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Does selective defoliation mediate competitive interactions in a semiarid savanna? A demographic evaluation

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Abstract. Three patterns of target-neighbor plant defoliation were imposed on a late-seral, perennial, C_4-grass, *Bouteloua curtipendula*, in three long-term grazing regimes to determine the influence of selective defoliation on competitive interactions and species replacement in a semiarid savanna on the Edwards Plateau, Texas, USA. Short-term (3-yr) target plant defoliation did not significantly affect either tiller or plant responses in any of the three grazing regimes. Neighbor plant defoliation, either alone or in combination with target plants, produced a significant defoliation interaction with time for tiller number and basal area per plant, but not for tiller recruitment or mortality. The minimal effect of selective defoliation on the intensity of competitive interactions in this semiarid community indicates that selective grazing has a less definitive role in mediating herbivore-induced species replacement than it does in mesic grasslands and savannas. This interpretation is discussed within the context of long-term (45-yr) change in herbaceous vegetation associated with grazing in this community.

Cumulative tiller recruitment in the intensively grazed regime was only 44 % of that in the ungrazed regime because of greater plant mortality and fewer surviving plants that recruited tillers. Target plant mortality (50 %) only occurred in the intensively grazed regime and the proportion of target plants that initiated tillers decreased by 70, 48 and 32 % in the ungrazed, moderately and intensively grazed regimes, respectively, during the final two years of the investigation. The decrease in cumulative tiller recruitment in all grazing regimes was probably mediated by a drought-induced increase in median tiller age the second year of the study. However, tiller per tiller recruitment rate among plants that recruited at least one tiller remained relatively constant among grazing regimes and years. Intensive, long-term grazing has modified the population structure of this late-seral perennial grass to the extent that population responses to both herbivory and periodic drought have been altered in comparison with those of ungrazed and moderately grazed populations. Ecological consequences of a herbivore-induced transition in population structure may be to minimize the effect of selective herbivory on competitive interactions and to function as an avoidance mechanism to reduce the probability of localized population extinction in response to intensive long-term herbivory.

Keywords: *Bouteloua curtipendula*; Grassland; Herbivory; Plant-animal interaction; Population structure; Selective grazing; Tiller demography.

Nomenclature: Hatch et al. 1990.

Introduction

Selective herbivory is capable of suppressing late-seral grass populations and contributing to species replacement in mesic grasslands of the true prairies (Brown & Stuth 1993; Anderson & Briske 1995) and mixed prairies of Texas (Heitschmidt et al. 1990) and mesic South African grasslands (O'Connor 1991). Selective herbivory originates from the differential expression of grazing avoidance mechanisms among plant species that influences the relative frequency and/or intensity of herbivory by reducing plant palatability and/or accessibility (Briske & Richards 1995; Briske 1996). Selective herbivory places plants at a competitive disadvantage by suppressing resource acquisition and growth relative to ungrazed or more leniently grazed plants (e.g. Mueggler 1972; Caldwell et al. 1987; Polley & Detling 1988).

Even though competitive interactions are generally assumed to mediate vegetation dynamics in semiarid communities (Fowler 1986), the intensity and duration of competitive interactions may be reduced by low resource availability (Fowler 1986, 1995) and extreme spatial- (Miller et al. 1995; Fuhlendorf & Smeins 1998) and temporal heterogeneity (Moloney 1990; Goldberg & Novoplansky 1997). A reduction in the intensity and duration of competitive interactions suggests that the effect of selective herbivory on competitive interactions may be diminished and overridden by abiotic variables in environments characterized by low and unpredictable resource availability (e.g. Grime 1979; Wilson & Keddy 1986). Climatic variability has been recognized to be a more important agent of vegetation change than grazing in various herbaceous communities (Milchunas et al. 1989; O'Connor 1991, 1994; Biondini et al. 1998).

Intensive herbivory may compromise competitive ability and population persistence of perennial grasses by reducing tiller recruitment, tiller longevity, plant longevity, seed production and seedling establishment (Briske & Richards 1995). Meristematic availability, including leaf and tiller initiation from apical meristems and axillary buds, respectively, is a critical variable determining herbivory tolerance in perennial grasses. A comparative investigation of a herbivory-tolerant and herbivory-sensitive C_3-perennial bunchgrass by Caldwell et al. (1981) demonstrated that the ability to replace leaf area by rapid tiller initiation and development of leaves with low specific mass were more important than compensatory photosynthesis (Nowak & Caldwell 1984) or size of reserve carbon pools (Richards & Caldwell 1985). Unfortunately, variation in species-specific herbivory tolerance is difficult to distinguish from that of herbivore-mediated competitive interactions in field settings (Caldwell 1984).

An experiment was conducted to evaluate the contribution of selective defoliation on competitive interactions and population persistence of a late-seral perennial grass, *Bouteloua curtipendula* var. *caespitosa*, in a semiarid savanna. Specific hypotheses tested were:

1. Tiller recruitment and mortality will be adversely affected by selective defoliation of *B. curtipendula*, but these variables will be relatively unaffected by uniform defoliation of both *B. curtipendula* and its immediate neighbors.
2. Selective defoliation of *B. curtipendula* will adversely affect tiller recruitment and mortality to a greater extent than tiller number and basal area per plant.
3. Selective defoliation of *B. curtipendula* will have a less adverse affect on plant and tiller variables in the more intensively grazed regimes because a greater proportion of the neighbors will be mid-seral, rather than late-seral species. The third hypothesis is based on the widely held assumption that late-seral species are more competitive than mid- or early seral species (Grime 1979).

