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Tiller dispersion in populations of the bunchgrass Schizachyrium scoparium: implications for herbivory tolerance

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We tested the hypothesis that a population structurally modified by herbivory, into a configuration consisting of a high density of small plants, possesses greater herbivory tolerance than a population composed of a low density of large plants. Three levels of tiller dispersion were established by transplanting *Schizachyrium scoparium* plants with basal areas of 30, 60 and 120 cm^2 at densities of 2, 4 or 8 plants per 0.25 m^2 plot, respectively, while maintaining constant tiller densities of approximately 250 per plot. Tiller dispersion did not significantly affect aboveground production in either defoliated or nondefoliated populations. However, populations constructed with maximum tiller dispersion (8 plants with 30 cm^2 basal areas) displayed greater relative increases in tiller density and basal area. These responses were apparently mediated through a mechanism regulating tiller recruitment, as opposed to the efficiency of resource acquisition, because annual aboveground production was comparable across the range of tiller dispersion evaluated. Neither morphometric variables nor water relations of tillers were significantly affected by the pattern of tiller dispersion. However, defoliated tillers had more favorable water potentials and stomatal conductances than nondefoliated tillers irrespective of dispersion treatment. The initial hypothesis was rejected indicating that the spatial arrangement of tillers in populations of *S. scoparium* was inconsequential in mediating plant responses to herbivory.

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Introduction

The ability of plants to cope with herbivory is dependent upon two broad categories of resistance mechanisms. Avoidance mechanisms reduce the probability of defoliation (e.g., biomass accessibility and mechanical deterrents) while tolerance mechanisms facilitate growth after defoliation (e.g., meristem availability and resource allocation patterns; Briske 1986). The ability of plants to survive grazing undoubtedly results from a combination of these two broad resistance mechanisms, but one mechanism may predominate over another in certain species and under specific environmental conditions. The relative expression of resistance mechanisms among species subjected to various frequencies and intensities of herbivory is eventually manifested at the population and community levels of vegetation organization (e.g., Archer and Tieszen 1986, Brown and Allen 1989).

Although herbivory resistance is most frequently viewed as an organismal attribute, species populations may also display structural attributes which influence their ability to cope with herbivory. For example, the density, size class distribution and spatial arrangement of plants and tillers in populations may potentially influence herbivory avoidance by influencing plant appearance and biomass accessibility (McNaughton 1978, Norton and Johnson 1983). Similarly, population structure may potentially affect herbivory tolerance by influencing tiller recruitment (Butler and Briske 1988, Olsen

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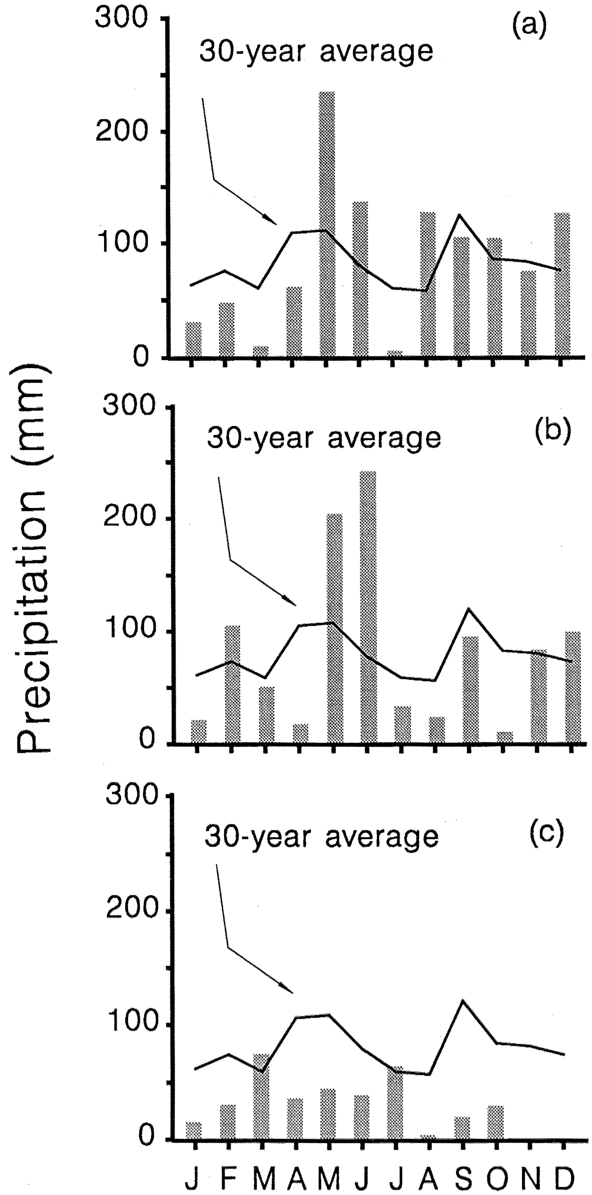

