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GRAZING HISTORY, DEFOLIATION, AND COMPETITION: EFFECTS ON SHORTGRASS PRODUCTION AND NITROGEN ACCUMULATION[1]

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Abstract. Plants of *Bouteloua gracilis* were collected from heavily grazed prairie dog (*Cynomys ludovicianus*) colonies (ON-colony) and lightly grazed uncolonized sites (OFF-colony) in Wind Cave National Park, South Dakota. Our objectives were to determine (1) how grazing history affected production, nitrogen uptake, and biomass and nitrogen allocation following defoliation; and (2) how such responses were affected by competing neighbors of the same population. The growth chamber experiment was factorial with three main treatments in 12 possible combinations. Main treatments were: population (plants from lightly and heavily grazed sites), defoliation (three intensities), and competition (with or without neighbors of the same population).

There were no significant interactions among treatments. OFF-colony plants produced 121% as much biomass and their N yield was 203% as great as ON-colony plants. ON-colony plants allocated a higher percentage of biomass and N to the roots than OFF-colony plants, while the latter allocated a greater percentage of resources to leaf sheaths and reproductive structures. In response to defoliation, plants from the two populations had an average increase of 122% in N uptake per unit of root biomass and a 141% increase in total leaf-blade N yield. Heavily defoliated plants from both populations increased biomass and N allocation to blades, but total biomass production was substantially reduced. Intrapopulation competition reduced biomass production and N yield in individuals of both populations, but it did not affect total and aboveground N concentrations (per unit biomass) or N uptake per unit of root biomass. Our results support the hypothesis that genetically based morphological and physiological differentiation has occurred in *B. gracilis* as a result of strong selection pressures from grazing mammals on prairie dog colonies. We suggest the ON-colony population displays a strategy that reduces grazing severity rather than a "grazing tolerance" response to aboveground herbivory.

Key words: blue grama; Bouteloua gracilis; *clipping;* Cynomys ludovicianus; *defoliation; grass; grassland; grazing history; nitrogen accumulation; nutrient accumulation; prairie dog.*

INTRODUCTION

A plant's response to herbivory may be controlled by a variety of physiological processes including altered photosynthetic rates, shifts in assimilate and nutrient allocation patterns, differential balance in vegetative and reproductive tissues, changes in nutrient uptake, and altered hormonal balance (Marshall and Sagar 1965, Youngner 1972, Detling et al. 1979, McNaughton 1979, Chapin 1980*b*, Caldwell et al. 1981, Detling and Painter 1983, Ruess et al. 1983). Increased nutrient uptake may allow defoliated plants to compensate for nutrient loss, and, coupled with shifts in nutrient and assimilate allocation patterns, it can contribute to successful recovery from repeated grazing (Chapin 1980*b*, Wallace et al. 1982, Ruess et al. 1983, McNaughton and Chapin 1985). This may be particularly true of nitrogen because of its importance both in mediating plant–herbivore interactions (Mattson 1980, Floate 1981, Ruess et al. 1983, White 1984) and in the photosynthetic machinery of the plant (Mooney and Gulmon 1982).

Only a few studies have focused on the relationship among defoliation, nitrogen uptake, and nitrogen yield. Ruess et al. (1983), Ruess (1984), and Ruess and McNaughton (1984) have shown that intense defoliation of the sedge *Kyllinga nervosa* Steud. increased nitrogen uptake and leaf nitrogen content and concentration. These studies, however, were done with plants growing in isolation. Because the presence of another plant may change the environment of its neighbors and alter their growth rate and form (Harper 1977), it is of interest to know how nitrogen uptake is affected when defoliated plants are growing with neighbors. A few experiments have determined the impact of defoliation on plants growing at contrasting densities, but they have not considered nutrient uptake or multiple defoliation events (Lee and Bazzaz 1980, Tripathi and Gupta 1980).

Research on several species from the northern mixed-grass prairie in Wind Cave National Park, South Da-

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kota, has shown that short, prostrate morphs, presumably genetically differentiated, grow on heavily grazed prairie dog (*Cynomys ludovicianus*) colonies (Detling and Painter 1983, Cid 1985, Detling et al. 1986, Painter 1987). Dwarf morphs of *Agropyron smithii* Rydb. may be better able to withstand defoliation and tend to have higher shoot-nitrogen concentration than taller morphs growing outside the prairie dog colonies (Coppock et al. 1983, Detling and Painter 1983, Krueger 1986). This suggested that grazing may enhance nitrogen uptake, and that this effect would be more pronounced in populations that had differentiated under heavy grazing pressure.

The objectives of this study on heavily and lightly grazed populations of *Bouteloua gracilis* (H.B.K.) Griffiths were to determine (1) how differences in grazing history affected plant production, nitrogen uptake, and biomass and nitrogen allocation following defoliation and (2) how such responses were affected by competing neighbors of the same population in a controlled environment. This species is a dominant or codominant in the short- and midgrass prairie of North America and constitutes a major dietary component of both wild and domesticated herbivores (Detling et al. 1979, Coppock et al. 1983*a*).

MATERIALS AND METHODS

The experiment was conducted with two populations of *Bouteloua gracilis* collected in Pringle Valley, Wind Cave National Park, South Dakota, on 7 July 1984. One population was from a heavily grazed 10–15 yr old prairie dog colony (Coppock et al. 1983*a*), the other was from a lightly grazed uncolonized site. The two sites were ≈300 m apart. Peak live aboveground biomass on the colonized site was ≈50% of that on the uncolonized site (Coppock et al. 1983*a*). The sods were brought to Colorado State University, planted in pots with potting soil, and maintained in a greenhouse for 6 mo prior to initiation of the experiment. Plants from the prairie dog colony and the uncolonized site will be referred to as ON-colony and OFF-colony populations, respectively.

Two months after potting, random samples of tillers were measured to the ligule of the uppermost leaf to check for population differences. On 9 January 1985, single tillers were planted in plastic pots 15 cm in diameter × 15 cm in height, singly and four per pot, in a 1:1 (by mass) mixture of potting soil and sand. Plants were then introduced into a Conviron E-15 plant growth chamber under 14 h light : 10 h dark photoperiods and a 30°:15°C temperature regime. Quantum flux density at canopy height was maintained at 550 μmol·m^{-2}·s^{-1}. Plants were watered as needed and grew for nearly 6 wk before the first defoliation.