Study area

Research was conducted at the Texas A&M University Agricultural Research Station 56 km south of Sonora, Texas (31° 18' N; 100° 28' W), in the southwestern portion of the Edwards Plateau Land Resource Area at an elevation of ca. 735 m. Topography of the research station is highly dissected and soils contain large amounts of limestone fragments, stones and gravel (Smeins & Merrill 1988; Fuhlendorf & Smeins 1997, 1998). The dominant soils are Tarrant stony clays that formed over fractured formations of Buda and Edwards Limestone and are classified as Lithic Haplustolls. The area is potentially a mid-grass grassland with individuals and clustered trees of *Quercus virginiana*, *Q. pungens* var. *vaseyana*, *Juniperus ashei* and *J. pinchotii*. However, long-term overgrazing by domestic herbivores has altered species composition by reducing the abundance of late-seral mid-grasses, including *B. curtipendula* and *Eriochloa sericea*, and increasing the abundance of mid-seral shortgrasses, including *Hilaria belangeri*, *Bouteloua trifida*, and *Erioneuron pilosum* and several woody species (Smeins & Merrill 1988; Fuhlendorf & Smeins 1997). The abundance of late-seral mid-grasses has increased following long-term (approximately 50 yr) protection from domestic herbivores.

This investigation was conducted in three long-term grazing regimes with contrasting grazing intensities. The ungrazed regime had been protected from domestic, but not native herbivores, since 1948 while the two grazed regimes had been either intensively or moderately grazed by cattle, sheep and goats since 1948 (Fuhlendorf & Smeins 1997). Sixty *B. curtipendula* target plants were located along transects in each of the three grazing regimes for a total of 180 plants. Target plants, within the grazed regimes, were protected from livestock grazing during the investigation by constructing two (10 m × 14 m) exclosures in each of the regimes.

Median long-term precipitation is 439 mm, but it is highly erratic within and between years (Smeins & Merrill 1988). May and September are typically the wettest months while November and January tend to be the driest. Mean annual precipitation was 73.6, 98.1, and 94.3% of the long-term mean for 1993, 1994, and 1995, respectively. However, precipitation was only 65 % of the long-term mean from October 1993 to September 1994. Mean annual precipitation for the 3-yr period prior to the investigation was 105 % of the long-term mean.

Methods

Three defoliation patterns were imposed to test the importance of selective versus uniform defoliation on plant and tiller demography of *B. curtipendula*. Defoliation patterns were: (1) defoliation of only the target plant; (2) defoliation of both the target plant and the five nearest neighbors; (3) defoliation of the five nearest neighbors, but not the target plant; and (4) a control treatment with no defoliation. Neighbor plants consisted of primarily late-seral species in the ungrazed regime and mid-seral species in the moderately and intensively grazed regimes. 15 target plants in each grazing regime were assigned to each of the three defoliation patterns and the control. Mid-grasses were manually defoliated to a height of 4 cm twice a year (May and October) with clippers and short-grasses were defoliated to a height of 2 cm to impose a comparable defoliation intensity on the shorter statured plants.

Whole-plant tiller number and basal area for *B. curtipendula* and its neighbors were evaluated in May-June and October of 1993, 1994 and 1995. Tillers were considered live when one green leaf was present. Basal area was calculated by determining plant circumference at the soil surface and converting it to an area. Density of *B. curtipendula* plants was measured in June 1994 by placing 50 quadrats along line transects in each of the three grazing regimes. Larger quadrats (0.25 m^2) were used in the ungrazed regime while smaller (0.18 m^2) quadrats were used to sample the higher density of smaller plants in the moderate and intensively grazed regimes.

Tiller demography of *B. curtipendula* was evaluated by monitoring four permanently marked vegetative tillers (2 - 4 leaf stage) on the periphery of each target plant. Permanently marked tillers were initially identified in June 1993 and censused for recruitment and mortality in October 1993 and in May and October of the following two years. Juvenile tillers were marked with different colored wire loops at each census interval. Monthly recruitment rate per tiller per plant was calculated for census time *t* as:

$$\frac{\text{juvenile tillers}\,/\,\text{plant at time } t}{\text{parental tillers}\,/\,\text{plant at time } t-1} \times \frac{1}{\text{census interval (months)}} \qquad (1)$$

Monthly mortality rate/tiller/plant was calculated similarly, except that the number of dead or missing tillers at time *t* were located in the numerator (Bullock et al. 1994, 1996).

Tiller replacement ratios were calculated to determine the net effect of tiller recruitment and mortality on tiller populations (Olson & Richards 1988). Replacement ratios were calculated for each defoliation pattern and the control as:

$$\frac{\text{initial tiller number} + \text{cumulative recruitment} - \text{mortality}}{\text{initial tiller number}} \qquad (2)$$

Increasing, constant, or decreasing tiller populations are indicated by ratios greater than, equal to, or less than one, respectively.

Absolute changes in plant variables and tiller recruitment and mortality rates were evaluated within each grazing regime as a split plot design with defoliation pattern as the main plot factor and time as the split plot factor. Data were analysed using ANOVA in the SAS statistical package (Anon. 1990). Main plot factors and interaction means were separated using Tukey's *w* procedure (Steele & Torrie 1980 p. 185). All main plot factors and interactions were considered significant at $P < 0.05$ unless stated otherwise. Survivorship curves were calculated for tiller cohorts both within and across defoliation patterns and tested with a log-rank test (Pyke & Thompson 1986; Hutchings et al. 1991). Log-rank analysis uses the χ^2-statistic to test for tiller survival at comparable time intervals. Significance of χ^2 values were evaluated using Bonferroni tests on all pairwise comparisons. Median tiller age for each cohort was calculated from the life spans of tillers initiated on specific sampling dates within individual grazing regimes.

Vegetation structure and composition among the three grazing regimes differed greatly (Smeins et al. 1976; Fuhlendorf & Smeins 1997) and the grazing regimes were not replicated (Hurlbert 1984). Therefore, each community was analysed independently. Inferences regarding plant and tiller responses among grazing regimes were based on the presence or absence of significant responses to defoliation patterns within communities, rather than on relative responses of plant and tiller variables among communities.

Results

Population structure

Population structure of *Bouteloua curtipendula* in the intensively grazed regime was characterized by a higher density of smaller plants compared with the other two grazing regimes. Mean basal area of *B. curtipendula* target plants in the intensively grazed regime was only 5 % of the mean basal area per plant in the ungrazed and moderately grazed regimes in June 1993 (Table 1). Mean tiller number per target plant in the intensively grazed regime was less than 22 % of mean tiller number per target plant in the ungrazed and moderately grazed regimes.

