Defoliation time and intensity of wall barley in the Mediterranean rangeland

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Abstract

Wall barley (*Hordeum murinum* L.) is the dominant species in northeastern rangeland of Jordan that decreases under grazing. We investigated the responses of wall barley to clipping time and height during 2 growing seasons in the semi-arid rangeland of Jordan. A natural stand was utilized to conduct the experiments that were arranged in a randomized complete block design during 1994/95 and 1995/1996 growing seasons. Treatments were combinations of clipping heights (5 or 10 cm above soil surface) and plant growth stages (tillering, jointing, or booting), in addition to unclipped check. Results showed that clipping to 5 and 10 cm stubble height at tillering produced 1,167 and 1,349 kg ha^{-1} dry matter, respectively, compared to 1,122 kg ha^{-1} for unclipped check. Clipping to 5 and 10 cm stubble height reduced shoot weight by 28 and 21% at jointing stage and 52 and 38% at booting stage. Defoliation during tillering stage did not impact plant height of regrowth nor seed yield. Weed biomass were higher when plant defoliation was delayed to the jointing and booting stages. Therefore, it is recommended to defoliate wall barley early at tillering stage but before plants reach jointing or reproductive stages.

Key Words: Jordan, *Hordeum murinum* L. clipping, plant height, shoot, seed, annual grass, weeds

Resumen

"Wall barley" (*Hordeum murinum* L.) es la especie dominante de los pastizales del noreste de Jordania y la cual decrece bajo el apacentamiento. En un pastizal semiárido de Jordania investigamos durante 2 estaciones de crecimiento, 1994/1995 y 1995/ 1996, la respuesta del "wall barley" a la época e intensidad de defoliación. Se utilizó una población natural para conducir los experimentos, los cuales se establecieron bajo un diseño de bloques completos al azar. Los tratamientos fueron combinaciones de alturas de corte (5 o 10 cm arriba de la superficie del suelo) y etapas de crecimiento de la planta (ahijamiento, encañe o embuche), y se tuvo un testigo si cortar. Los resultados mostraron que el corte a los 5 o 10 cm efectuados en el ahijamiento produjeron 1,167 y 1,349 kg ha^{-1} de materia seca respectivamente, comparado con 1122 kg ha^{-1} producidos por el testigo sin defoliar. Cortar a 5 o 10 cm de altura del rastrojo remanente redujo el peso de los tallos en 28 y 21 % cuando los cortes se realizaron en la etapa de encañe y en 52 y 38% cuando se efectuaron en la etapa de embuche. La defoliación durante la etapa de ahijamiento no impactó la altura del rebrote ni la producción de semilla. La biomasa de la maleza fue mayor cuando la defoliación fue retrasada hasta los estados de encañe o embuche. Por lo tanto, es recomendable defoliar a "wall barley" en la etapa de ahijamiento, pero antes de que las plantas alcancen el estado de encañe o la etapa reproductiva.

Jordanian grassland is located within the 200 to 350 mm rainfall zone of the eastern Mediterranean region. This semi-arid rangeland occupies an important part of the country and needs to be well understood to achieve optimum management. Vegetation dynamics and seasonal growth patterns need special attention as many plant communities are exposed to long-term overgrazing. Wall barley (*Hordeum murincum* L.) is an annual native grass that is the key species for many local plant communities in semiarid rangelands. Wall barley withstands the harsh climatic conditions of dry areas by its ability to reproduce readily from seed and to recover quickly from drought events.

Deciding when and to what extent plants should be defoliated are considered the most critical and difficult tasks that a range manager must undertake. Understanding plant responses

to defoliation allows manager to choose the proper timing for plant use and rest which permits better management of range plant communities (Jameson and Huss 1959). Plant response to green material removal varies greatly among seasons and defoliation intensities. Defoliation timing and frequency affects range grass development (Mullahey et al. 1990). Miller and Donart (1979) reported that forage production and crown diameters of 2 grass species were affected by forage removal season and quantity. The most critical period was during the reproductive stage. Plants become more sensitive to defoliation as reproductive stage is approached (Tarassoum 1982, Moser and Perry 1983). Dual purpose barley (*H. spontaneum* L) yield was reduced by late clipping (AL-Rawi et al. 1995). The ability of grasses to regrow after defoliation depends on plant genotype and the amount of green leaf tissue remaining in the stubble (Davies 1974). Plant injuries decreased with

increasing stubble heights after clipping *Agropyron spicatum* (Sullivan and Sprague 1953, Mclean and Wikeen 1985). Dual purpose barley is becoming more popular in Iraq because it tolerates grazing at the pre-stem elongation stage (AL-Rawi et al. 1995). Grazing barley at pre-stem elongation stage can recover and produce grain equivalent to ungrazed stand (Morey 1961). However, severe defoliation of many semiarid range species was detrimental when defoliated plants relied upon nutrient reserves for regrowth (Trlica and Cook 1971). Therefore, knowledge of defoliation extent and timing is crucial for successful management of annual species such as wall barley range.

Jordanian rangeland is subjected to continuous livestock overgrazing, and thorough understanding of vegetation dynamics is not available. The responses of wall barley to defoliation has not been reported. The objective was to determine the responses of wall barley to clipping time and height in the semiarid rangelands of Jordan.

Materials and Methods

Study Area

Field studies were conducted on the Jordan University of Science and Technology Experimental Station (JUSTES) located 22 km east of Irbid (32° 34' N, 36° 0' E) in the 1994/95 and 1995/96 growing seasons. The site has an altitude of 520 m and is characterized by a flat to gently rolling topography with less than 8% slope. The soil is brown weakly cracked, calcareous, deep silty clay with a pH of 6.8. Natural vegetation at JUSTES is a typical Mediterranean semiarid grassland with the dominating species being *Hordeum* spp., *Avena fatua* L. and *Trigonella* spp. This site was subjected to long term overgrazing and cultivation until 1986, after that it was partially protected from
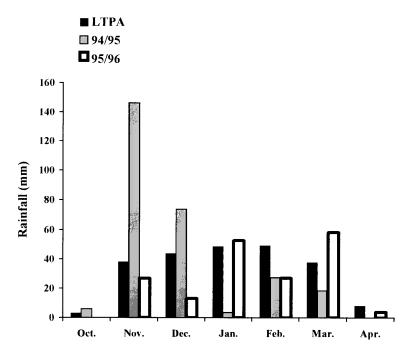

Fig. 1. Rainfall distribution for 1994/95, 1995/96 growing seasons and long-term precipitation average (LTPA) at JUSTES.