A $2^2 \times 3$ factorial, randomized complete block design was used with the following treatments: two populations (ON- and OFF-colony), two densities (one or four plants of the same population per pot), and three levels of defoliation (heavy, light, and no defoliation). Within each block, individual tillers were as homogeneous in size as possible. The defoliation treatments were imposed at different heights in each population because of their different plant sizes. Tiller heights to the ligule of the uppermost fully expanded leaf were measured 2 d prior to defoliation, and these means were used to set the heavy defoliation intensity: 25 mm above the ground for the ON-colony and 32 mm for the OFF-colony population. The height for the light defoliation treatment was double that of the heavy defoliation: 50 mm for the ON-colony and 64 mm for the OFF-colony population. These defoliation treatments, which were repeated every two weeks, removed an average of 81.3% (light) and 93.3% (heavy) of total aboveground biomass produced by plants of both populations over the 8-wk duration of the experiment. In the high-density treatment, all four plants in each pot were treated the same, and one was randomly selected as the target plant for subsequent measurements. Overall, the experiment consisted of five replicates of each of 12 treatments. Blocks were randomly assigned to a location within the growth chamber and pots were rerandomized within each block weekly.

Although clipping experiments have been criticized for their more even and greater severity of foliage removal compared with actual grazing (Jameson 1963, Hart and Balla 1982, Stroud et al. 1985), our treatments did resemble the way prairie dogs consume vegetation, and the frequency imposed approximates that experienced by plants in the field (K. Krueger and E. L. Painter, *personal communication*).

After 8 wk (2 wk after the fourth and final defoliation), plants were harvested; separated into roots, crowns (shoot bases 1 cm above soil level plus underground portion), sheaths, blades, and reproductive structures (culms and inflorescences); dried for at least 24 h at 60°; and weighed. Material removed at each defoliation was sorted in the same way and summed to estimate total plant production and total nitrogen yield. Nitrogen concentration was determined by the micro-Kjeldahl technique. Nitrogen yield of each plant part was calculated by multiplying its dry mass by the nitrogen concentration. Root-specific nitrogen accumulation was total nitrogen yield of the plant divided by the root biomass present at time of harvest. At each sampling date, number of tillers, culms, and inflorescences per culm were also recorded.

All data were statistically analyzed with a three-way ANOVA with SPSS (Nie et al. 1975). Biomass and nitrogen-yield data were log-transformed for analysis to satisfy homogeneity of variances assumptions in the ANOVA, and percent allocation data were analyzed upon arcsine $\sqrt{x}$ transformation.

RESULTS

Although there were no significant interactions among treatments, in two cases (biomass root : shoot ratio and

TABLE 1. ANOVA results for the main effects of the three treatments. There were no significant interactions.

Trait	Population effect	Competition effect	Defoliation effect
Biomass			
Total	**	**	**
Aboveground	***	***	*
Belowground (roots)	*	***	***
Root : shoot ratio	*	NS	*†
Blades	***	***	NS
Sheaths	***	***	NS
Reproductive structures	***	**	***
Crowns	***	**	***
Blade : sheath ratio	**	**	**
% blade	NS	NS	***
% sheaths	***	NS	NS
% reproductive structures	**	**	***
% crown	NS	***	NS
% roots	**	NS	*†
Nitrogen yield			
Total	**	**	NS
Aboveground	***	***	NS
Belowground (roots)	***	***	***
Root : shoot ratio	*	NS	***
Whole-plant N concentration	*	NS	***
Aboveground N concentration	NS	NS	***
Root-specific N accumulation	**	NS	***
Blades	**	***	**
Sheaths	**	***	NS
Reproductive structures	***	*	*
Crown	***	***	*
Blade : sheath ratio	*	**	**
% blade	NS	NS	***
% sheaths	**	*	NS
% reproductive structures	***	*	***
% crown	NS	**	***
% roots	*	NS	***

* $P < .05$; ** $P < .01$; *** $P \leq .001$; NS = nonsignificant ($P > .05$).

† Significant for the ON-colony population only. See Results for explanation.

percent biomass allocation to roots) the data strongly suggested differential responses of the populations of defoliation. These two variables were therefore analyzed with polynomial contrasts, partitioning the defoliation treatment into linear and quadratic components. A significant interaction ($P \leq .05$) between the population treatment and the linear contrast indicated the need to partition the response within the population treatment. The appropriate contrast was performed, and in both cases the ON-colony population showed a significant response to defoliation, and the OFF-colony population did not (Table 1). With the exception of these two variables, the presentation and discussion of results involve only the main effects (Table 1).

Whole-plant response

Both total biomass production and total N yield differed significantly between populations and level of competition. However, of these two variables only total biomass was significantly reduced by defoliation (Table 1; Fig. 1). OFF-colony plants averaged 121 and 203% as great biomass and N yield, respectively, as ON-colony plants, and competition caused an average decrease of 58% of both yields in the two populations. In three of the four cases, light defoliation produced a slight but nonsignificant increase in total N content. Thus, even though biomass production suffered significant reductions, nitrogen content was kept relatively constant, indicating a net increase in N concentration of the plants with defoliation (Fig. 1). The OFF-colony population showed significantly higher N concentration (22%) than the ON-colony population (Table 1; Fig. 1), and competition did not significantly affect it ($P > .05$).

Aboveground and belowground subsystems

The aboveground subsystem includes all aerial biomass components plus the crown, while the belowground subsystem is synonymous with roots. As

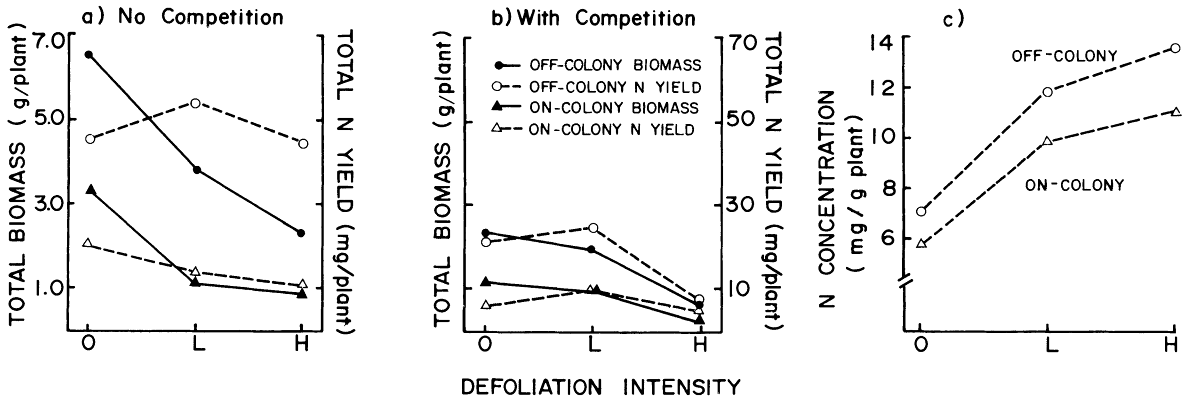

FIG. 1. Defoliation effect on total biomass and total N yield (a) without and (b) with competition (one or four tillers per pot), and defoliation effect on (c) N concentration of OFF-colony and ON-colony populations of *Bouteloua gracilis*. Each point represents the mean of 5 (a and b) or 10 (c) replicates. Defoliation intensity symbols: 0 = no defoliation, L = light defoliation, H = heavy defoliation. Significance levels for the three treatments are indicated in Table 1.