Plant variables

The defoliation pattern did not significantly affect main factor tiller or plant variables in any of the grazing regimes and defoliation pattern × time interactions were significant for plant, but not tiller, variables in the

Table 1. Population structure of *Bouteloua curtipendula* and neighboring plants in three grazing regimes with contrasting grazing intensities. Mean (± SE) basal area, tiller numbers and species composition were determined in June 1993 and plant density was evaluated in June 1994. $N = 60$ for basal area and tiller number and $N = 50$ for density values.

	Target plant			Neighbor plants		
Grazing regime	Basal area/ plant (cm^2)	Tillers/ plant	Density/ m^2	Basal area/ plant (cm^2)	Tillers/ plant	Seral status
Ungrazed	38.5 ± 4.4	28.0 ± 1.7	4.0 ± 1.3	13.6 ± 1.2	19.4 ± 1.0	Late-seral
Moderate	47.7 ± 3.8	35.7 ± 2.6	1.5 ± 0.8	10.7 ± 1.1	23.6 ± 1.5	Mid-seral
Intensive	1.9 ± 0.8	5.9 ± 0.9	15.6 ± 7.0	4.5 ± 0.6	11.5 ± 0.7	Mid-seral

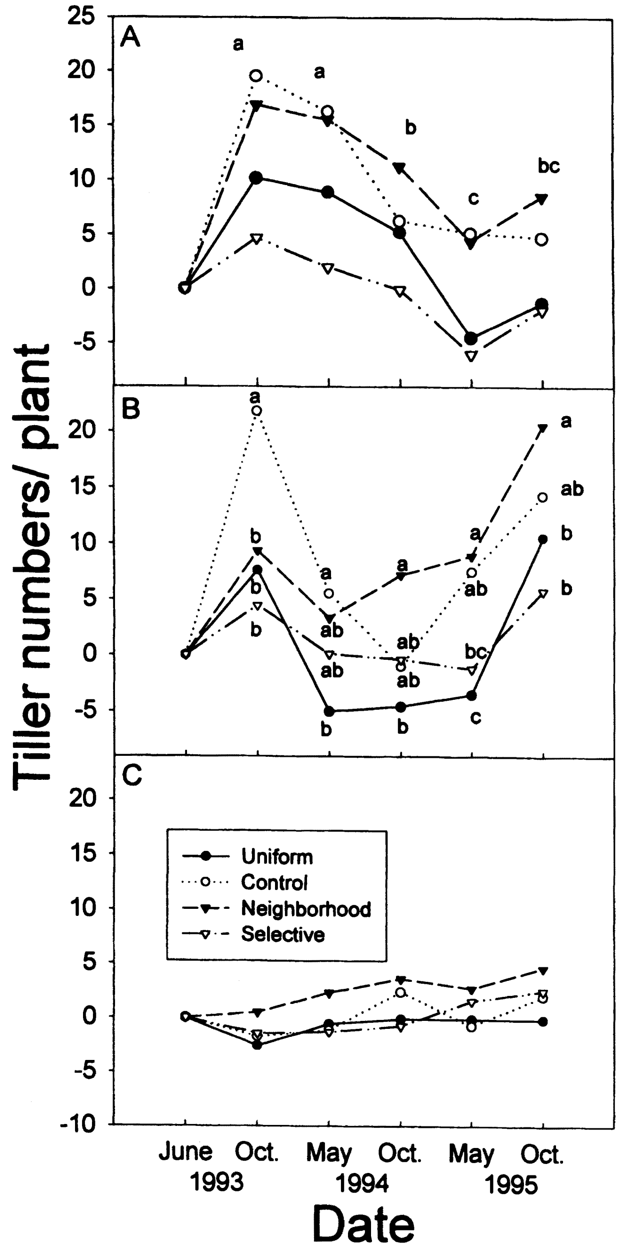

Fig. 1. Mean absolute change in tiller number per *Bouteloua curtipendula* target plant in response to three defoliation patterns and control plants in an **A.** ungrazed, **B.** moderately grazed, and **C.** intensively grazed regime. Defoliation patterns were (1) defoliation of only the target plant (Selective); (2) defoliation of both target and neighbor plants (Uniform); (3) defoliation of only the neighbor plants (Neighbor); and (4) undefoliated target and neighbor plants (Control). Defoliation patterns marked with different letters indicate significant differences ($P \leq 0.10$) among time periods across defoliation patterns (A) and among defoliation patterns at each time period (B). $N = 15$ plants per defoliation pattern per grazing regime.

neighborhood defoliation pattern. Neighbor defoliation modified plant variables of *B. curtipendula* to the greatest extent in the ungrazed and moderately grazed regimes, but these variables were unresponsive to the same defoliation patterns in the intensively grazed regime.

Target plants

A significant time × defoliation pattern interaction occurred in the moderately grazed regime when tiller number per target plant was significantly greater in the neighborhood than in the selective or uniform defoliation patterns during the last two sampling dates (Fig. 1B). Target plant tiller number in the control was also significantly greater than those in the uniform pattern in May 1995. In the ungrazed regime, tiller number per target plant, averaged over all defoliation patterns, was significantly greater in October 1993 and May 1994 than it was in the following three sampling periods (Fig. 1A). The lowest tiller number per target plant occurred in May 1995 when tiller number in the selective and uniform defoliation patterns decreased below initial values recorded in June 1993. In the ungrazed and moderately grazed regimes, mean tiller number per target plant decreased between October 1993 and May 1994, but increased from May to October 1995 (Fig. 1A,B). Tiller number per target plant was consistently low in all defoliation patterns in the intensively grazed community (Fig. 1C).