intensive agricultural use. The long-term precipitation average (LTPA) for the site is 230 mm, whereas annual rainfall for the 1994/95 and 1995/96 growing seasons were 275 and 182 mm, respectively (Fig. 1).
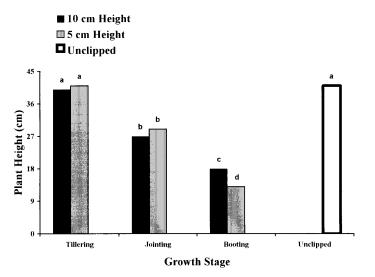
Treatment and Statistical Analysis

Field plots of 6 x 5 m were established on a native stand of wall barley. Treatments were combinations of clipping height (5 or 10 cm above soil surface) and timing, that corresponded to plant growth stages of tillering, jointing, and booting. Tillering is the growth stage at which 50% of the plant tillers have 4 leaves per tiller; jointing is the stage at which the second node appear in 50% of the tillers; and booting is the stage that immediately precedes the emergence of the inflorescence from the sheath of the flag leaf in approximately 30% of tillers. Treatment combinations and an unclipped check were replicated
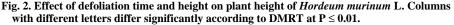
3 times and arranged in a randomized complete block design. All plots were harvested to 5 cm stubble height at seed maturity.
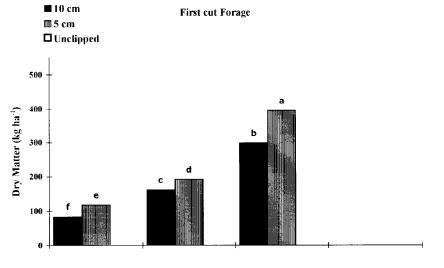
Data collected each year included; plant height (average of 3 vertical measurements from the soil surface to the highest point in the plant and soil surface recorded at physiological seed maturity); total oven-dry forage weight determined by adding the weight of tops removed at the time of defoliation to the total forage weight (vegetative shoot part weight) at time of harvest. Oven dry weight was obtained by heating shoot at 70°C for 48 hours. Seed yield was determined by threshing and cleaning dry heads. Weed biomass was also determined at the end of the season by weighing aboveground weeds after drying at 70°C for 48 hours. All weight measurements were collected for 1 m² quadrats. Analysis of variance (Table 1.) for data combined over the 2 years were performed as outlined for a randomized
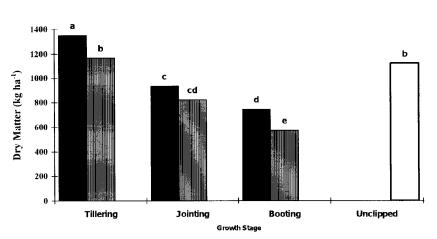
Table 1. Mean square and source of variation table showing the effect of defoliation time and height of *Hordeum murinum* L.

Source of Variation	df	Plant height		Forage yield		First cut forage		Seed yield		Weed biomass	
						Mean Square					
Year	1	0.46		7817.36		9102.26		11270.10		586.90	
Error (a)	4	4.12		1798.43		229.17		1074.70		725.00	
Treatment	6	788.00	**	436388.80	**	638564.07	**	266279.30	**	53457.30	**
Treatment*Year	6	11.00		11221.47		3476.45	**	699.90		246.20	*
Error (b)	24	5.13		4943.71		3088.52		1182.00		707.04	

Fig. 2. Effect of defoliation time and height on plant height of *Hordeum murinum* L. Columns with different letters differ significantly according to DMRT at P ≤ 0.01.

Fig. 3. Effect of defoliation time and height on first cut (top) and total forage yield (bottom) of *Hordeum mirinum* L. Columns with different litters differ significantly according to DMRT at P ≤ 0.01.
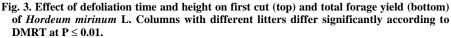
complete block design using MSTATC computer program (Michigan State University). Means were separated by Duncan's Multiple Range Test (DMRT) at P<0.01 (Steel and Torrie 1980).

Results and Discussion

Rainfall

Variation in rainfall total and distribution were high between the 2 seasons which is expected for semiarid lands (Noy-Meir and Seligman 1979). In 1994/95, more than 50 % of rain occurred during November, whereas March and April were dry months (Fig. 1). This poor distribution masked the effect of high precipitation on plant growth. Although the precipitation for 1995/96 was lower than LTPA, the distribution was better especially during the period from January to April. This allowed the plant to produce forage yields equivalent to that produced in 1994/95.

Plant Height

Clipping plants during the tillering stage did not affect plant height when measured at physiological maturity (Fig. 2). However, wall barley height was significantly reduced when clipping was performed at the jointing (27 and 29 cm) and boot stage (13 and 18 cm). Clipping height effects were only observed when cutting was practiced at boot. Wall barley height was greatly reduced when plants were clipped 5 cm above soil surface at the boot stage.

Forage Yield

Forage production from the first cut increased with decreasing clipping height (Fig. 3). The greatest forage yield (1349 kg ha⁻¹) was obtained when wall barley plants were clipped to 10 cm above soil surface at tillering stage (Fig. 3). However, clipping wall barley plants to 5 cm above soil surface at tillering lower ed forage yield (1,167 kg ha⁻¹) but was equivalent to unclipped checks. This indicates that clipping heights of 5 and 10 cm at tillering stage did not impede regrowth following clipping in wall barley. Barley herbage at tillering stage has high protein content equivalent to that of forage legumes (Droushiotis and Wilman 1987) which may also improve animal feed quality. Similar results were
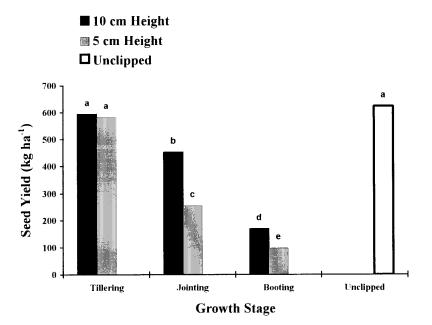
Fig. 4. Effect of defoliation time and height on seed yield of *Hordeum murinum* L. Columns with different letters differ significantly according to DMRT at P ≤ 0.01.

obtained where clipping heights of 4 and 10 cm did not affect forage yield of meadow foxtail stand (Smith et al. 1973). However, a 10 cm stubble height clipping improved plant forage yield but this yield was reduced when plants were clipped down to 5 cm stubble height (Leyshon and Campbell 1992). Previous observations indicated that plant responses to defoliation were highly variable among time and intensity of defoliation (Miller and Donart 1979), and the most critical defoliation time was either during the reproductive stage or under unsuitable environmental conditions (Mullahey et al. 1990). In addition, clipping height generally has less influence on forage yield than clipping time (Dovel 1996). This agrees with our result where plant defoliation during jointing or booting stages reduced forage yield. These reductions were more severe when clipping was practiced at lower stubble heights (Fig. 3). Clipping during booting stage coincided with high temperature and low precipitation at the end of the rainy season. This lead to reduction in plant regrowth at booting stage. Italian ryegrass (*Lolium multiflorum*) regrowth rate and tillering capacity were minimized at high temperature, whereas primary growth rate was at maximum (Hill and Pearson 1985). These results agree with data reported by Kennett et al. (1992) where early season defoliation of bluebunch wheatgrass

(A*gropyron spicatum*) produced higher shoot biomass due to better opportunity to regrow through the growing season.