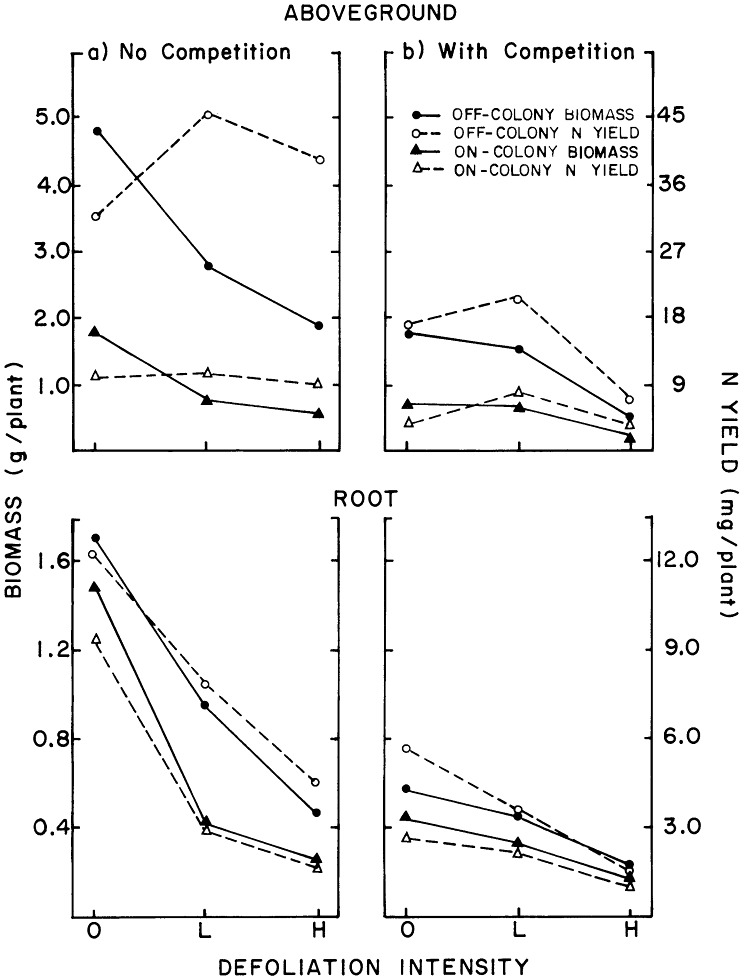

FIG. 2. Defoliation effect on aboveground and root biomass and on N yield of OFF-colony and ON-colony populations of *Bouteloua gracilis* (a) without and (b) with competition (one or four tillers per pot). Each point represents the mean of five replicates. Significance levels in Table 1. Defoliation intensity symbols as in Fig. 1.

with the whole-plant response, OFF-colony plants significantly (Table 1) outproduced ON-colony plants in both biomass and N yields in both subsystems, but the differences were much greater aboveground than belowground (Fig. 2). Aboveground biomass and N yields were, respectively, 173 and 256% as high in the OFF-colony population, and belowground values were 41 and 44% as high, as in the ON-colony population. Competition reduced above- and belowground biomass an average of 56 and 58%, and N yield an average of 60 and 57%, respectively, in the OFF- and ON-colony populations.

Biomass production of the two subsystems in both populations was significantly reduced with increasing defoliation intensity, but only belowground N yield was significantly reduced (Table 1; Fig. 2). Although light defoliation appeared to increase aboveground N yield slightly, the effect was not statistically significant (Table 1). Aboveground N concentration, however, did increase with defoliation, but it did not differ between populations (Table 1). While defoliation decreased root biomass (Fig. 2), it increased N uptake per unit of root biomass in both populations (Fig. 3). However, contrary to what was expected, the OFF-colony population had approximately twice the root-specific N accumulation as the ON-colony population at all three defoliation intensities (Fig. 3). The effect of competition was nonsignificant (Table 1).

Root : shoot ratios for biomass production and N yield were significantly greater in the ON-colony population (Table 1; Fig. 4). Although ON-colony plants exhibited reductions in both biomass and N root : shoot ratios following defoliation, only the N root : shoot ratio was significantly decreased by defoliation in OFF-colony plants (Table 1; Fig. 4). The N root : shoot ratio had a greater drop than the biomass ratio.

Individual plant parts

The OFF-colony population had significantly higher biomass and N yields than the ON-colony population

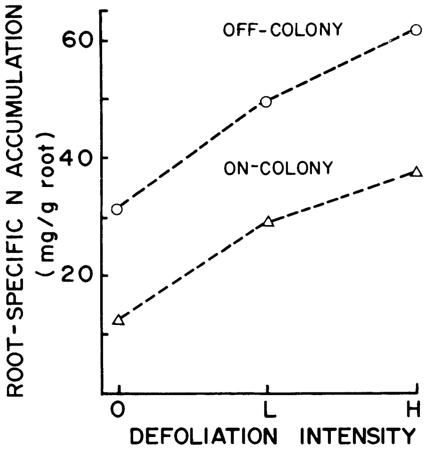

FIG. 3. Defoliation effect on root-specific N accumulation [(total plant N) ÷ (root biomass at harvest)] for OFF-colony and ON-colony populations of *Bouteloua gracilis*. Each point represents the mean of 10 replicates averaged over both competition treatments. Significance levels in Table 1. Defoliation intensity symbols as in Fig. 1.