Mean basal area of the target plant had a significant time × defoliation pattern interaction in the ungrazed regime. Basal area per target plant was significantly greater in the neighborhood than in the selective or control patterns in October 1995 (Fig. 2A). Mean basal area per target plant was significantly greater in the control compared to target plants in the selective pattern, after May 1994. Basal area per target plant, averaged across defoliation patterns, was significantly greater in May and October 1995 than in October 1993 or May 1994 in the moderately grazed regime (Fig. 2B). Mean basal area per target plant increased throughout the investigation in both the ungrazed and moderately grazed regimes, but not in the intensively grazed regime (Fig. 2A-C).

Neighbor plants

Tiller number per neighbor plant exhibited a time × defoliation pattern interaction in all three grazing regimes (Fig. 3A-C). Mean tiller number per neighbor plant was lower when neighbor plants were defoliated (neighborhood and uniform patterns) compared to when they were undefoliated (selective treatment and control) for all sampling dates in the ungrazed regime (Fig. 3A) and for the last two sampling dates in the intensively grazed regime (Fig. 3C). In the moderately grazed

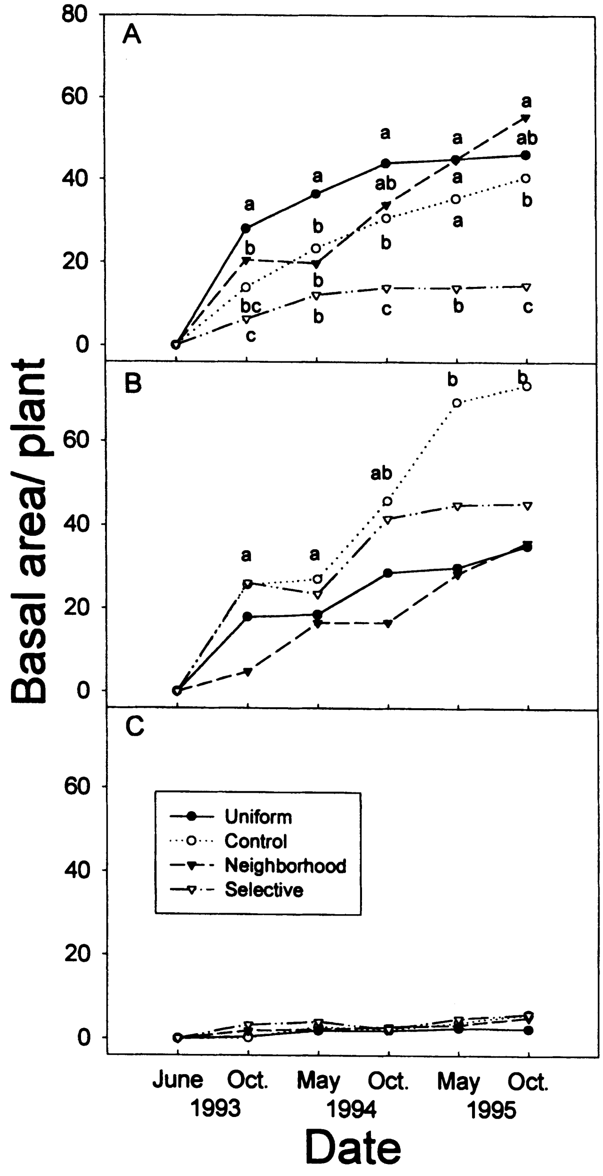

Fig. 2. Mean absolute change in basal area per *Bouteloua curtipendula* target plant in response to three defoliation patterns and control plants in an **A.** ungrazed, **B.** moderately grazed, and **C.** intensively grazed regime. Defoliation patterns are described in Fig. 1. Defoliation patterns marked with different letters indicate significant differences ($P \leq 0.10$) among defoliation patterns at each time period (A) and among time periods across defoliation patterns (B). $N = 15$ plants per defoliation pattern per grazing regime.

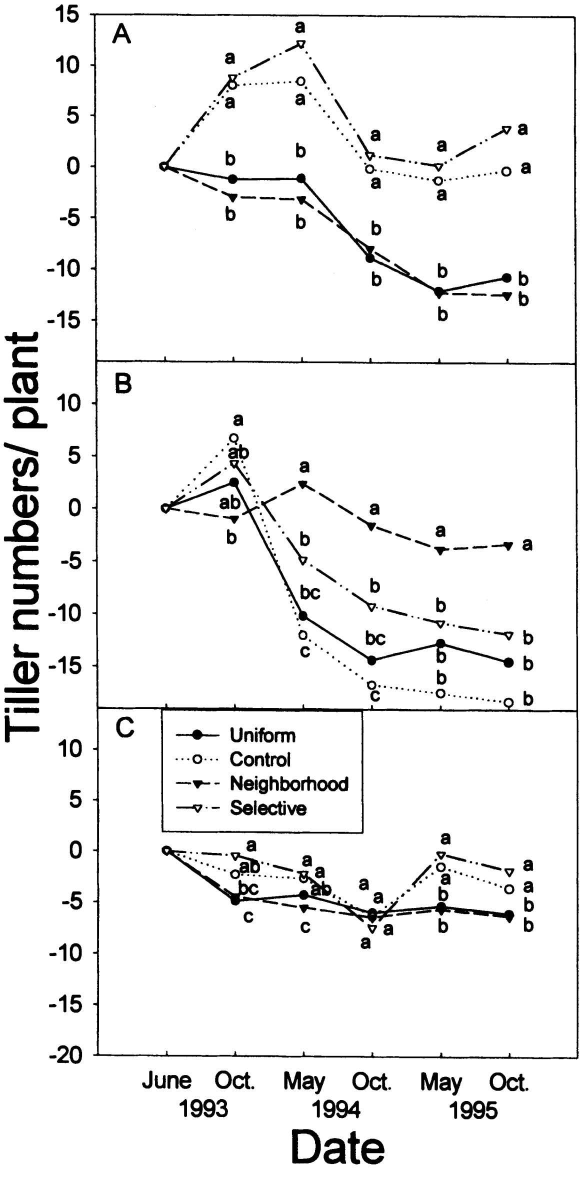

Fig. 3. Mean absolute change in tiller number per neighbor plant in response to three defoliation patterns and control plants in an **A.** ungrazed, **B.** moderately grazed, and **C.** intensively grazed regime. Defoliation patterns are described in Fig. 1. Defoliation patterns marked with different letters indicate significant differences ($P \leq 0.10$) among defoliation patterns at each time period (A,B and C). $N = 15$ plants per defoliation pattern per grazing regime.

regime, the neighborhood pattern significantly increased neighbor plant tiller number compared to the other three defoliation patterns after October 1993 (Fig. 3B).

