically-active leaf tissue (Wareing et al. 1968), extending photosynthetic capabilities in ageing leaves (Gifford and Marshall 1973), translocating nutrients from below-ground to above-ground (Kinsinger and Shaulis 1961), and lowering respiratory costs through a reduction of transpiring surfaces (Baker and Hunt 1961). While these plant responses may occur in individual plants, they are likely to be mediated by the physical and biological consequences of specific defoliation events that occur at the community scale. Turner et al. (1993) suggested 3 mechanisms that may be occurring at the community level. First, defoliation of plant communities may provide greater light availability to all constituents by changing the structure to a more open canopy. While this may be important in mesic grasslands like the tallgrass prairie, the high-elevation grasslands of this study are comprised of plants with relatively low stature and it's unlikely that light is limiting. Second, in the case of grazing by herbivores, soil N availability may increase due to feces, urine, or increased root mortality (Frank and Groffman 1998). Again, this mechanism seems unlikely in this study because our findings showed increased above-ground biomass with clipping and no

manipulation of soil N availability. The final mechanism proposed by Turner et al. (1993) suggests that clipping may allow for greater water availability by decreasing the amount of vegetation that intercepts and, subsequently, loses precipitation due to evapotranspiration. The latter may be the most important mechanism and explanation of patterns found in this study. Soil water has been shown to have a positive relationship with the productivity of semi-arid range plants (Eneboe et al. 2002). However, our current study did not evaluate differences in soil water because of defoliation. Ongoing research at this site may shed light on soil water dynamics.

In addition to the community-level consequences of a single defoliation event, the history of defoliation can affect the degree to which plants are able to compensate. In this study, the lowest compensation response was found in the grazing enclosures (20% increase over non-defoliated control), an intermediate response (27% increase over non-defoliated controls) for the subplots with 2 consecutive years of defoliation, and maximum response (31% increase over non-defoliated controls) for subplots with no recent history of defoliation. Our results corroborate the findings of other studies (Aldous 1930, Turner et al. 1993, Varnamkhasti et al. 1995). In the significantly more mesic tallgrass prairie

Aldous (1930, reprinted in Turner et al. 1993) found that repeated mowing decreased over compensation above-ground biomass by as much as 85% over the course of 3 years. Turner et al. (1993) found grazing history lessened the compensatory response of a tallgrass prairie to a greater extent in a drought year than in a year with average precipitation. Similar findings were reported by Varnamkhasti et al. (1995), who showed long-term, heavy grazing in shortgrass prairie lowered above-ground productivity compared to long-term, light grazing when water was a limiting resource. It is likely that defoliation history interacts with resource supply (Heitschmidt et al. 1999, Maschinski and Whitham 1989, Varnamkhasti et al. 1995) and species characteristics (Diaz et al. 2001) to determine compensatory responses.

ANPP responses of dominant species – Three plant species comprised 82% of the above-ground biomass in this semi-arid grassland. Prairie sagewort, a perennial forb that reproduces rhizomatously, represented 34% of the total above-ground biomass. The native perennial grasses, western wheatgrass and squirreltail, represented 35% and 13% of above-ground biomass, respectively. Western wheatgrass and squirreltail are considered native grasses of the western U.S., however both are thought to have greatly expanded their distribution across northern Arizona within the last 100 years (M. Loeser, unpublished data). Western wheatgrass has been frequently seeded in rangelands across the Southwest, however there is no evidence that this study site was directly seeded (J. Metzger, pers. comm.).

The ANPP of these 3 species and a fourth category comprised of all other plant species was evaluated. In our study, 2 of 3 dominant species accounted for the majority of the above-ground overcompensation. Defoliating squirreltail resulted in twice as much ANPP as in the control treatment ($df = 46$, $t = -3.359$, $P = 0.0016$; Fig. 4). Although prairie sagewort showed higher average ANPP in the defoliated treatment than in the non-defoliated treatment the difference was not statistically significant ($df = 46$, $t = -1.501$, $P = 0.140$; Fig. 4). The ANPP of western wheatgrass and the Other category were not significantly different from the control (western wheatgrass: $df = 46$, $t = -0.554$, $P = 0.582$; Other: $df = 46$, $t = -0.002$, $P = 0.998$; Fig. 4). This suggests that increases in community-level ANPP were driven primarily by squirreltail and, to a lesser degree, prairie sagewort.