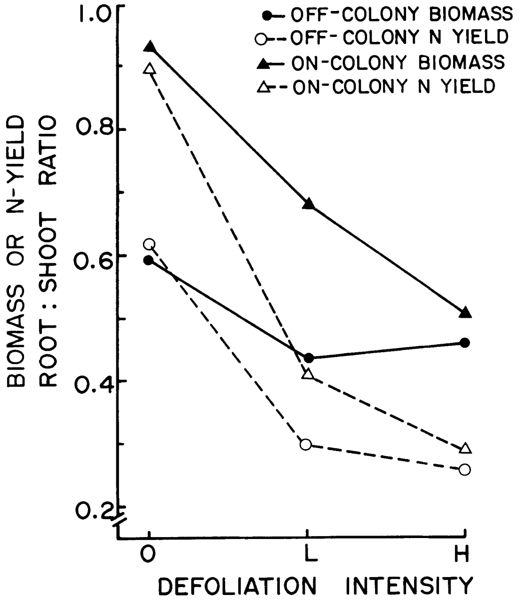

FIG. 4. Defoliation effect on biomass and nitrogen root: shoot ratios of OFF-colony and ON-colony populations of *Bouteloua gracilis*. Each point represents the mean of 10 replicates. Significance levels in Table 1. Defoliation intensity symbols as in Fig. 1.

for the five parts considered: roots, crowns, sheaths, blades, and reproductive structures (Table 1; Figs. 2 and 5). Similarly, plants growing without competition outyielded, in both biomass and nitrogen of every plant part, plants growing with neighbors (Table 2). Defoliation, however, affected biomass and N yields of the plant parts in different ways. Increasing intensity of defoliation reduced biomass and N yields of reproductive structures, crowns, and roots (Table 1; Figs. 2 and 5C, D). Sheath and blade biomass and sheath N yield were not affected by defoliation, but blade N yield increased (Table 1; Fig. 5A).

Blade : sheath ratios calculated for biomass and N yields were higher in the ON-colony population (Table

TABLE 2. Competition effects on plant parts ($\bar{X}$ ± SE; $n = 15$). W.O.C. = without competition; W.C. = with competition; * $P < .05$; ** $P \leq .01$; *** $P \leq .001$; NS = nonsignificant ($P > .05$). P for within-population comparison. There were no significant population × competition interactions in the variables measured.

	OFF-colony population		ON-colony population		
Trait	W.O.C.	W.C.	W.O.C.	W.C.	*P*
Biomass (g)					
Blades	0.85 ± 0.12	0.4 ± 0.08	0.38 ± 0.26	0.22 ± 0.05	***
Sheaths	0.61 ± 0.13	0.24 ± 0.10	0.18 ± 0.04	0.08 ± 0.03	***
Reproductive structures	0.90 ± 0.34	0.28 ± 0.14	0.19 ± 0.07	0.05 ± 0.03	**
Crowns	0.79 ± 0.17	0.32 ± 0.07	0.30 ± 0.06	0.21 ± 0.07	**
Roots	1.04 ± 0.25	0.43 ± 0.08	0.74 ± 0.18	0.31 ± 0.05	***
% blade	24.0 ± 2.2	26.8 ± 1.8	26.9 ± 2.6	27.2 ± 2.3	NS
% sheath	13.5 ± 1.4	11.6 ± 1.8	9.6 ± 0.8	6.8 ± 1.1	NS
% reproductive structures	14.8 ± 3.7	7.4 ± 2.6	6.4 ± 1.5	2.7 ± 1.0	**
% crown	18.9 ± 1.4	21.8 ± 1.4	17.4 ± 0.9	22.9 ± 1.3	***
% roots	28.8 ± 3.9	32.4 ± 3.0	39.2 ± 2.3	40.4 ± 3.1	NS
Blade : sheath ratio	2.2 ± 0.4	3.7 ± 0.9	3.1 ± 0.4	5.2 ± 0.7	**
Nitrogen yield (mg)					
Blades	17.6 ± 4.2	6.4 ± 1.7	5.7 ± 1.5	3.1 ± 1.0	***
Sheaths	7.4 ± 1.8	3.0 ± 1.1	1.5 ± 0.3	0.6 ± 0.2	***
Reproductive structures	7.7 ± 2.3	2.8 ± 1.5	1.0 ± 0.3	0.2 ± 0.1	*
Crowns	6.9 ± 1.6	2.7 ± 0.7	1.9 ± 0.3	1.3 ± 0.4	***
Roots	8.3 ± 1.8	3.6 ± 1.0	4.7 ± 1.1	1.9 ± 0.4	***
% blade	36.3 ± 4.2	38.7 ± 3.8	40.9 ± 4.2	40.7 ± 4.4	NS
% sheath	12.4 ± 1.4	10.1 ± 1.7	9.4 ± 0.9	5.7 ± 0.8	*
% reproductive structures	12.8 ± 3.3	6.8 ± 2.5	5.0 ± 1.1	1.9 ± 0.7	*
% crown	14.9 ± 0.9	17.7 ± 1.7	13.5 ± 0.7	18.3 ± 1.5	**
% roots	23.6 ± 4.0	26.8 ± 3.3	31.1 ± 3.4	33.4 ± 3.7	NS
Blade : sheath ratio	3.7 ± 1.0	6.7 ± 0.7	4.9 ± 0.7	9.0 ± 1.4	**