Seed Yield

Seed yield was low when plants were clipped at jointing or booting stages (Fig. 4). Clipping at booting stage resulted in a severe reduction in seed production. Seed yields at booting stage were 98 and 169 kg ha^{-1} for clipping height of 5 and 10 cm, respectively.

Tiller production was inhibited when the wall barley plants were defoliated at the booting stage therefore seeds produced at the end of the season were from late maturing tillers, due to hot and dry condition during April. Large reductions in *H. murinum* L. seed production might eliminate this grass from range communities since it depends on soil seed bank for continuity and persistence. Seed production was not adversely affected when clipping occurred at tillering stage regardless of clipping height (594 and 583 kg ha^{-1} for 10 and 5 cm clipping height, respectively). This indicate that seed reserve will not be depleted if defoliation occurred early in the season. Mowing range grasses early in spring did not affect seed head production, whereas, late spring mowing progressively reduced the density of seed heads (Sims et al. 1971). Day time temperature (Franke et al. 1992), moisture supply (Thakur and Shands 1954), and proper grazing management (Morey 1961), contribute to high forage and seed yields of small grain crops under simulated grazing.

Weed Biomass

The dominating weed species on the site were *Cardaria draba* (L.) Desv., *Sinapis arrensis* L., and *Diplotaxis erucoides* (L.) D.C. Weed interference as detected by weed biomass significantly increased as defoliation was delayed and
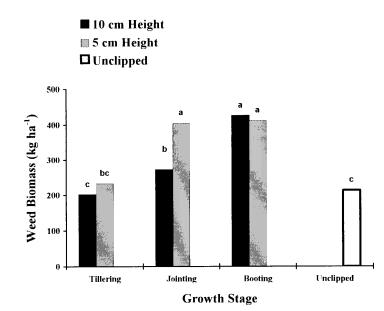

Fig. 5. Effect of *Hordeum murinum* L. defoliation time and height on weed biomass. Columns with different letters differ significantly according to DMRT at P ≤ 0.01.

clipping intensity (5 vs 10) increased (Fig. 5). Weed biomass was 201 and 223 kg ha^{-1} in stands subjected to 10 and 5 cm clipping heights at tillering stage, respectively. Clipping at booting stage reduced wall barley stand and led to increased weed infestation (412 to 426 kg ha^{-1}). Clipping during tillering did not reduce wall barley competing ability and this prevented weed invasion. This negative impact of clipping on competitive ability was stronger when range plants were clipped at later growth stages. Kennett et al. (1992) also reported that spotted knapweed (*Centaurea maculosa* Lam.) growth and density were influenced by bluebunch wheatgrass defoliation treatments. Weed invasion to any range site is associated with reduction in desirable species range cover and normally reduces the grazing value of that site. Defoliation alters plant competitive ability and influences its role in the community (Maschinski and Whitham 1989).

Conclusion

Maximum forage production was achieved when wall barley was defoliated at either at the early tillering stage or at plant maturity. Adequate soil moisture and temperature will encourage optimal plant regrowth. Defoliation during jointing or booting stages of wall barley reduces forage and seed yield and increases weed interference. Severe reduction in seed yield occurs when plants are defoliated at the booting stage which threatens a possible elimination of the species from the rangeland as a result of heavy unplanned grazing practices. Future studies are needed to determine the optimum number of seeds in the seed bank that are required to maintain a healthy natural wall barley population.

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Plant responses to defoliation and resource supplementation in the Pryor Mountains

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Abstract

Field studies were conducted in 2 types of grasslands in the Pryor Mountain Wild Horse Range of northern Wyoming and southern Montana to examine plant biomass production and nitrogen responses to the separate and combined effects of graminoid defoliation and increased environmental resource (water or nutrients) supply. Short-term plant responses were monitored over 2 years which differed substantially in growing season precipitation. In the arid, low elevation grassland, total grass biomass was significantly lower in the dry year than the wet year in all treatments. Defoliation of the grasses did not reduce their aboveground biomass production in the wet year, but severely reduced it in the dry year, primarily because of a decrease in tiller density. Mass of remaining individual tillers increased with clipping in the dry year, and nitrogen concentrations of the grasses increased with clipping in both years. Irrigation alone increased total belowground biomass compared to the other treatments, but did not increase the aboveground biomass production of any plant functional group. Clipping plus irrigation resulted in greater total aboveground biomass production and higher nitrogen concentrations of the grasses than control or irrigated treatments. Clipping graminoids in the more mesic montane grassland did not decrease their biomass production in either year, but did increase their nitrogen concentrations and increase the collective aboveground biomass production of the other plant functional groups. Fertilization and fertilization plus clipping significantly increased total aboveground biomass production in both years, and total belowground biomass was greatest in fertilized plots.

Resumen

Se condujeron estudios de campo en 2 tipos de pastizal en el pastizal Pryor Mountain Wild Horse ubicado en el noreste de Wyoming y sureste de Montana. El objetivo de estos estudios fue examinar los efectos individuales y combinados de la defoliación de gramíneas y el incremento de recursos ambientales (agua o nutrientes). Las respuestas de la planta a corto plazo fueron monitoreadas durante 2 años, los cuales difirieron substancialmente en precipitación durante la estación de crecimiento. En la parte árida, pastizal de baja elevación, la producción total de biomasa de gramíneas en todos los tratamientos fue significativamente menor en el año seco que en el año húmedo. En el año húmedo, la defoliación de los zacates no redujó su producción de biomasa aérea, sin embargo, fue severamente reducida en el año seco, debido principalmente a la disminución de la densidad de hijuelos. Durante el año seco, la biomasa remanente de los hijuelos individuales se incrementó con la defoliación. En ambos años, las concentraciones de nitrógeno de los zacates se incrementó con la defoliación. Comparado con los otros tratamientos, la irrigación sola incrementó la biomasa total subterránea, pero no incrementó la producción de biomasa aérea en ninguno de los grupos funcionales de plantas. La defoliación mas irrigación produjó mayores cantidades de biomasa total aérea y concentraciones de nitrógeno que los tratamientos control o de irrigación. La defoliación de gramíneas en el pastizal montano más mésico no disminuyó su producción de biomasa en ninguno de los años de estudio, pero si incrementó su concentración de nitrógeno e incrementó la producción colectiva de biomasa aérea de los otros grupos funcionales de plantas. En ambos años de estudio, la fertilización y la fertilización mas defoliación incrementaron significativamente la producción total de biomasa aérea y la producción total de biomasa subterránea fue superior en las parcelas fertilizadas.