Variation in responses of grassland plant communities to defoliation may be

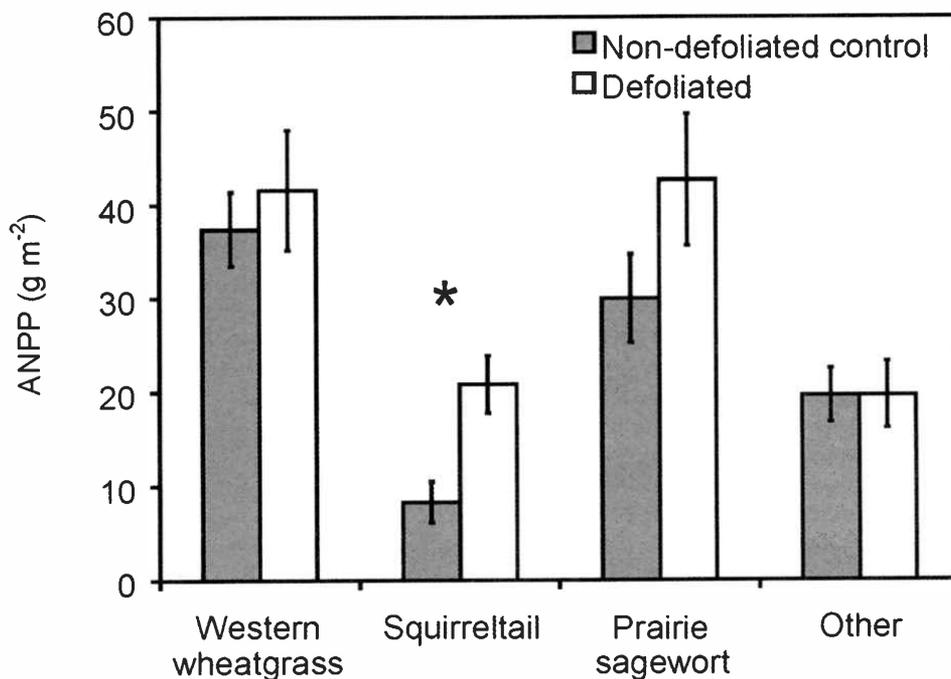


Fig. 4. Average ANPP of 3 dominant species and all other species combined for non-defoliated and defoliated treatments. The comparison of squirreltail showed the only statistically significant difference ($df = 46$, $t = -3.359$, $p = 0.0016$), but all 3 dominant species contributed to the observed community-level effects. The asterisk represents a statistically significant difference.

explained by individual species responses in a given environment. While all 3 dominant species are considered native, observations by local ranchers suggest that squirreltail became dominant in this grassland only within the last 90 years (J. Metzger, pers. comm., see 1912 plant surveys in Noel and Hill 1912). Squirreltail and the subshrub, prairie sagewort, have a high tolerance to grazing (Bai and Romo 1996, Jones 1998). While western wheatgrass has also shown tolerance to grazing (Eneboe et al. 2002), its biomass was relatively stable with defoliation in our study. Our results show that individual grazing events may enhance productivity, but long-term (decadal or more) increases in productivity may be more directly the result of increases in abundance of grazing-tolerant species. In this positive feedback model, grazing intolerant species would be replaced by more tolerant species, and landscape level productivity would be increased at the expense of plant diversity.

Root productivity of squirreltail – Comprehensive understanding of the effects of grazing on grassland functioning requires studies of whole-plant productivity, but research efforts on below-ground responses have not kept pace with those on above-ground responses. We compared root productivity of squirreltail in the defoliation treatment with non-defoliated

controls and found no statistically significant difference ($df = 22$, $t = -1.689$, $P = 0.105$; Fig. 5). Average root productivity of squirreltail in the defoliated treatment was $0.051 \text{ g root-core}^{-1} \text{ growing season}^{-1}$ while the average root productivity of the non-defoliated plants was $0.076 \text{ g root-core}^{-1} \text{ growing season}^{-1}$.