Fig. 1. Mean monthly precipitation for (a) 1986, (b) 1987, and (c) 1988 and the long-term average annual precipitation at the study site where experimental populations of *Schizachyrium scoparium* were established.

and Richards 1988a), resource acquisition (Nobel 1981, Soriano et al. 1987), and inter- and intra-specific competitive interactions within the community (Fowler 1986, Briske and Butler 1989).

Herbivory reduced individual plant basal area and concomitantly increased plant density in populations of the perennial bunchgrass *Schizachyrium scoparium* (Butler and Briske 1988). Intensive herbivory apparently increased plant density and tiller number per unit of plant basal area by fragmenting individual large plants and eliminating areas of low tiller density in the plant interior. These herbivore-mediated modifications in population structure collectively influence the number and spatial distribution of tillers in the population. Similar responses have been observed in other bunchgrass species, including *Festuca idahoensis* (Pond 1960), *Agropyron desertorum* (Hickey 1961) and several grasses in the pampas of Argentina (Sala et al. 1986). However, the ecological consequences of herbivore-mediated modifications in population structure remain unexplored.

This investigation was designed to test the hypothesis that a population modified structurally by herbivory, into a configuration consisting of a high density of small plants, would possess greater herbivory tolerance than a population composed of a low density of large plants at comparable tiller densities. Both plant and tiller variables were evaluated to accurately access population responses to herbivory (e.g., Butler and Briske 1988, Brown and Allen 1989).

Materials and methods

Transplant garden and abiotic variables

Individual, intact plants of *Schizachyrium scoparium* var. *frequens* F. T. Hubb. were collected from a remnant southern true prairie community near Caldwell, Texas in February 1986, and established in a transplant garden located at the Texas A&M University Native Plant and Animal Conservancy. The Conservancy is located 2 km W of the Texas A&M main campus, College Station, Texas and is classified as part of the Post Oak Savanna natural resource region (Gould 1975). The collection site was located 45 km W of Texas A&M University, and had been intensively grazed by cattle for approximately 20 yr. Plants that did not survive the initial transplanting during February were replaced in March. Sprinkler irrigation was used to augment natural precipitation during February and March to increase transplanting success.

Long-term (30 yr; 1951–1988) and actual precipitation received during the investigation were recorded at a weather station 2 km S of the transplant garden. Long-term average annual precipitation is 993 mm and is bimodally distributed with maxima in the spring and autumn (NOAA 1986–1988). Total annual precipitation during 1986 and 1987 approximated the 30-yr average, but distribution was proportionately greater during May through July (Fig. 1). Total annual (351.0 mm) and May through August precipitation (151.8 mm) in 1988 were 58 and 50% less than the 30-yr average, respectively. The entire garden was irrigated during May and June 1988 with a total of 50 mm of water to insure plant survival and maintain live biomass throughout the season. The 30-yr mean daily temperature was 20.0°C with the minimum occurring in January (9.4°C) and maxi-