Key Words: wild horses, Pryor Mountain Wild Horse Range, primary production, nitrogen, *Pseudoroegneria spicata*

Many large ungulate herbivores preferentially consume grasses relative to their proportion in the plant community (Schwartz and Ellis 1981, Vinton et al. 1993). This not only changes the relative ability of grasses to acquire resources, but also alters the competitive interactions within the community as plant species or functional groups are differentially affected by the direct and indirect effects of selective herbivory. For example, selective grazing of dominant grasses by bison in tallgrass prairie can increase photosynthesis and growth of neighboring ungrazed plants of the same and other species (Fahnestock and Knapp 1993, 1994).

The ability of grasses to compensate for biomass consumed

by large herbivores is controlled in part by the availability of environmental resources that can readily be acquired by the plants (Chapin and McNaughton 1989). When resources such as water, light, and mineral nutrients are abundant and readily available to plants, increased aboveground productivity of grasses in response to moderate grazing levels is possible (Archer and Tieszen 1980, McNaughton 1985, Seastedt 1985, Hik and Jeffries 1990, Pandey and Singh 1992, Frank and McNaughton 1993). Conversely, when environmental resources are limited, the ability of grasses to replace tissue lost to grazers is reduced. The persistence of plants in grassland ecosystems, therefore, largely depends on the ability of individuals to cope with complex and dynamic interactions between herbivory and limitations of environmental resources.

The environmental resources that most frequently limit the growth of plants and their ability to recover from grazing and other disturbances often differ with the type of grassland being studied. In arid and semi-arid grasslands, water availability most often limits plant growth (Lauenroth 1979, Sala et al. 1988), while in more humid grasslands, or in wet years, light and nutrients, especially nitrogen availability, are more likely to limit plant growth (Knapp and Seastedt 1986, Burke et al. 1991). The response of plants to grazing may also differ between and within species, depending on the nutrient and water stress tolerance of the species present, and on the type of herbivory and its intensity and frequency (Crawley 1983, Wallace et al. 1984, Coughenour et al. 1985a, 1985b, Polley and Detling 1988).

In the Pryor Mountain Wild Horse Range in southern Montana and northern Wyoming, grasses comprise over 70% of the annual diet of wild horses (Kissell 1996). Little is known, however, about the ability of the grasses in this system to maintain production in response to this potentially substantial grazing pressure, or about the interaction of herbivory with water or nutrient availability in the Pryor Mountains. The principal objective of this research, therefore, was to determine if the dominant grasses in the Pryor Mountain Wild Horse Range could acquire the resources necessary to maintain biomass and nitrogen production in response to selective grass defoliation, or whether there were environmental

resource limitations (i.e., water or nutrient limitations) to growth following defoliation. Because the relative competitive ability of other plants may be differentially affected by selective grass herbivory, we also investigated whether selective defoliation of the grasses would result in increased biomass production or nitrogen content of other plant functional groups, particularly forbs. We hypothesized that biomass production and nitrogen concentrations would increase in plants with additional resource supply, and that the potential negative effects of defoliation on grass growth would be ameliorated with increased resource supply.

Materials and Methods

Site description

The experiments took place during the summers of 1993, a year with above average growing season precipitation, and 1994, a relatively dry year, in the Pryor Mountain Wild Horse Range, an 18,000 ha refuge located 80 km south of Billings, Mont. Elevation ranges from 1,190 m to 2,440 m in the Pryor Mountains, and annual precipitation varies from about 130 mm in some lowland areas to over 500 mm at upper elevations. Our research was carried out in 2 types of grasslands in the Pryor Mountains—a low elevation arid grassland and a more mesic montane grassland—in which plant growth was presumed to be limited, respectively, by water and nutrient availability. To control for grazing, both experiments were established in long-term (>20 years) fenced areas that precluded wild horse use but were similar in botanical composition as those currently grazed by wild horses (Fahnestock 1998).

The first experiment was conducted in an arid lowland community at 1,300 m above sea level that receives only ca. 230 mm of precipitation annually. Precipitation data (1982–1994) for this community were obtained from a weather station located about 1 km south of our study site. Aboveground biomass in this community averages about 128 g m^{-2} (Fahnestock 1998) and is dominated by perennial grasses (51% of total plant cover) and forbs (26% of total plant cover), with lesser quantities of cushion plants, dwarf shrubs and succulents. *Pseudoroegneria spicata* (Pursh) A.

Löve (bluebunch wheatgrass) is the most abundant plant in these lowland communities, accounting for nearly 50% of the total herbaceous plant cover and over 90% of the total grass cover (Fahnestock 1998). Since water presumably limits plant growth in these lowlands, a grass defoliation and water supplementation experiment was carried out in this community.

The second experiment was conducted in a more mesic, montane meadow at 2,400 m above sea level that receives over 500 mm of precipitation annually. This site is located approximately 4 km north-west of the lowland site and precipitation data for this community were obtained from a weather station located about 1 km north of this site. Vegetation in this community is more abundant than the lowlands, averaging about 177 g m^{-2}, and consists primarily of grasses and sedges (44% of total plant cover) and forbs (51% of total plant cover). Much of the precipitation at this site comes from frequent summer showers, and thus the availability of nutrients, rather than water, presumably limits plant growth here. We carried out a graminoid (grasses and sedges) defoliation and nutrient supplementation experiment at this site.

Experimental design and treatments

A completely randomized 2 X 2 factorial design with 20 replicate plots was utilized for each experiment. Each experiment was established in a representative area of the upland or lowland grassland community at that site, and plots were selected that were relatively uniform in terms of plant cover and species composition to control for differences within and between plots. Each 3.2 m X 3.2 m plot was subdivided into 4 equal subplots to which a particular treatment was randomly assigned. In the arid lowlands the treatments were grass defoliation (D), irrigation (W), grass defoliation plus irrigation (DW), or untreated control (C). In the more mesic uplands the treatments were graminoid defoliation (D), fertilization (F), graminoid defoliation plus fertilization (DF), or control (C).