Root responses to defoliation have widely varied responses in the literature. A review by Dawson et al. (2000) concluded that above-ground defoliation commonly results in a decline in root mass (e.g. Holland and Detling 1990, Mawdsley and Bardgett 1997, Ruess et al. 1998). There is specific evidence suggesting defoliation may trigger a shift from below-ground carbon allocation to above-ground shoot production in some species (Richards 1984), which may lower root productivity in the short-term. The long-term consequences are difficult to predict because increased shoot growth may stimulate greater photosynthate production and subsequent below-ground productivity. In a temperate grassland, long-term grazing increased below-ground productivity by 35% (Frank et al. 2002). However McNaughton et al. (1998) found long-term grazing had no significant effect on root productivity, but environmental factors such as soil type and precipitation influenced differences over 6 orders of magnitude. In this study, the substantial variabil-

ity in root responses may have lessened our ability to detect a response. Further studies should include more extensive replication.

Management implications – The history of research and debate regarding the “overcompensation hypothesis” includes considerable hyperbole (Painter and Belsky 1993). Our study indicates that this high-elevation, semi-arid grassland in northern Arizona exhibits some level of resilience to herbivory. The clipping used in this experiment may differ qualitatively from livestock grazing, yet effects were evident in combination with intensive livestock grazing. We do not, however, suggest that all forms of grazing would yield increases in above-ground productivity. The very high impact, short duration grazing style practiced in this study was implemented to mimic dense herding behavior along with associated dramatic changes of plant communities and soil structure. This particular management style involves logistical obstacles that limit its practical application as a management tool and the appropriateness of high-impact grazing practices in arid grasslands has been contested. Moreover, our results on the influence of defoliation history are consistent with other studies that have shown a decline of compensatory responses after multiple defoliation events (Turner et al. 1993, Varnamkhasti et al. 1995) suggesting that repeated overgrazing may inhibit

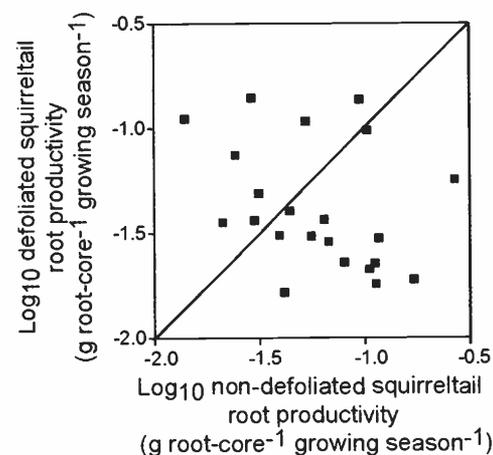


Fig. 5. The relationship of root productivity of squirreltail in defoliated and non-defoliated treatments. Root productivity of defoliated squirreltail did not differ significantly from non-defoliated plants ($df = 22$, $t = -1.689$, $p = 0.1054$). These data were log transformed to improve normality of the distribution. The reference line represents a 1:1 correlation. Data points above the line represent overcompensation while those below the line represent undercompensation.

plant recovery and community resilience. Nonetheless, the significant increases in productivity in these intensively grazed plots suggest that these grasslands can tolerate some livestock management regimes. Thus our results provide insight about short-term responses of high-elevation, semi-arid grasslands to herbivory, while continuing studies at this site should address many of the additional processes that determine the suitability or sustainability of particular grazing practices.