Basal area per neighbor plant displayed a significant time × defoliation pattern interaction in the ungrazed regime because basal area was significantly lower when the neighbor plants were defoliated than when they were undefoliated in October 1994 and May and October 1995 (Fig. 4A). Mean basal area per neighbor plant was not significantly affected by defoliation pattern or time in the moderately grazed regime because of high variability among sample means (Fig. 4B). The coefficient of variation for neighbor basal area was five times greater in the moderately grazed regime than in the

Table 2. Initial number of target plants of *Bouteloua curtipendula* in June 1993, cumulative plant mortality, percent of live plants that recruited tillers, and tiller/tiller recruitment rate (± SE) of plants that recruited tillers in October of 1993, 1994 and 1995 for three grazing regimes with contrasting grazing intensities. Tiller recruitment rate is expressed as tillers/tiller/plant/month.

Grazing regime	Initial plant No.	Cumulative plant mortality 1993	1994	1995	Plants recruiting tillers 1993	1994	1995	Tiller/Tiller recruitment rate 1993	1994	1995
Ungrazed	60	0	1	1	92 %	52 %	22 %	0.4 ± 0.04	0.4 ± 0.04	0.5 ± 0.06
Moderate	60	0	0	0	83 %	60 %	35 %	0.4 ± 0.06	0.3 ± 0.05	0.4 ± 0.08
Intensive	60	5	19	30	62 %	56 %	30 %	0.4 ± 0.05	0.3 ± 0.05	0.3 ± 0.09

intensively grazed regime which had the next highest coefficient of variation. Basal area per neighbor plant differed significantly between sampling dates in the intensively grazed regime. Basal area per neighbor plant was greatest in October 1994 and lowest in May 1995 compared to the other sampling dates (Fig. 4C).

The number of target plants that initiated juvenile tillers declined by 70, 48, and 32 % in the ungrazed, moderately grazed and intensively grazed regimes, respectively, between October 1993 and October 1995 (Table 2). Plant mortality only occurred in the intensively grazed regime, with the exception of one plant in the ungrazed regime. The percentage of plants that died in the intensively grazed regime in October of 1993, 1994, and 1995 was 8, 32, and 50, respectively.

Tiller variables

Cumulative tiller recruitment and mortality significantly ($P < 0.10$) increased each successive year as anticipated in all three grazing regimes (Fig. 5A-C). In the ungrazed and moderately grazed regimes, cumulative recruitment exceeded mortality until October 1994 which resulted in a net increase in tiller numbers. However, by October 1995, cumulative mortality exceeded cumulative recruitment and tiller numbers decreased in these two grazing regimes. In the intensively grazed regime, cumulative recruitment never exceeded cumulative mortality which resulted in a net decrease in tiller numbers over the 3-yr investigation. Cumulative tiller recruitment in the intensively grazed regime was only 44 % of that in the ungrazed regime.

Tiller per tiller recruitment and mortality rates in 1993 were significantly greater ($P = 0.09$ for mortality in the moderately grazed regime) than in either of the following 2 years in all three grazing regimes (Fig. 6A-C). Tiller per tiller recruitment rates were 85 % lower in October 1995 compared to October 1993 in all three grazing regimes. Mortality was significantly ($P < 0.05$) different between years and decreased more than 45 % from October 1993 to October 1995 in all three grazing regimes. However, the tiller per tiller recruitment rate of plants that recruited tillers remained constant among grazing regimes and years (Table 2).

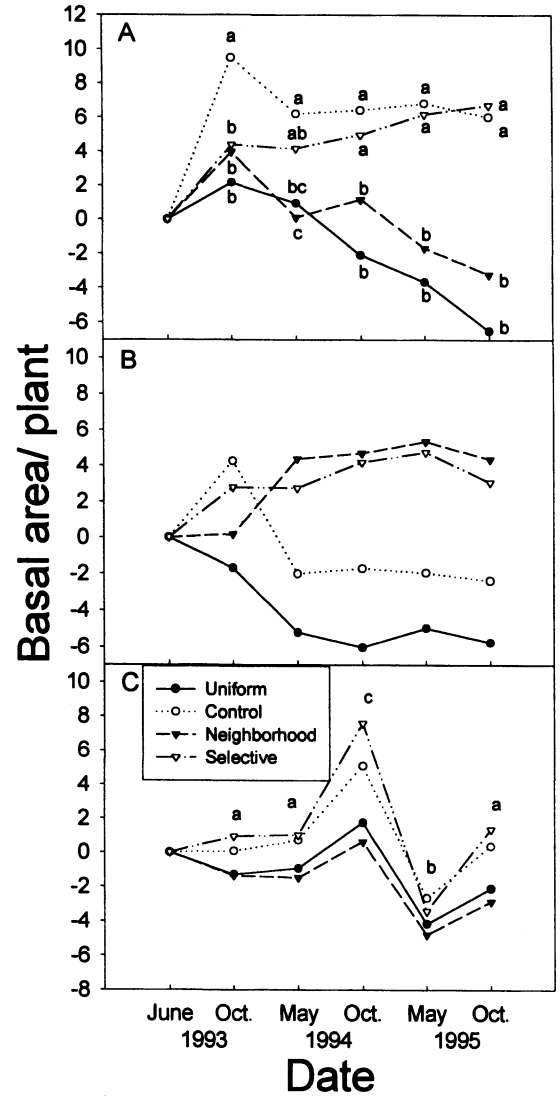

Fig. 4. Mean absolute change in basal area per neighbor plant in response to three defoliation patterns and control plants in an **A.** ungrazed, **B.** moderately grazed, and **C.** intensively grazed regime. Defoliation patterns are described in Fig. 1. Defoliation patterns marked with different letters indicate significant differences ($P \leq 0.10$) and among defoliation patterns at each time period (A) and among time periods across defoliation patterns (C). $N = 15$ plants per defoliation pattern per grazing regime.