Vegetation was sampled in each subplot with 0.25 m^2 circular quadrats that were randomly placed in one of 4 possible locations in each subplot. No vegetation sample was collected within 20 cm

of the edge of each subplot to avoid edge effects. To simulate recurrent, selective ungulate herbivory, all graminoid biomass in entire defoliated and defoliated plus irrigated or defoliated plus fertilized subplots of each experiment was clipped to a height of 2 cm once a month in May, June, July, and August of 1993 and 1994, and clipped biomass within the 0.25 m² quadrats of each treatment was retained. This level of defoliation was equivalent to 60–70% utilization of the graminoids over the course of the growing season. Additionally, at the lowland site, tillers of *P. spicata* were counted in the 0.25 m² quadrats of each plot, and individual tiller mass was quantified by weighing 100 tillers from each treatment in August (i.e., 5 randomly selected tillers from each of the 20 plots).

All aboveground biomass in the 0.25 m² quadrats of each treatment was harvested to ground level in August of both years and oven-dried at 60°C for 48 hours. Because all aboveground biomass was harvested to ground level in 1993, alternate 0.25 m² quadrats within each subplot were sampled in 1994. These alternate plots had received the same treatments except for the ground level harvest in 1993. Biomass and total offtake values for each treatment were sorted by functional group (e.g., live and dead graminoids, forbs, etc.) and weighed. Pooled biomass samples (n=5) of each functional group were ground through an 850 µm (20-mesh) screen in a Wiley mill, subsampled, and nitrogen concentrations were determined by cou-

pled combustion/reduction and gas chromatography (CHN-1000, LECO Corporation, St. Joseph, Mich.). Aboveground N yield was calculated by multiplying the N concentration by the aboveground biomass of each functional group. Root biomass was estimated at the time of final harvest in 1994 by excavating 5 alternate 0.25 m² quadrats to the depth of 30 cm for each treatment. Soils were air-dried and roots and rhizomes were separated from soil by sieving.

In the lowland experiment, irrigated subplots were watered with hand-held sprinklers with water obtained from a nearby well. A 26.6 mm rainfall event was simulated in May, June, and July of each year, approximating a small increase in the number of large rainfall events this lowland area receives during the growing season. A total of 80 mm of water was added to irrigated plots during each growing season, resulting in a near doubling of the long-term average precipitation received at this site in May–July. Each watering event was applied over a 30-hour span so that there was no significant puddling or runoff, and water appeared to uniformly infiltrate the soil to a depth of at least 25 cm (pers. obs. based on excavations). This irrigation scheme appeared to increase the availability of soil water to irrigated plants by nearly 3 weeks during the growing season (i.e., irrigated soils were appreciably more moist at 20 cm than non-irrigated soils for about 1 week following each watering event). In the upland experiment, a moderate level (39 g m⁻²) of slow-release fertilizer (20-10-5 of N-P-

K) was surface-broadcast applied to the appropriate randomly selected subplots once near the beginning (late-May) of the 1993 and 1994 growing seasons. Soils were moist at the time of fertilization and rain fell on the site within 10 days of fertilization. All fertilizer was dissolved into the soil within 4 weeks of application.

Statistical analyses

In each experiment, total biomass (i.e., May–August clipped biomass plus final August harvest biomass) and nitrogen responses to each treatment were compared using the General Linear Models procedure of the Statistical Analysis System (SAS 1989). Models included the main effects of treatment by functional group and the interaction of treatments. Type III sums-of-squares were used for significance ($P < 0.05$) testing, and least squares methods were used to examine associations between treatments by functional group. We used t-test procedures to compare biomass and nitrogen responses of each functional group to treatments between years.

Results

Biomass responses

Growing season (ca. March–July) precipitation in the lowland site was 202 mm in 1993, well above the long-term average of 143 mm, while in 1994 it was only 101 mm. Live grass biomass and live plus dead grass biomass were significantly lower in all lowland treat-

Table 1. Mean aboveground biomass (g m⁻²) ±1 SE of grasses, forbs, and total biomass in control plots and defoliated, irrigated, and defoliated plus irrigated treatments from arid lowland sites (n = 20 for each functional group x treatment). Values shown are for final harvest in August 1993 and 1994 and include clipped grass biomass from May through August (see text for additional details).

	Control	Defoliated	Irrigated	Defoliated and Irrigated
	- (g m⁻²) -			
1993				
Grasses	31.8 ± 1.0ᵃ*‡	33.3 ± 1.1ᵃ*	33.4 ± 1.0ᵃ*	27.5 ± 0.8ᵃ*
Live	10.5 ± 1.1ᵃ*	13.2 ± 1.4ᵃ*	12.5 ± 1.4ᵃ*	11.8 ± 1.2ᵃ*
Dead	21.3 ± 0.8ᵃ	20.1 ± 3.3ᵃ*	20.9 ± 2.8ᵃ*	15.7 ± 2.0ᵃ
Forbs	25.8 ± 2.9ᵃ	33.3 ± 3.4ᵃ	30.0 ± 2.6ᵃ	27.2 ± 3.2ᵃ
Total aboveground biomass	137.2 ± 4.5ᵃ	135.6 ± 4.7ᵃ	135.4 ± 4.5ᵃ	126.8 ± 5.2ᵃᵃ
1994				
Grasses	22.7 ± 1.0ᵃ*	8.6 ± 0.4b*	19.0 ± 0.6ᵃ*	14.2 ± 0.7ᵃᵇ*
Live	6.2 ± 1.1ᵃ*	3.1 ± 0.3b*	5.6 ± 0.7ᵃᵇ*	4.4 ± 0.6ᵃᵇ*
Dead	16.6 ± 3.0ᵃ	5.5 ± 1.2b*	13.4 ± 1.9ᵃ	9.8 ± 2.3ᵃᵇ
Forbs	21.0 ± 2.8ᵃ	24.4 ± 3.7ᵃ	30.3 ± 4.5ᵃ	29.8 ± 3.4ᵃ
Total aboveground biomass	119.2 ± 7.2ᵃ	123.3 ± 12.2ᵃ	134.6 ± 10.2ᵃᵇ	149.5 ± 8.5b