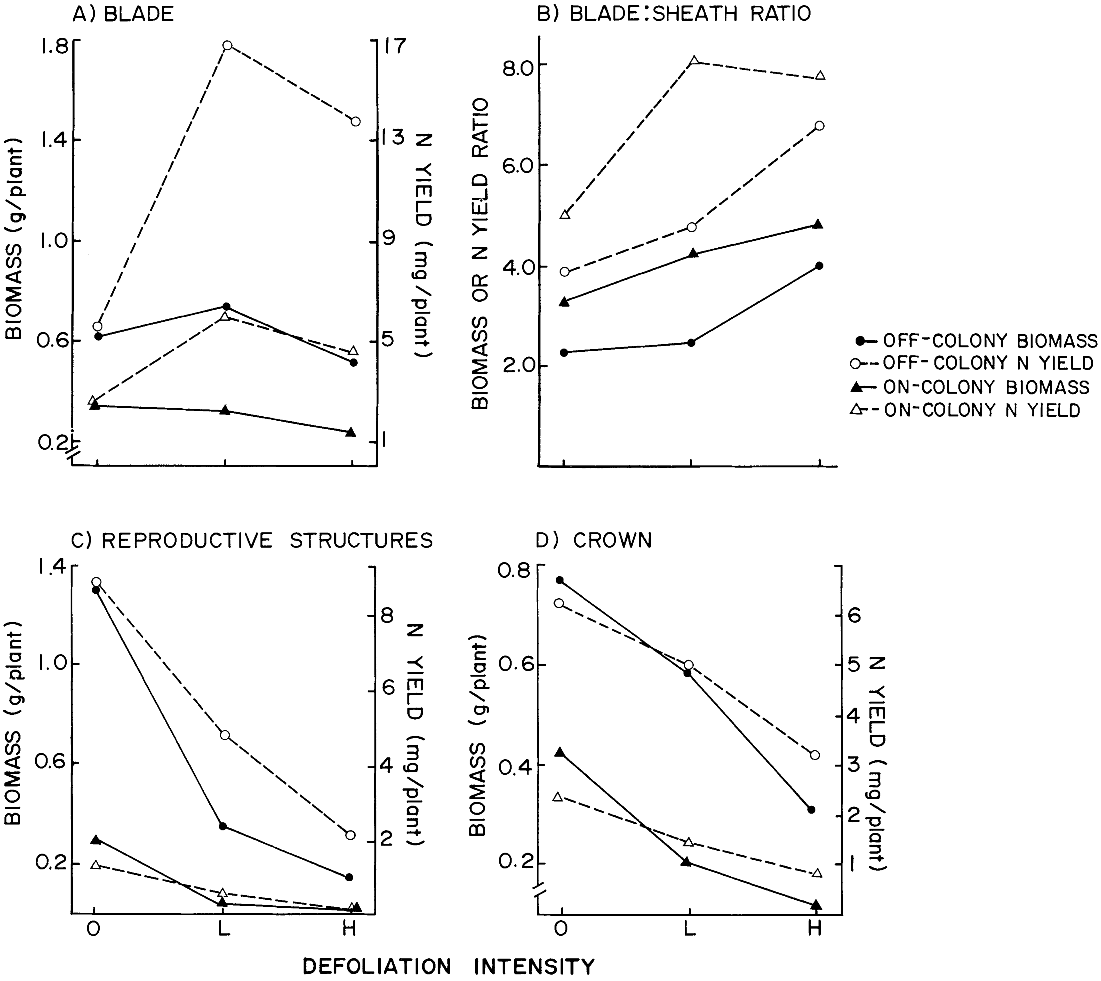

FIG. 5. Defoliation effect on biomass and N yields of (a) blades, (b) blade : sheath ratios, (c) reproductive structures, and (d) crowns of OFF-colony and ON-colony populations of *Bouteloua gracilis*. Each point represents the mean of 10 replicates averaged over both competition treatments. Significance levels in Table 1. Defoliation intensity symbols as in Fig. 1.

1; Fig. 5B). Defoliation (Fig. 5B) and competition (Tables 1 and 2) significantly increased the ratios for both populations.

Analysis of relative biomass and nitrogen allocation patterns revealed population differences in three plant parts: sheaths, reproductive structures, and roots (Table 1; Figs. 4 and 5). Overall, OFF-colony plants allocated a higher percentage of their biomass and N to sheaths (4.4 and 3.7% more, respectively) and to reproductive structures (6.5 and 6.4% more), whereas ON-colony plants allocated a greater percentage of their biomass and N to roots (9.2 and 7.1% more). The two populations did not differ in percent allocation of biomass and N to leaf blades or crowns. Apparently, the higher root : shoot biomass and N ratios of the ON-colony population (Fig. 4) resulted from a greater percentage of resources allocated to roots at the expense of sheaths and reproductive structures.

Relative biomass and N allocation were differentially affected by defoliation (Table 1). Biomass and N allocation to leaf blades increased to an average of 35 and 53% of the plant's biomass and nitrogen in the blades of heavily defoliated plants. Both N allocation to the remaining plant parts (except sheaths) and biomass allocation to reproductive structures were reduced with defoliation. However, in contrast to the OFF-colony population, the ON-colony population showed a significant reduction in root biomass allocation with defoliation (Table 1; Fig. 4).

Competition reduced biomass and N allocation to reproductive structures, reduced sheath N allocation, and increased both biomass and N allocation to the crown (Table 2).

DISCUSSION

The two populations of *Bouteloua gracilis*, with contrasting grazing histories, were significantly different in both whole-plant and individual plant part biomass and N yields. In every case, the taller OFF-colony population outyielded ON-colony plants. Previous work in

Wind Cave National Park has shown that populations of *Bouteloua gracilis* and *Agropyron smithii* Rydb. growing on prairie dog colonies are not only less productive, but are also shorter and more prostrate than plants from lightly grazed or ungrazed populations, even after 3 yr of growth in the greenhouse (Detling and Painter 1983, Cid 1985, Painter 1987). Furthermore, both populations occur throughout the grassland, with the shorter morph predominating on the prairie dog colonies and the taller morph on the uncolonized sites (Painter 1987). This suggests that genetic differentiation has occurred as a result of strong selection pressure from heavy grazing favoring shorter morphs on prairie dog colonies (Detling and Painter 1983, Detling et al. 1986). Other investigations have also shown genetic differences among populations subjected to different grazing or mowing regimes (Gregor and Sansome 1926, Stapledon 1928, Kemp 1937, Brougham and Harris 1967, McNeilly 1981, Scott and Whalley 1984, Carman and Briske 1985). Although our results are consistent with these previous reports, we cannot rule out completely the possibility of phenotypic plasticity, because our plants were collected only 6 mo prior to initiation of the experiment.

Our finding that nondefoliated plants outproduced heavily defoliated plants from both populations is consistent with most previous reports (Jameson 1963), and for *B. gracilis* in particular (Santos and Trlica 1978, Detling et al. 1980, Detling and Dyer 1981). Although defoliation reduced total biomass production, blade and sheath production were not significantly affected (Table 1, Fig. 5A). Resistance to grazing has been associated with the plants' ability to replace lost leaf tissue (Hyder 1972), and our results agree with those of other studies in which defoliated plants exhibited increased allocation of biomass (Detling et al. 1979, Caldwell et al. 1981, Ruess et al. 1983, Ruess and McNaughton 1984), photosynthate (Detling et al. 1980), and nitrogen (Wallace et al. 1982, Ruess et al. 1983, Ruess and McNaughton 1984) to leaves.

In our study, despite root biomass reductions, nitrogen uptake per unit of root biomass and N yield per unit of plant production increased in response to defoliation (Figs. 1, 2, 3). A few other investigators have documented increases in nutrient uptake in response to defoliation (Ruess et al. 1983, McNaughton and Chapin 1985). They proposed that the greater sink strength of grazed shoots results in increased nutrient acquisition per unit of root biomass. We propose an alternative mechanism: phloem retranslocation of mineral nutrients from shoots to roots is known to regulate uptake rates by the roots (Marschner 1986). A decline in retranslocation rate of a given mineral nutrient (because of defoliation) may constitute a "signal" for increasing the rate of uptake of the nutrient.