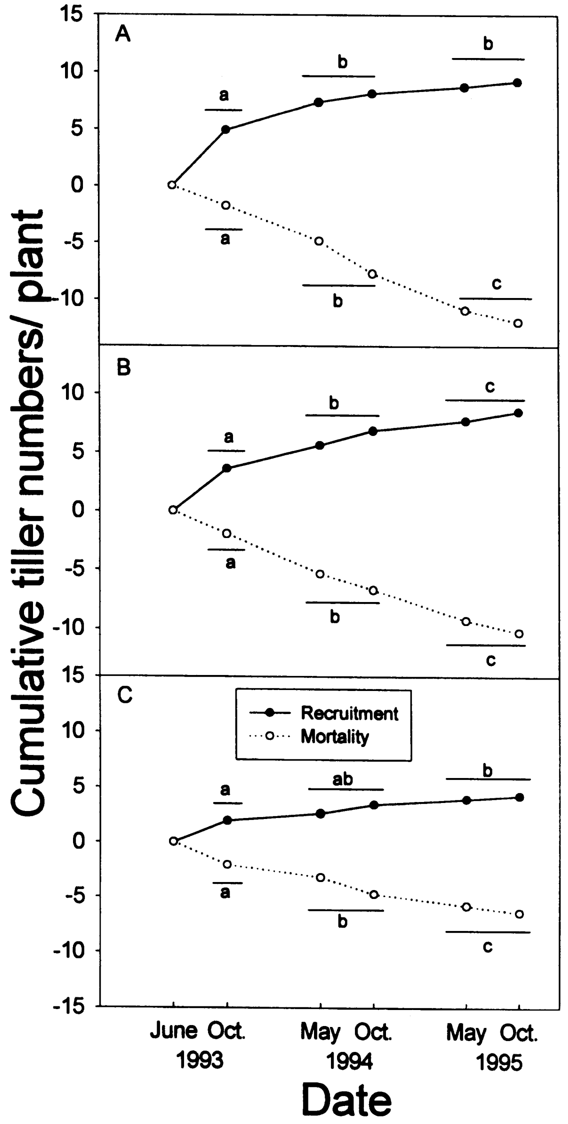

Fig. 5. Mean cumulative tiller recruitment (upper lines) and mortality (lower lines) for *Bouteloua curtipendula* in an **A.** ungrazed; **B.** moderately grazed; **C.** intensively grazed regime. Defoliation patterns were pooled within each grazing regime. Years marked with different letters indicate significant differences ($P \leq 0.10$). $N = 60$ plants per grazing regime and 228, 226 and 195 tillers were initially marked in June 1993 in the ungrazed, moderately grazed, and intensively grazed regimes, respectively.

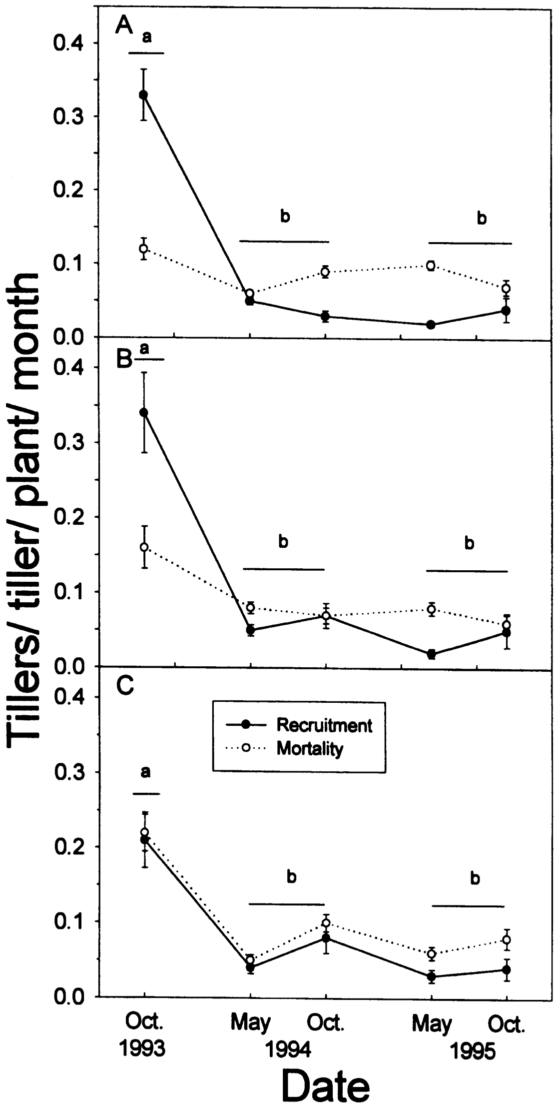

Fig. 6. Mean tiller recruitment rate and tiller mortality rate for *Bouteloua curtipendula* plants in an **A.** ungrazed; **B.** moderately grazed; **C.** intensively grazed regime. Defoliation patterns were pooled within each grazing regime. Years marked with different letters indicate significant differences ($P \leq 0.10$). $N = 60$ plants per grazing regime and 228, 226 and 195 tillers were initially marked in June 1993 in the ungrazed, moderately grazed and intensively grazed regimes, respectively.

Tiller replacement ratios for *B. curtipendula* target plants decreased throughout the investigation for all defoliation patterns in all three grazing regimes (Table 3). In October 1995, tiller replacement ratios, averaged across all defoliation patterns, were 17, 36 and 34 % of the ratios in October 1993 for the ungrazed, moderately grazed and intensively grazed regimes, respectively. Tiller replacement ratios were greatest following defoliation of neighbor plants, except in the intensively grazed regime in October 1995. In the moderately grazed regime, neighborhood defoliation was the only pattern in which the tiller population approached replacement level at the end of the investigation. Median tiller age, including all tiller cohorts, for the ungrazed, moderately grazed and intensively grazed regimes was 9.5 months in May 1995 and 8.5 months in October 1995.