‡Columns with different letters within a functional group indicate significant differences ($P < 0.05$) between treatment means. Asterisks indicate significant differences ($P < 0.05$) between 1993 and 1994 values.
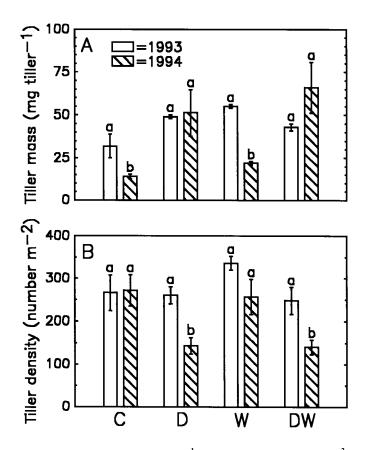
Fig. 1. (a) Individual grass tiller mass (mg tiller^{-1}) and (b) tiller density (no. m^{-2}) in 1993, a wet year, and 1994, a dry year, in the lowland experimental site of the PMWHR. Measurements were made on Pseudoroegneria spicata, the dominant grass in these lowlands. Different letters above bars indicate significant (P < 0.05) differences in means between treatments and years. Treatments are control (C), grasses defoliated (D), irrigated (W), and defoliated plus irrigated (DW).

tiller density in control plots was about 270 tillers m^{-2} in both years. In defoliated treatments, density averaged 260 tillers m^{-2} in 1993, but only 140 tillers m^{-2} in 1994 (Fig. 1b).

Irrigation did not increase aboveground biomass production of any plant functional group in either year (Table 1). Total belowground biomass, however, was greatest in irrigated plots by the end of the experiment (Fig. 2a). Total belowground biomass in irrigated plots was 158 g m^{-2}, while that in control, defoliated, and defoliated plus irrigated plots averaged 98 g m^{-2} (Fig. 2a). Irrigation apparently also enabled the grasses to compensate, at least in part, for tissue lost to clipping during the dry year; that is, in the dry year defoliation alone reduced live and dead aboveground grass biomass, but biomass of grasses in defoliated plus irrigated plots was not different from that of control plots (Table 1). The combined effects of defoliation and irrigation did not significantly alter aboveground biomass of any individual plant functional groups, but did result in greater total aboveground biomass production than control and defoliated treatments by the end of the experiment in 1994.

In the upland study site, growing season (ca. April–August) precipitation was also lower in 1994 (193 mm) than in 1993 (399 mm). Nevertheless, we found no interannual differences in aboveground biomass production of any plant functional group in control plots (Table

ments in 1994 than 1993 (Table 1). However, forb and total aboveground biomass were not significantly lower in 1994 than 1993 in any treatment. In the lowland experiment, there was not a significant effect of any of the treatments (defoliated, irrigated, or defoliated plus irrigated) on biomass production of any plant functional group in 1993, the wet year (Table 1). This was not the case, however, in 1994, where grass biomass production was much lower in defoliated plots (9 g m^{-2}) than in control plots (23 g m^{-2}; Table 1).

Much of the lower live grass biomass production in 1994, the dry year, was the result of lower mass of individual live grass tillers. In control plots, mass was 32 mg tiller^{-1} in 1993 but only 14 mg tiller^{-1} in 1994 (Fig. 1a). A similar reduction in tiller mass was seen in grasses that were irrigated. In contrast, individual mass of grass tillers that were defoliated (both defoliated and defoliated plus irrigated treatments) were not

reduced, but defoliation did reduce tiller density in the dry year (Fig. 1b). Grass

Table 2. Mean aboveground biomass (g m^{-2}) ±1 SE of grasses, forbs, and total biomass in control plots and defoliated, fertilized, and defoliated plus fertilized treatments from montane sites (n = 20 for each functional group x treatment). Values shown are for final harvest in August 1993 and 1994 and include clipped graminoid biomass from May through August (see text for additional details).

	Control	Defoliated	Fertilized	Defoliated and Fertilized
	\- (g m^{-2}) \- \- \- \- \- \- \- \- \- \- \- \- \- \- \- \- \- \- \-			
1993				
Graminoids	48.5 ± 6.4[a]‡	54.2 ± 5.0[a]	61.7 ± 7.2[a]*	65.4 ± 6.6[a]
Live	25.4 ± 2.9[a]	30.9 ± 2.6[a]	42.0 ± 4.8[b]*	45.2 ± 4.6[b]
Dead	23.0 ± 4.2[a]	23.2 ± 2.7[a]	19.7 ± 4.1[a]*	20.1 ± 3.1[a]
Forbs	82.0 ± 10.7[a]	84.0 ± 7.0[a]	93.6 ± 11.3[a]*	110.3 ± 17.9[a]
Total aboveground biomass	175.6 ± 11.1[a]	193.1 ± 13.1[ab]	234.9 ± 17.4[bc]*	234.5 ± 15.2[bc]*
1994				
Graminoids	49.7 ± 6.0[a]	41.2 ± 6.2[a]	105.6 ± 8.1[b]*	59.6 ± 6.5[a]
Live	27.8 ± 3.1[ab]	21.8 ± 2.4[a]	57.5 ± 4.9[c]*	36.1 ± 4.4[b]
Dead	21.9 ± 3.2[a]	19.4 ± 3.5[a]	48.1 ± 6.3[b]*	23.5 ± 2.5[a]
Forbs	90.1 ± 12.0[a]	101.2 ± 12.8[ab]	146.8 ± 16.8[c]*	137.4 ± 13.7[bc]
Total aboveground biomass	177.7 ± 18.2[a]	211.7 ± 22.5[b]	338.3 ± 19.8[c]*	282.8 ± 17.4[c]*

‡Columns with different letters within a functional group indicate significant differences (P < 0.05) between treatment means. Asterisks indicate significant differences (P < 0.05) between 1993 and 1994 values.

2). Selective defoliation of the graminoids also did not significantly reduce their biomass production in either year. However, defoliated plots did have greater total aboveground biomass than control plots by the end of the experiment (Table 2).

Fertilization increased live graminoid biomass in both years, and total live and dead graminoid biomass was highest in fertilized plots by the end of the experiment in 1994. At that time, live (58 g m^{-2}) and dead (48 g m^{-2}) graminoid biomass in fertilized plots was more than twice that in control or defoliated plots (Table 2). Aboveground biomass production of all plant functional groups was higher in fertilized plots in 1994 than in 1993 (Table 2). Total belowground biomass in fertilized plots (620 g m^{-2}) was greater than that of control (391 g m^{-2}) or defoliated (306 g m^{-2}) plots by the end of the experiment, but was not significantly different from defoliated plus fertilized plots (453 g m^{-2} Fig. 2b). The defoliation plus fertilization treatment increased live graminoid biomass in 1993 compared to control plots, but total grass biomass was not significantly changed by this treatment (Table 2). Additionally, total aboveground biomass was significantly higher in defoliated plus fertilized plots than in control plots in both years.