Increases in foliage nitrogen concentration, in response to grazing, have been known to occur in grasses (Jameson 1963, Everson 1966, Chapin 1980*b*, Detling and Painter 1983). However, in contrast to results from previous field studies in Wind Cave National Park (Coppock et al. 1983*a*, Krueger 1986), ON-colony plants did not have greater shoot N concentrations than OFF-colony plants (Table 1). Possibly the higher shoot N concentration of ON-colony populations in the field results from the potentially greater nitrogen input from excretion products of herbivores that graze on prairie dog colonies (Coppock et al. 1983*b*, Krueger 1986), from greater N availability resulting from increased N mineralization rates (E. Holland, *personal communication*), and from greater intensity of defoliation (Krueger 1986).

Contrary to our expectations, OFF-colony plants had greater nitrogen uptake per unit of root than ON-colony plants (Fig. 3). Because they attained a larger size and had a greater number of tillers and culms than ON-colony plants ($P \leq .01$) when planted from similar-sized single tillers (Jaramillo 1986), we assume that OFF-colony plants had greater growth rates. Rapid biomass accumulation can result in high root absorption capacity and rapid mineral accumulation (Chapin 1980*a*), which would account for the higher root-specific N accumulation, nitrogen yield, and nitrogen concentration of the OFF-colony population.

Analysis of the relative allocation patterns of biomass and nitrogen (root : shoot ratios and percent allocation to plant parts) revealed important differences between the two populations (Figs. 4 and 5). ON-colony plants allocated a greater percentage of resources than OFF-colony plants to the root system, whereas the latter allocated a higher percentage to sheaths and reproductive structures. A higher investment in roots has been considered necessary to offset the negative effects of limited water or nutrient availability, or of frequent shoot removal by fire or grazing (Marshall and Sagar 1965, Mooney 1972, Chapin and Slack 1979, Chapin 1980*a*, Redmann and Reekie 1982, Mooney and Gulmon 1983). In addition to defoliation by prairie dogs, ON-colony plants face heavier grazing pressure than plants at other sites because of preferential feeding by bison and pronghorn on the prairie dog colonies (Coppock et al. 1983*b*, Krueger 1986). Furthermore, they also experience greater removal of root biomass by nematodes than OFF-colony plants (Ingham and Detling 1984). Such interacting biotic pressures may have played an important role in selecting for ON-colony *B. gracilis* plants devoting a greater proportion of their resources to roots than plants from uncolonized sites. On the other hand, plants growing off the prairie dog colonies are taller (Detling and Painter 1983, Brizuela 1985), and canopy cover in these sites is greater than on colonized sites (Coppock et al. 1983*a*, Krueger 1986, Archer et al. 1987). Therefore, plants growing off the prairie dog colonies probably experience a more light-limiting environment. A greater investment in sheaths would allow the plants to hold their blades up higher in the canopy.

For most grasses, grazing may remove not only foliage but reproductive structures as well. Our results show that, although defoliation reduced production of reproductive tissue in both populations, OFF-colony plants consistently allocated both more biomass and more N (absolute and relative) to reproduction than ON-colony plants (Fig. 5). Reproductive structures should not face serious predation risk in lightly grazed OFF-colony sites. In fact, field studies have shown that flowering and seed production are reduced by heavy grazing on prairie dog colonies (Brizuela 1985). Reproductive differences have also been documented for grazed and ungrazed populations of *Danthonia* spp., but in this case plants from heavily grazed sites have increased fecundity (Scott and Whalley 1984).

Although nondefoliated plants of both populations had similar biomass and N allocation patterns, as has been shown for other grasses (Pavlik 1983, Adams and Wallace 1985), defoliation altered them substantially (Figs. 4 and 5). The significant increases in the percentage of biomass and N allocated to leaf blades (from 17 to 35% and from 20 to 53%, respectively), as well as in blade N yield and blade : sheath ratios (Fig. 5), suggest that defoliated plants from both populations have the ability to rapidly restore photosynthetic capacity. However, following defoliation, plants from the prairie dog colony reduced both biomass and nitrogen allocation to the root system, while OFF-colony plants reduced only nitrogen allocation to the roots. Such a response may allow the ON-colony plants to more rapidly restore root : shoot equilibrium, which presumably should enhance their ability to tolerate herbivory (Caldwell et al. 1981, Richards 1984).

Plants show both plastic and mortality responses to increased density (Harper 1977). Both populations showed plastic responses by decreasing biomass and N yields between 50 and 60%. Similar density effects have been noted in other grasses (Donald 1963, Harper 1977, Williams and Ingber 1977, Tripathi and Gupta 1980).

Very few studies have focused on the interactive effects of density and herbivory or defoliation (Dirzo and Harper 1980, Lee and Bazzaz 1980, Tripathi and Gupta 1980). In contrast to Lee and Bazzaz (1980), we did not find a significant interaction between heavy defoliation and competition. Possibly, the absence of interaction occurred because all plants in each pot were evenly clipped. Thus, a single clipped plant was not in a disadvantageous position with regard to nondefoliated neighbors. However, another study with species mixtures has also shown independent effects of defoliation and competition, in which defoliated plants were not in a disadvantageous position with regard to nondefoliated neighbors of different species (Fowler and Rausher 1985).

Biomass reductions caused by increased density in nondefoliated plants were similar in magnitude to those caused by heavy defoliation on isolated individuals (Figs. 1 and 2). This supports the conclusion of Dirzo and Harper (1980) that grazing may substitute for density as the cause of death or plastic change in plant populations. Our study also supports their argument that results from field studies using exclosures are the consequence not only of grazing prevention but also of a concomitant increase in interference between the ungrazed plants.

Capacity to make use of nutrients may influence the competitive ability of a plant species (Donald 1963, Tilman 1982). Root-specific N accumulation, a measure of the plant's ability to capture nitrogen, was not impaired by the presence of neighbors of the same population. This suggests that N-yield reductions by competition may have resulted principally from plants in the high-density treatment drawing nutrients from a relatively smaller pool, compared with a plant growing alone in a pot.

Results from studies of *Agropyron smithii* from Wind Cave National Park (Detling and Painter 1983, Detling et al. 1986) suggested that ON-colony plants would withstand defoliation better than OFF-colony plants. However, this was not the case with the ON-colony population of *B. gracilis,* which has seemingly been selected more for a strategy that reduces grazing severity than for a "grazing tolerance" strategy. We suggest this because the lack of a significant population × defoliation interaction means the two populations have similar responses to defoliation (except for the two cases already discussed). Plants of both populations are capable of both effectively replacing their lost photosynthetic structures and increasing their aboveground N concentration. In this context, the short stature and more prostrate growth form of ON-colony plants should enable them to reduce the proportion of aboveground structures consumed by herbivores and enhance their probabilities of survival and persistence under heavy grazing. This may be especially so, considering that ON-colony populations have greater blade : sheath ratios (Fig. 5B; Detling and Painter 1983), which makes them, potentially, a more rewarding resource for herbivores. The growth form advantage, however, was not examined in our study.