Table 3. Tiller replacement ratios for target plants of *Bouteloua curtipendula* in response to three defoliation patterns and a control in three grazing regimes with contrasting grazing intensities. Defoliation patterns were (1) defoliation of only the target plant (Selective); (2) defoliation of both target and neighbor plant (Uniform); (3) defoliation of only the neighbor plants (Neighbor); and (4) undefoliated target and neighbor plants (Control). Ca. 228, 226 and 195 tillers were initially marked in June 1993 in the ungrazed, moderately grazed and intensively grazed regimes, respectively.

Grazing regime	Defoliation pattern	Tiller replacement ratios Oct. 1993	Oct. 1994	Oct. 1995
Ungrazed	Selective	1.64	1.04	0.26
	Uniform	1.42	0.77	0.27
	Neighbor	2.19	1.27	0.34
	Control	**2.00**	**1.43**	**0.32**
	Mean	1.81	1.13	0.30
Moderately	Selective	1.45	1.17	0.60
	Uniform	1.48	0.81	0.29
	Neighbor	1.64	1.33	0.92
	Control	**1.18**	**0.89**	**0.29**
	Mean	1.44	1.05	0.52
Intensively	Selective	0.85	0.58	0.44
	Uniform	0.93	0.61	0.41
	Neighbor	1.04	0.67	0.29
	Control	**1.02**	**0.56**	**0.20**
	Mean	0.96	0.60	0.33

Cohort survivorship, averaged across defoliation patterns, showed significant differences ($P < 0.001$) within regimes because of reduced survivorship of the May-1994 cohort compared to the October-1993 and October-1994 cohorts (data not shown). Median tiller ages of the various cohorts were similar in all three grazing regimes. Tiller cohorts had median ages of 9.5, 8.5, and 9.5 months in October 1993, May 1994 and October 1994, respectively.

Discussion

Selective defoliation had a minimal affect on competitive interactions and population persistence of this late-seral perennial grass in a semiarid environment. Consequently, all three of the original hypotheses were rejected. Selective defoliation of *Bouteloua curtipendula* did not adversely affect tiller recruitment and mortality to a greater extent than uniform plant defoliation (hypothesis 1), selective defoliation of *B. curtipendula* did not adversely affect tiller recruitment and mortality to a greater extent than tiller number and basal area per plant (hypothesis 2), and selective defoliation of *B. curtipendula* did not have a less adverse affect on plant and tiller variables in the more intensively grazed regimes because a greater proportion of the neighbors were mid-seral, rather than late-seral (hypothesis 3). Long-term grazing history had a greater affect on competitive interactions and population persistence of *B. curtipendula* than did short-term defoliation patterns because of the influence of long-term grazing on population structure of both target and neighbor plants in the intensively grazed regime.

Even though we were unable to statistically test differences among grazing regimes, the different responses of plant variables, cumulative tiller recruitment, and plant mortality of *B. curtipendula* to comparable defoliation patterns within the various grazing regimes indicate that long-term modifications in population structure and neighborhood species composition affected the ability of *B. curtipendula* to respond to defoliation. For example, a significant time effect or time by defoliation interaction occurred for basal area and/or tiller number of *B. curtipendula* plants when neighbor plants were defoliated in the ungrazed and moderately grazed regimes, but plants in the intensively grazed regime were unresponsive to both defoliation pattern and time.

The limited ability of selective defoliation to modify competitive interactions and population persistence of this late-seral, perennial grass is contrary to results of comparable investigations in mesic grasslands (O'Connor 1991; Brown & Stuth 1993; Anderson & Briske 1995). However, these results do support the interpretation of a reduction in the intensity and duration of competitive interactions in semiarid grasslands and savannas (Fowler 1995; McPherson 1997; but see Moretto & Distel 1997). Contrasting responses of selective defoliation in mesic and semiarid communities support the notion that the mechanisms contributing to herbivore-induced species replacement may vary along a precipitation gradient (e.g. Milchunas et al. 1988). The influence of selective grazing on the intensity and duration of competitive interactions may be minimized by low and unpredictable resource availability (Grime 1979; Wilson & Keddy 1986). Therefore, selective grazing may not modify competitive interactions to a sufficient extent to have a major influence on species replacement in semiarid systems in most years. This interpretation of greater abiotic involvement in species replacement in semiarid communities is consistent with the occurrence of stronger correlations between precipitation (3-yr mean) and total basal area of perennial grasses than between grazing intensity and total basal area in this plant community (Fuhlendorf et al. in rev.).

The inference that selective grazing has a limited influence on species replacement is not entirely consistent with the interpretation of herbivory-induced vegetation change derived from long-term (45 yr) data for this herbaceous community (Fuhlendorf & Smeins 1997;

Fuhlendorf et al. in rev.). Long-term data indicate that grazing intensity is the primary process determining the relative proportion of mid-grass and short-grass species within this community. We were unable to identify the specific processes contributing to this inconsistency, but several plausible mechanisms exist to reconcile these seemingly contrasting roles of competititon on vegetation change. First, the brief temporal scale associated with this investigation may have minimized the influence of selective grazing on interspecific competition by limiting the occurrence of seasons or years in which the intensity and duration of competition was sufficient to induce a detectable response. Even though grazing intensity determined the general pattern of vegetation change in the long-term data, compositional shifts were expressed as periodic events rather than as gradual continuous change (Fuhlendorf et al. in rev.). Second, the defoliation intensity imposed in our investigation may not have been sufficiently severe to be representative of grazing regimes historically implemented in this region and grazing may have induced vegetation change only after it had been imposed for a series of years (Fuhlendorf & Smeins 1997). Third, long-term grazing may have contributed to species replacement by affecting processes other than vegetative growth and interspecific competition. For example, long-term grazing may have suppressed sexual reproduction of various species to affect their population demography and composition within the community (e.g. O'Connor 1991). Inconsistent interpretations between short- and long-term investigations within the same community illustrate the importance of long-term data as a reference for accurate interpretation of mechanisms contributing to vegetation change in semiarid environments.