Literature Cited

- Agrawal, A. A. 2000.** Overcompensation of plants in response to herbivory and the by-product benefits of mutualism. *Trends in Plant Sci.* 5:309–313.
- Aldous, A. E. 1930.** Effect of different clipping treatments on the yield and vigor of prairie grass vegetation. *Ecology* 11:752–759.
- Bai, Y. and J. T. Romo. 1996.** Fringed sagebrush response to sward disturbances: seedling dynamics and plant growth. *J. Range Manage.* 49:228–233.
- Baker, J. N. and O. J. Hunt. 1961.** Effects of clipping treatments and clonal differences on water requirement of grasses. *J. Range Manage.* 14:216–219.
- Bartolome, J. W. 1993.** Application of herbivore optimization theory to rangelands of the western United States. *Ecol. Appl.* 3:27–29.
- Belsky, A. J. 1986.** Does herbivory benefit plants? A review of the evidence. *The American Nat.* 127:870–892.
- Brown, D. E. 1994.** Biotic communities: southwestern United States and northwestern Mexico. University of Utah Press, Salt Lake City, Ut.
- Curtin, C. G. 2002.** Livestock grazing, rest, and restoration in arid landscapes. *Cons. Bio.* 16:840–842.
- Dawson, L. A., S. J. Grayston, and E. Paterson. 2000.** Effects of grazing on the roots and rhizosphere of grasses, p. 61–84 *In:* G. Lemaire, J. Hodgson, A. de Moraes, C. Nabinger, and P. C. de F. Carvalho, (ed.) *Grassland ecophysiology and grazing ecology.* CABI Publishing, Cambridge, U.K..
- Diaz, S., I. Noy-Meir, and M. Cabido. 2001.** Can grazing response of herbaceous plants be predicted from simple vegetative traits? *J. Appl. Ecol.* 38:497–508.
- Dyer, M. I., J. K. Detling, D. C. Coleman, and D. W. Hilbert. 1982.** The role of herbivores in grasslands, p. 255–295 *In:* J. R. Estes, R. N. Tylr, and J. N. Brunken, (ed.) *Grasses and grasslands: systematics and ecology.* University of Oklahoma Press, Norman, Okla..
- Eneboe, E. J., B. F. Sowell, R. K. Heitschmidt, M. G. Karl, and M. R. Haferkamp. 2002.** Drought and grazing: IV. blue grama and western wheatgrass. *J. Range Manage.* 55:73–79.
- Fahey, T. J., C. S. Bledsoe, F. P. Day, R. W. Ruess, and A. J. M. Smucker. 1999.** Fine root production and demography, p. 437–451 *In:* G. P. Roberston, D. C. Coleman, C. S. Bledsoe, and P. Sollins, (ed.) *Standard soil methods for long-term ecological research.* Oxford University Press, New York, N.Y..
- Fahnestock, J. T. and J. K. Detling. 1999.** Plant responses to defoliation and resource supplementation in the Pryor Mountains. *J. Range Manage.* 52:263–270.
- Fleischner, T. L. 1994.** Ecological costs of livestock grazing in western North America. *Cons. Bio.* 8:629–644.
- Frank, D. A. and P. M. Groffman. 1998.** Ungulate vs. landscape control of soil C and N processes in grasslands of Yellowstone National Park. *Ecol.* 79:2229–2241.
- Frank, D. A., M. M. Kuns, and D. R. Guido. 2002.** Consumer control of grassland plant production. *Ecol.* 83:602–606.
- Gifford, R. M. and C. Marshall. 1973.** Photosynthesis and assimilate distribution in *Lolium multiflorum* Lam. following differential tiller defoliation. *Aus. J. Bio. Sci.* 26:517–526.
- Heitschmidt, R. K., M. R. Haferkamp, M. G. Karl, and A. L. Hild. 1999.** Drought and grazing: I. Effects on quantity of forage produced. *J. Range Manage.* 52:440–446.
- Holland, E. A. and J. K. Detling. 1990.** Plant response to herbivory and belowground nitrogen cycling. *Ecol.* 71:1040–1049.
- Jones, T. A. 1998.** Viewpoint: The present status and future prospects of squirreltail research. *J. of Range Manage.* 51:326–331.
- Kinsinger, F. E. and N. Shaulis. 1961.** Carbohydrate content of underground parts of grasses as affected by clipping. *J. Range Manage.* 14:9–12.
- Mack, R. N. and J. N. Thompson. 1982.** Evolution in steppe with few large, hooved mammals. *The Amer. Nat.* 119:757–773.