Finally, our study showed population differences in biomass and nitrogen yields, in relative allocation patterns and their plasticity in response to defoliation, and in the plants' ability to take up nitrogen. We suggest the differences we observed may have been the result of a strong selection pressure, heavy grazing by mammals, that has produced genetic differentiation of the populations in a relatively short time. The occurrence of rapid genetic changes in populations has been documented by a number of workers (Brougham and Harris 1967, Antonovics 1976, Snaydon 1978), and it is likely that other processes associated with grazing on the prairie dog colonies (e.g., increased nutrient inputs) have also contributed to the differentiation of the nutrient physiology of *B. gracilis* populations.

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Literature Cited

Adams, D. E., and L. L. Wallace. 1985. Nutrient and biomass allocation in five grass species in an Oklahoma tallgrass prairie. American Midland Naturalist **113**:170–181.

Antonovics, J. 1976. The input from population genetics: "the new ecological genetics." Systematic Botany **1**:233–245.

Archer, S. R., M. G. Garrett, and J. K. Detling. 1987. Rates of vegetation change associated with prairie dog (*Cynomys ludovicianus*) grazing in North American mixed-grass prairie. Vegetatio **72**:159–166.

Brizuela, M. A. 1985. Silicon concentration of grasses from sites with different prairie dog and bison grazing histories. Thesis. Colorado State University, Fort Collins, Colorado, USA.

Brougham, R. W., and W. Harris. 1967. Rapidity and extent of changes in genotypic structure induced by grazing in a ryegrass population. New Zealand Journal of Agricultural Research **10**:56–65.

Caldwell, M. M., J. H. Richards, D. A. Johnson, R. S. Nowak, and R. S. Dzurec. 1981. Coping with herbivory: photosynthetic capacity and resource allocation in two semiarid *Agropyron* bunchgrasses. Oecologia (Berlin) **50**:14–24.

Carman, J. G., and D. D. Briske. 1985. Morphologic and allozymic variation between long-term grazed and nongrazed populations of the bunchgrass *Schizachyrium scoparium* var. *frequens*. Oecologia (Berlin) **66**:332–337.

Chapin, F. S. 1980*a*. The mineral nutrition of wild plants. Annual Review of Ecology and Systematics **11**:233–260.

———. 1980*b*. Nutrient allocation and responses to defoliation in tundra plants. Arctic and Alpine Research **12**:553–563.

Chapin, F. S., and M. Slack. 1979. The effect of defoliation upon root growth, phosphate absorption and respiration in nutrient-limited tundra graminoids. Oecologia (Berlin) **42**:67–79.

Cid, M. S. 1985. Effects of grazing exposure history and defoliation on silicon concentration of *Agropyron smithii*. Thesis. Colorado State University, Fort Collins, Colorado, USA.

Coppock, D. L., J. K. Detling, J. E. Ellis, and M. I. Dyer. 1983*a*. Plant-herbivore interactions in a North American mixed-grass prairie. I. Effects of black-tailed prairie dogs on intraseasonal aboveground plant biomass and nutrient dynamics and plant species diversity. Oecologia (Berlin) **56**:1–9.

Coppock, D. L., J. E. Ellis, J. K. Detling, and M. I. Dyer. 1983*b*. Plant-herbivore interactions in a North American mixed-grass prairie. II. Responses of bison to modification of vegetation by prairie dogs. Oecologia (Berlin) **56**:10–15.

Detling, J. K., and M. I. Dyer. 1981. Evidence for potential plant growth regulators in grasshoppers. Ecology **62**:485–488.

Detling, J. K., M. I. Dyer, C. Procter-Gregg, and D. T. Winn. 1980. Plant-herbivore interactions: examination of potential effects of bison saliva on regrowth of *Bouteloua gracilis* (H.B.K.) Lag. Oecologia (Berlin) **45**:26–31.

Detling, J. K., M. I. Dyer, and D. T. Winn. 1979. Net photosynthesis, root respiration, and regrowth of *Bouteloua gracilis* following simulated grazing. Oecologia (Berlin) **41**:127–134.

Detling, J. K., and E. L. Painter. 1983. Defoliation responses of western wheatgrass populations with diverse histories of prairie dog grazing. Oecologia (Berlin) **57**:65–71.

Detling, J. K., E. L. Painter, and D. L. Coppock. 1986. Ecotypic differentiation resulting from grazing pressure: evidence for a likely phenomenon. Pages 431–433 *in* P. J. Joss, P. W. Lynch, and O. B. Williams, editors. Rangelands: a resource under siege. Proceedings of the Second International Rangelands Congress, Australian Academy of Science, Canberra, Australia.

Dirzo, R., and J. L. Harper. 1980. Experimental studies on slug-plant interactions. II. The effect of grazing by slugs on high density monocultures of *Capsella bursa-pastoris* and *Poa annua*. Journal of Ecology **68**:999–1011.

Donald, C. M. 1963. Competition among crop and pasture plants. Advances in Agronomy **15**:1–118.

Everson, A. C. 1966. Effects of frequent clipping at different stubble heights on western wheatgrass (*Agropyron smithii* Rydb.). Agronomy Journal **58**:33–35.

Floate, M. J. S. 1981. Effects of grazing by large herbivores on nitrogen cycling in agricultural ecosystems. *In* F. E. Clark and T. Roswall, editors. Terrestrial nitrogen cycles. Ecological Bulletins–NFR **33**:585–601.

Fowler, N. L., and M. D. Rausher. 1985. Joint effects of competitors and herbivores on growth and reproduction in *Aristolochia reticulata*. Ecology **66**:1580–1587.

Gregor, J. W., and F. W. Sansome. 1926. Experiments on the genetics of wild populations. Part I. Grasses. Journal of Genetics **17**:349–364.

Harper, J. L. 1977. Population biology of plants. Academic Press, London, England.

Hart, R. H., and E. F. Balla. 1982. Forage production and removal from western and crested wheatgrasses under grazing. Journal of Range Management **35**:362–366.