A herbivore-induced shift in population structure to a greater density of small, uniformily arranged plants may have altered the intensity and mode of interspecific competition in the intensively grazed regime (e.g. Briske & Anderson 1990; Colegrave 1997). A higher density of smaller plants for both *B. curtipendula* and its immediate neighbors may have more uniformly distributed the detrimental effects of competition among species (i.e. symmetric competition) as opposed to the disproportionate suppression of smaller plants by larger plants (i.e. asymmetric competition) (Weiner 1993; Connally & Wayne 1996). Competition for light is generally assumed to be asymmetric because light is a unidirectional resource that can be effectively preempted by larger plants (Connally & Wayne 1996; Schwinning 1996). Intensive grazing may have reduced the height advantage of the mid-grasses for light interception and intensified competition for belowground resources. Belowground competition is assumed to be symmetric because soil resources are less effectively preempted by competing plants (Connally & Wayne 1996; Schwinning 1996). An important ecological consequence of a herbivore-induced shift toward symmetric competition would be to minimize the effect of herbivory on interspecific competitive interactions.

Size of neighbor plants had a greater influence on the response of *B. curtipendula* target plants to neighbor defoliation than did composition of neighbors. The contrasting size of mid-seral neighbors may explain why tiller number per *B. curtipendula* target plant increased when the larger mid-seral neighbors in the moderately grazed regime were defoliated, but not when smaller mid-seral neighbors in the intensively grazed regime were defoliated. Larger target plants and mid-seral neighbors in the moderately grazed regime compared to the intensively grazed regime may have increased the intensity of competition between target and neighbor plants (e.g. Caldwell et al. 1996). Greater tiller number per *B. curtipendula* target plant following defoliation of mid-seral neighbors in the moderately grazed regime, but not following defoliation of late-seral neighbors in the ungrazed regime does not support the hypothesis of greater competitive ability of late- compared to mid-seral species. This demonstrates that long-term herbivore-induced modifications to the spatial arrangement and size class distribution of plants can alter competitive interactions to an equal or greater extent than compositional changes.

Greater plant mortality in the intensively grazed regime supports the community level interpretation that herbaceous plant density is more strongly correlated with grazing intensity than it is with precipitation in this community (Fuhlendorf et al. in rev.). However, plant mortality is very likely mediated by a herbivory × drought interaction because drought has been recognized to disproportionately increase mortality of perennial grasses that have small basal areas (O'Connor 1994; Hodgkinson 1995). The intensively grazed regime had the greatest density of small plants and was the only grazing regime that had substantial plant mortality.

Tiller populations of *B. curtipendula* displayed two distinct demographic responses during the investigation. First, cumulative tiller recruitment was substantially lower in the intensively grazed regime because of greater plant mortality and a smaller proportion of surviving plants that recruited juvenile tillers compared to the ungrazed and moderately grazed regimes. The relatively smaller number of plants recruiting tillers maintained tiller populations below replacement level in the intensively grazed regime throughout the investigation. Second, tiller per tiller recruitment decreased in all three grazing regimes during the second and third years. A drought during the second year of the investigation reduced both tiller per tiller recruitment and survivorship of the May-1994 tiller cohort. The year following the drought was characterized by a more normal precipitation pattern, but both cumulative and tiller per tiller recruitment remained low. Limited tiller recruitment the year following the drought resulted from a reduction in the total number of plants that recruited tillers in the ungrazed and moderately grazed regimes because plant mortality was minimal. However, tiller per tiller recruitment rates among plants that recruited at least one tiller remained relatively constant among grazing regimes and years suggesting that tiller recruitment was at least partially regulated by plant as well as tiller level processes. This response is inconsistent with previous interpretations suggesting that tiller recruitment is regulated at the individual tiller level, rather than at the tiller level (Briske & Butler 1989; de Kroon & Kwant 1991; but see Laterra et al. 1997).

Delayed tiller recruitment the year following a drought period indicates the occurrence of a carry-over effect at the tiller and/or plant level (Bullock et al. 1995). A reduction in tiller recruitment may have resulted from an increase in median age of existing tillers associated with limited tiller recruitment during the previous drought period (e.g. Bastrenta et al. 1995; Bullock et al. 1996). A relatively constant median tiller age of ca. 9 months in all three grazing regimes suggests that tiller populations may have been responding to a larger-scale disturbance (i.e. drought) than the specific grazing intensities within individual grazing regimes. Greater median tiller age may have limited tiller recruitment by reducing the availability of recently developed axillary buds that comprise the primary source of tiller initiation in this species (Hendrickson & Briske 1997). Proximal axillary buds remain attached to the base of parental tillers for 18 - 24 months, but only a small proportion (ca. 6 %) of these older buds grow out to form tillers. This interpretation of an age-induced reduction of tiller recruitment is consistent with the conclusion of Bullock et al. (1996) that grazing affects tiller demography of perennial grasses by altering the relationship between vital demographic rates and tiller age.

These data collectively indicate that long-term, intensive grazing has modified the population structure of this late-seral perennial grass to the extent that population responses to both herbivory and periodic drought have been altered in comparison to those in ungrazed or moderately grazed regimes. Plant and tiller demography were less responsive to herbivory, but plants encountered a greater probability of mortality during drought in populations characterized by a high density of small plants. Long-term species composition and population structure data from this community indicate that this modified population structure can be maintained for long periods and that these populations retain sufficient viability to reestablish dominance within several decades when grazing is eliminated or substantially reduced (Smeins et al. 1976; Fuhlendorf & Smeins 1997). Important ecological consequences of a herbivore-induced transition in population structure may be to minimize the effect of selective herbivory on interspecific competitive interactions and to function as an avoidance mechanism to reduce the probability of localized population extinction in response to intensive long-term herbivory.

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