Nitrogen responses

In the arid lowland grassland, N concentrations of both live and dead grass in defoliated and defoliated plus irrigat-

Table 3. Nitrogen concentrations (%) of live and dead grass and forbs in 1993, a wet year, and 1994, a dry year, from the lowland experimental site (n = 5 for each functional group x treatment).

	Control	Defoliated	Irrigated	Defoliated and Irrigated
	- (%) -			
1993				
Live grass	0.81 ± 0.01^{a}*‡	1.26 ± 0.05^{b}*	0.85 ± 0.04^{a}*	1.25 ± 0.03^{b}*
Dead grass	0.45 ± 0.01^{a}*	0.62 ± 0.02^{b}*	0.46 ± 0.02^{a}*	0.61 ± 0.03^{b}*
Forbs	0.78 ± 0.03^{a}	0.84 ± 0.03^{a}	0.82 ± 0.02^{a}	0.95 ± 0.04^{a}
1994				
Live grass	0.66 ± 0.02^{a}*	0.80 ± 0.02^{b}*	0.62 ± 0.02^{a}*	0.78 ± 0.02^{b}*
Dead grass	0.53 ± 0.03^{a}*	0.76 ± 0.01^{b}*	0.55 ± 0.04^{a}*	0.75 ± 0.01^{b}*
Forbs	0.80 ± 0.03^{a}	0.95 ± 0.19^{a}	0.79 ± 0.04^{a}	0.81 ± 0.03^{a}

‡Columns with different letters within a functional group indicate significant differences (P < 0.05) between treatment means. Asterisks indicate significant differences (P < 0.05) between 1993 and 1994 values.

ed plots were higher in both years than those in either control or irrigated plots (Table 3). The N concentration of live grasses was significantly lower in all treatments in 1994, the dry year, than in 1993, the wet year (Table 3). In contrast, the N concentration of dead grasses was higher in all treatments in 1994 than in 1993. The N concentrations of the forbs were not significantly affected by selective grass defoliation in either year.

In the more mesic montane grassland, all treatments (defoliated, fertilized, and defoliated plus fertilized) resulted in increased N concentrations in the live graminoids, and defoliated and defoliated plus fertilized increased the N concentration of the dead graminoids, in both years (Table 4). As at the lowland site, N concentrations of live graminoids

were higher in all treatments in 1993 than in 1994, and N concentrations of the forbs were not affected by any treatment in either year.

Total aboveground nitrogen yield (g N m^{-2}) of the lowland and upland graminoids was increased by defoliation only in 1993, the wetter year (Fig. 3). Aboveground N yield of all lowland plants combined was increased in the defoliated plus irrigated treatment by the end of the experiment in 1994, and in the upland experiment, fertilization and defoliation and fertilization increased the aboveground N yield of the graminoids and of all plants combined in both years.

Discussion and Conclusions

In the wet year, 1993, selective defoliation of the lowland grasses, primarily *P. spicata*, had no effect on their aboveground biomass production; that is, the grasses fully compensated for the shoot biomass removed. In the dry year, however, defoliation in the absence of water supplementation severely reduced grass biomass production. Irrigation in that year enabled *P. spicata* to compensate for shoot biomass lost to clipping. Consistent with our hypothesis, these data suggest that in the arid lowlands of the Pryor Mountain Wild Horse Range, regrowth following grazing is closely linked to water availability.

Similar reductions in grass biomass production in response to the simultaneous pressures of clipping and water stress have also been found in other studies (e.g., Toft et al. 1987, Georgiadis et al. 1989, Simoes and Baruch 1991, Busso and Richards
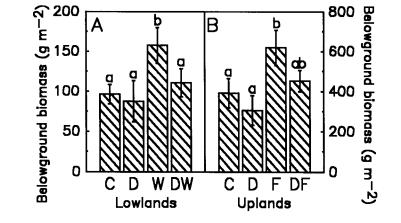

Fig. 2. Total belowground biomass (g m^{-2}) in the (a) lowland and (b) upland experimental sites at the conclusion of the experiment in August, 1994. Columns headed by different letters indicate significant (P < 0.05) differences between treatments. Treatments are control (C), graminoids defoliated (D), irrigation (W) or fertilization (F), and graminoids defoliated plus irrigation (DW) or graminoids defoliated plus fertilization (DF). Note different scales for the 2 sites.
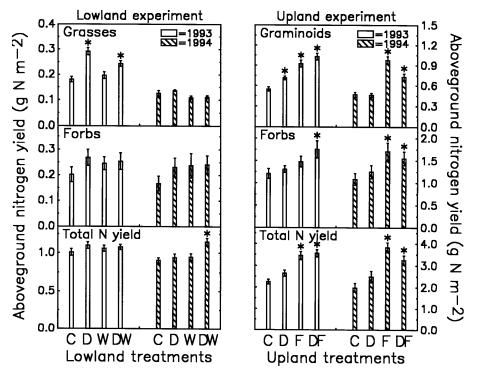
Fig. 3. Aboveground nitrogen yield (g N m⁻²; n = 5 for each vertical bar) for graminoids, forbs, and total N yield in the lowland and upland experiments in August, 1993 and August, 1994. Treatments as in Fig. 2. Asterisks denote significantly higher N yields (calculated as N concentration multiplied by aboveground biomass) in treatment than control. Note different scales for each graph.

either the dry or wet year. Why *P. spicata* failed to increase its aboveground biomass production in response to artificially increased water supply is not known. Although bare ground evaporation was undoubtedly high, soil excavations showed that soil moisture was appreciably higher in irrigated compared to non-irrigated plots for at least 1 week following each watering event. It is possible that the grasses in these arid lowlands are rather insensitive to large pulses of increased water availability, such as those simulated in this study, and that frequent, smaller rainfall events may be more important to their growth (e.g., Sala and Lauenroth 1982, but see Weaver 1985). Additionally, the overall environment in these lowlands was still arid which may have negated the effects of our irrigation treatment. Nevertheless, total root biomass was significantly higher in the lowland irrigated plots than in the other treatments by the end of the experiment, indicating that plant growth responses to our levels of irrigation may have been belowground only.