Hyder, D. N. 1972. Defoliation in relation to vegetative growth. Pages 304–317 *in* V. B. Youngner and C. M. McKell, editors. The biology and utilization of grasses. Academic Press, New York, New York, USA.

Ingham, R. E., and J. K. Detling. 1984. Plant–herbivore interactions in a North American mixed-grass prairie. III. Soil nematode populations and root biomass on *Cynomys ludovicianus* colonies and adjacent uncolonized areas. Oecologia (Berlin) **63**:307–313.

Jameson, D. 1963. Responses of individual plants to harvesting. Botanical Review **29**:532–594.

Jaramillo, V. J. 1986. The effect of grazing history and competition on the response of *Bouteloua gracilis* to defoliation. Thesis. Colorado State University, Fort Collins, Colorado, USA.

Kemp, W. B. 1937. Natural selection within plant species. Journal of Heredity **28**:329–333.

Krueger, K. 1986. Feeding relationships among bison, pronghorn and prairie dogs: an experimental analysis. Ecology **67**:760–770.

Lee, T. D., and F. A. Bazzaz. 1980. Effects of defoliation and competition on growth and reproduction in the annual plant *Abutilon teophrasti*. Journal of Ecology **68**:813–821.

Marschner, H. 1986. Mineral nutrition of higher plants. Academic Press, New York, New York, USA.

Marshall, C., and M. G. Sagar. 1965. The influence of defoliation on the distribution of assimilates in *Lolium multiflorum* Lam. Annals of Botany **29**:365–371.

Mattson, W. J., Jr. 1980. Herbivory in relation to plant nitrogen content. Annual Review of Ecology and Systematics **11**:119–161.

McNaughton, S. J. 1979. Grazing as an optimization process: grass-ungulate relationships in the Serengeti. American Naturalist **113**:691–703.

McNaughton, S. J., and F. S. Chapin. 1985. Effects of phosphorus nutrition and defoliation on C_4 graminoids from the Serengeti plains. Ecology **66**:1617–1629.

McNeilly, T. 1981. Ecotypic differentiation in *Poa annua*: interpopulation differences in response to competition and cutting. New Phytologist **88**:539–547.

Mooney, H. A. 1972. The carbon balance of plants. Annual Review of Ecology and Systematics **3**:315–346.

Mooney, H. A., and S. L. Gulmon. 1982. Constraints on leaf structure and function in reference to herbivory. BioScience **32**:198–206.

Mooney, H. A., and S. L. Gulmon. 1983. The determinants of plant productivity—natural versus man-modified communities. Pages 146–158 *in* H. A. Mooney and M. Godron, editors. Disturbance and ecosystems: components of response. Ecological Studies 44. Springer-Verlag, Berlin, West Germany.

Nie, N. H., C. H. Hull, J. G. Jenkins, K. Steinbrenner, and D. H. Bent. 1975. Statistical package for the social sciences. Second edition. McGraw-Hill, New York, New York, USA.

Painter, E. L. 1987. Grazing and intraspecific variation in four North American grass species. Dissertation. Colorado State University, Fort Collins, Colorado, USA.

Pavlik, B. M. 1983. Nutrient and productivity relations of the dune grasses *Ammophila arenaria* and *Elymus mollis*. II. Growth and patterns of dry matter and nitrogen allocation as influenced by nitrogen supply. Oecologia (Berlin) **57**:233–238.

Redmann, R. E., and E. G. Reekie. 1982. Carbon balance in grasses. Pages 195–213 *in* J. R. Estes, R. J. Tyrl, and J. N. Brunken, editors. Grasses and grasslands: systematics and ecology. University of Oklahoma Press, Norman, Oklahoma, USA.

Richards, J. H. 1984. Root growth response to defoliation in two *Agropyron* bunchgrasses: field observations with an improved root periscope. Oecologia (Berlin) **64**:21–25.

Ruess, R. W. 1984. Nutrient movement and grazing: experimental effects of clipping and nitrogen source on nutrient uptake in *Kyllinga nervosa*. Oikos **43**:183–188.

Ruess, R. W., and S. J. McNaughton. 1984. Urea as a promotive coupler of plant–herbivore interactions. Oecologia (Berlin) **63**:331–337.

Ruess, R. W., S. J. McNaughton, and M. B. Coughenour. 1983. The effects of clipping, nitrogen source and nitrogen concentration on the growth responses and nitrogen uptake of an East-African sedge. Oecologia (Berlin) **59**:253–261.

Santos, G. L., and M. J. Trlica. 1978. Clipping effects on production and carbohydrate reserves of blue grama and western wheatgrass. Journal of Range Management **31**:384–386.

Scott, A. W., and R. D. B. Whalley. 1984. The influence of intensive sheep grazing on genotypic differentiation in *Danthonia linkii, D. richardsonii* and *D. racemosa* on the New England tablelands. Australian Journal of Ecology **9**:419–429.

Snaydon, R. W. 1978. Genetic changes in pasture populations. Pages 253–269 *in* J. R. Wilson, editor. Plant relations in pastures. Commonwealth Scientific and Industrial Research Organization (CSIRO), Melbourne, Australia.

Stapledon, R. G. 1928. Cocksfoot grass (*Dactylis glomerata* L.): ecotypes in relation to the biotic factor. Journal of Ecology **16**:71–104.

Stroud, D. O., R. H. Hart, M. J. Samuel, and J. D. Rodgers. 1985. Western wheatgrass responses to simulated grazing. Journal of Range Management **38**:103–108.

Tilman, D. 1982. Resource competition and community structure. Princeton University Press, Princeton, New Jersey, USA.

Tripathi, R. S., and G. T. Gupta. 1980. The growth of *Bothriochloa pertusa* and *Dichanthium annulatum* in relation to crowding and herbage removal. Oikos **34**:219–226.

Wallace, L. L., S. J. McNaughton, and M. B. Coughenour. 1982. The effects of clipping and fertilization on nitrogen nutrition and allocation by mycorrhizal and nonmycorrhizal *Panicum coloratum* L., a C_4 grass. Oecologia (Berlin) **54**:68–71.

White, T. C. R. 1984. The abundance of invertebrate herbivores in relation to the availability of nitrogen in stressed food plants. Oecologia (Berlin) **63**:90–105.

Williams, R. D., and B. F. Ingber. 1977. The effect of intraspecific competition on the growth and development of Johnson-grass under greenhouse conditions. Weed Science **25**:293–297.

Youngner, V. B. 1972. Physiology of defoliation and regrowth. Pages 292–303 *in* V. B. Youngner and C. M. McKell, editors. The biology and utilization of grasses. Academic Press, New York, New York, USA.