- Maschinski, J. and T. G. Whitham. 1989.** The continuum of plant responses to herbivory: the influence of plant association, nutrient availability, and timing. *The Amer. Nat.* 134:1–19.
- Mawdsley, J. L. and R. D. Bardgett. 1997.** Continuous defoliation of perennial ryegrass (*Lolium perenne*) and white clover (*Trifolium repens*) and associated changes in the microbial population of an upland grassland soil. *Biol. and Fert. Soils* 24:52–58.
- McNaughton, S. J. 1979.** Grazing as an optimization process: grass-ungulate relationships in the Serengeti. *The Amer. Nat.* 113:691–703.
- McNaughton, S. J., F. F. Banyikwa, and M. M. McNaughton. 1998.** Root biomass and productivity in a grazing ecosystem: the Serengeti. *Ecol.* 79:587–592.
- Milchunas, D. G. and W. K. Lauenroth. 1993.** Quantitative effects of grazing on vegetation and soils over a global range of environments. *Ecol. Monog.* 63: 327–366.
- Noel, J. S. and R. R. Hill. 1912.** Forest atlas of the national forests of the United States: Coconino. U.S. Geol. Surv.
- Owen, D. F. 1980.** How plants may benefit from the animals that eat them. *Oikos* 35:230–235.
- Owen, D. F. and R. G. Wiegert. 1976.** Do consumers maximize plant fitness? *Oikos* 27:488–492.
- Owen, D. F. and R. G. Wiegert. 1981.** Mutualism between grasses and grazers: an evolutionary hypothesis. *Oikos* 36:376–378.
- Painter, E. L. and A. J. Belsky. 1993.** Application of herbivore optimization theory to rangelands of the western United States. *Ecol. Appl.* 3:2–9.
- Patten, D. T. 1993.** Herbivore optimization and overcompensation: does native herbivory on western rangelands support these theories? *Ecol. Appl.* 3:35–36.
- Reardon, P. O., C. L. Leinweber, and L. B. Merrill. 1972.** The effect of bovine saliva on grasses. *J. Animal Sci.* 34:897–898.
- Richards, J. H. 1984.** Root growth response to defoliation in two *Agropyron* bunchgrasses: field observations with an improved root periscope. *Oecologia* 64:21–25.
- Ruess, R. W., R. L. Hendrick, and J. P. Bryant. 1998.** Regulation of fine root dynamics by mammalian browsers in early successional Alaskan Taiga forests. *Ecol.* 79:2706–2720.
- Savory, A. 1988.** Holistic resource management. Island Press, Washington, D.C., USA.
- SAS Institute. 2001.** JMP version 4.0.4. SAS Institute Inc., Cary, N.C..
- Sisk, T. D., T. E. Crews, R. T. Eisefeldt, M. King, and E. Stanley. 1999.** Assessing impacts of alternative livestock management practices: raging debates and a role for science, p. 89–103 *In:* C. van Riper, III and M. A. Stuart, (ed.) *Fourth Biennial Conference of Research on the Colorado Plateau.* U.S.G.S., Flagstaff, Ariz.
- Sokal, R. R. and F. J. Rohlf. 1995.** *Biometry.* W.H. Freeman and Co., New York, N.Y..
- Strauss, S. Y. and A. A. Agrawal. 1999.** The ecology and evolution of plant tolerance to herbivory. *Trends in Res. in Ecol. and Evol.* 14:179–185.
- Turner, C. L., T. R. Seastedt, and M. I. Dyer. 1993.** Maximization of aboveground grassland production: the role of defoliation frequency, intensity, and history. *Ecol. Appl.* 3:175–186.
- Van Devender, T. R. 1995.** Desert grassland history, changing climates, evolution, biogeography, and community dynamics, p. 68–99 *In:* M. P. McClaran and T. R. Van Devender, (ed.) *The desert grassland.* The University of Arizona Press, Tucson, Ariz.
- Varnamkhasti, A. S., D. G. Milchunas, W. K. Lauenroth, and H. Goetz. 1995.** Production and rain use efficiency in short-grass steppe: grazing history, defoliation, and water resource. *J. Veg. Sci.* 6:787–796.
- Wareing, P. F., M. M. Khalifa, and K. J. Treharne. 1968.** Rate limiting processes in photosynthesis at saturating intensities. *Nature* 220:453–457.