In the lowland site, the reduction in grass biomass with clipping that was measured in the dry year was the result of a decrease in grass tiller density and not individual tiller mass, which was much higher in clipped than control plots that year. Bluebunch wheatgrass, the dominant grass in these lowlands, has been shown to be a decreaser under increasing grazing pressure (Williams 1963). A decrease in tiller number resulting from grazing has frequently been reported (Branson 1956, Ellison 1960, Caldwell et al. 1981, Carman and Briske 1985, Polley and Detling 1989), although an increase in tiller production (Richards et al. 1988, Zhang and Romo 1995) and

1995). This response, however, is in contrast to the prediction of Hilbert et al. (1981) that plants which are stressed in some way, and consequently growing slowly compared to their potential rates, are most likely to increase production following grazing. The response of the lowland grasses in the Pryor Mountains was also not consistent with those of McNaughton et al. (1983) and Coughenour et al. (1985 a, 1985b, 1990); in their studies, the effects of water stress and defoliation were found to often act singly and 1 factor could reduce or ameliorate the negative effect of the other. In our study, additional water supply ameliorated the negative effects of defoliation in the dry year. In the semiarid shortgrass steppe, Milchunas et al. (1994) have found that long-term primary production across 50 years of cattle grazing treatments was most sensitive to precipitation and least sensitive to grazing intensity.

In the dry year, decreased live grass biomass in the lowland control plots was the result of lower individual tiller mass, not tiller density. Busso and

Richards (1995) similarly found that mass of individual unclipped tillers of *P. spicata* was severely reduced under drought conditions compared to more average precipitation levels. They also found that plants that were irrigated showed lower tiller height, leaf area, and mass compared to plants under more average precipitation conditions. Our levels of irrigation did not increase individual grass tiller mass of *P. spicata* in

Table 4. Nitrogen concentrations (%) of live and dead graminoids and forbs in 1993, a wet year, and 1994, a dry year, from the montane experimental site (n = 5 for each functional group x treatment).

	Control	Defoliated	Fertilized	Defoliated and Fertilized
	- (%) -			
1993				
Live graminoids	1.37 ± 0.04[a]*	1.50 ± 0.02[b]*	1.72 ± 0.02[c]*	1.76 ± 0.06[c]*
Dead graminoids	0.90 ± 0.03[a]*	1.08 ± 0.05[b]	1.04 ± 0.05[ab]*	1.17 ± 0.05[b]
Forbs	1.47 ± 0.05[a]	1.56 ± 0.03[a]	1.58 ± 0.07[a]	1.59 ± 0.06[a]
1994				
Live graminoids	1.13 ± 0.02[a]*‡	1.27 ± 0.05[bc]*	1.24 ± 0.02[b]*	1.37 ± 0.06[c]*
Dead graminoids	0.70 ± 0.07[a]*	0.94 ± 0.08[b]	0.55 ± 0.01[a]*	1.00 ± 0.10[b]
Forbs	1.27 ± 0.03[a]	1.33 ± 0.08[a]	1.35 ± 0.05[a]	1.25 ± 0.06[a]

‡Columns with different letters within a functional group indicate significant differences (P < 0.05) between treatment means. Asterisks indicate significant differences (P < 0.05) between 1993 and 1994 values.

increased regrowth of surviving tillers (Branson 1956, Caldwell et al. 1981, McNaughton et al. 1983, Carman and Briske 1985), has also been observed. In this system there appears to be an inverse relationship between tiller size and density, as is generally the case (Risser 1969, Gorham 1979, Christiansen and Svejcar 1988). The simultaneous pressures of clipping and water stress reduced tiller density of *P. spicata*, but increased the mass of the surviving tillers relative to those of unclipped plants. Additions of water to clipped plots in the dry year did not prevent a reduction in tiller density following clipping, providing further evidence to suggest that *P. spicata* is not very responsive to the large, infrequent rainfall events simulated in this short-term study.

In the upland defoliation-fertilization experiment, the decrease in growing season precipitation in 1994 compared to 1993 did not result in a decrease in aboveground biomass production of any plant functional group, suggesting that water did not limit plant growth at this site during the study. This was not true at all upland sites in the Pryor Mountain Wild Horse Range, however, since decreases in plant cover and biomass were measured at some sites in the dry year (Peterson et al. 1997, Fahnestock 1998). At this site, our finding that defoliation did not reduce live or total graminoid biomass production in either year indicates that the graminoids are apparently able to compensate for biomass lost to grazers without additional resource supply.

Fertilization increased the growth of most plant functional groups such that total above- and belowground biomass production were higher in fertilized only plots than unfertilized plots by the end of the experiment. In individual plants, nutrient limitation is recognized by an increase in growth in response to an addition of the limiting nutrient. The analogous response at the community level is an increase in total community production in response to fertilization (Chapin et al. 1986). In this experiment only, the upland graminoids increased their aboveground biomass production in response to fertilization in the first year, but by the second year all plant functional groups had increased biomass production. These results suggest that species or functional groups differed in their ability to respond to increased nutrient supply or that nutrient limitations were not the same for all

plants (Chapin 1980, Jaramillo and Detling 1992). Fertilization also resulted in defoliated graminoids producing more live, but not dead, biomass in 1993, than unclipped, unfertilized plants. Therefore, the effect of increased nutrient supply on defoliated graminoids in the uplands may be to decrease their rate of senescence, and to increase their belowground biomass production (see above).

Our results suggest that the dominant graminoids in the Pryor Mountains are able to withstand fairly heavy levels of defoliation through compensatory growth. In the uplands, the graminoids are able to compensate for tissue lost to grazers without additional resource supply. In the lowlands, however, their ability to fully regrow following grazing is only possible when water availability is not too low. Increased water availability in the lowlands of the Pryor Mountains will most likely stimulate belowground growth in these plant communities, and will increase the nitrogen concentrations of all plants except perhaps the forbs.

In both the lowland and upland communities, selective graminoid defoliation increased the N concentrations of graminoids in both years, and increased total aboveground N yield of graminoids in the wet year. This may have resulted from increased N uptake by defoliated grasses, increased allocation of N to aboveground plant tissue, or both. Nitrogen uptake, N concentration, and physiological activity are often higher in plants that have been grazed or otherwise defoliated than in plants from ungrazed areas (e.g., Jameson 1963, Detling et al. 1979, McNaughton 1979, Coppock et al. 1983, McNaughton et al. 1983, Ruess et al. 1983, Detling and Painter 1983, Polley and Detling 1988, Jaramillo and Detling 1988). Increased N concentrations in grazed graminoids results in higher quality forage available to herbivores. This may have important consequences for subsequent food preference by herbivores in the Pryor Mountain Wild Horse Range. In addition, the higher N-yield of defoliated graminoids suggests that herbivores may, via their grazing activities, increase not only the quality of their forage but also the quantity of crude protein subsequently available to them when they regraze the same patch. Defoliation of the graminoids did not change the aboveground biomass production or nitrogen concentrations of the

other plant functional groups in the Pryor Mountains, indicating that the relative competitive abilities of plants in the upland and lowland communities are not greatly, or at least rapidly, altered by selective graminoid defoliation.

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