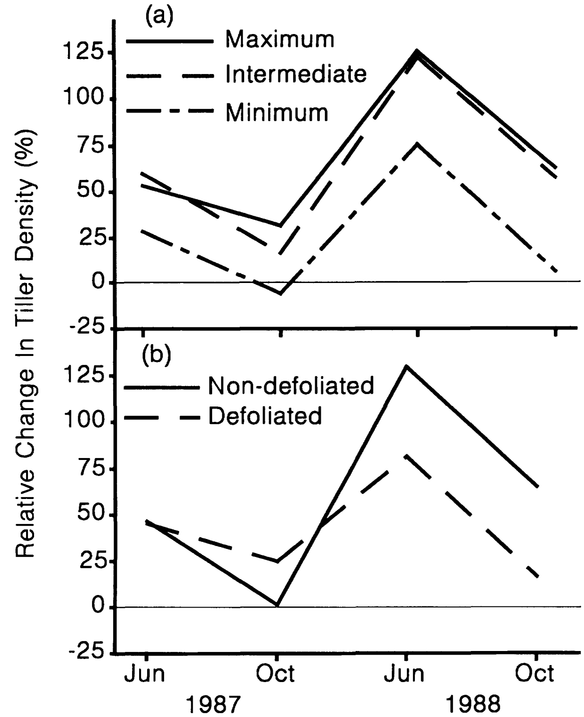

Fig. 2. Relative change in tiller densities of *Schizachyrium scoparium* on a per plot basis during 1987 and 1988 as influenced by (a) tiller dispersion ($P < 0.001$) and (b) defoliation ($P = 0.016$). Percentages are based on absolute values of 233, 298 and 255 tillers per plot for maximum, intermediate and minimum dispersion treatments and 242 and 249 tillers per defoliated and nondefoliated plot, respectively, in September 1986.

mum in July (29.4°C). Temperatures during the investigation did not deviate appreciably from the 30-yr mean.

Soils in the garden were a Lufkin fine sandy loam with an A horizon not exceeding 23 cm in depth (USDA 1958). The B horizon is characterized as a dense clay with limited permeability to water. The transplant garden was tilled to a depth of approximately 15 cm in preparation for transplanting. Interspaces between plots were tilled periodically for weed control.

Treatments and experimental design

Tiller dispersion treatments were designed to represent decreasing plant basal areas and increasing plant densities associated with intensive herbivory in this species (see Butler and Briske 1988). Three patterns of tiller dispersion were established by transplanting two plants with basal areas of 120 cm^2 (minimum dispersion), four plants with basal areas of 60 cm^2 (intermediate dispersion) or eight plants with basal areas of 30 cm^2 (maximum dispersion) into 0.25 m^2 plots at a constant tiller density of approximately 250 tillers. The number of live tillers per plant was proportional to the basal area estimates in cm^2 (i.e., approximately one tiller per cm^2). Each of the 0.25 m^2 plots were confined on all sides by a metal barrier to a depth of 35 cm to standardize the soil volume accessible to each dispersion treatment. Lateral root development below the metal barriers was assumed to be minimal because of the dense clay pan at this depth.

Approximately 70% (by weight) of the above-ground biomass was removed with hand clippers from all plants within one-half of the plots in mid-April, early June, mid-August and early October to simulate herbivory. Height-weight relationships were constructed from 15 tillers per treatment at three stages of phenological development (vegetative, culmed and flowering) by regressing cumulative height against cumulative percent weight on an incremental basis. These relationships were used to implement a uniform intensity of defoliation. The remaining plots containing non-defoliated plants served as controls.

Data collection

Baseline data were collected in September 1986, eight months after transplanting. Plant responses were monitored by estimating tiller number and basal area on each plant within a plot in June (peak production period) and October (end of growing season) of both years. Tiller number per plant was determined by counting all tillers that had attained the two leaf stage. Plant basal area was calculated from the circumference of the plant base. Tiller number and basal area were analyzed on the basis of percent change from their respective September 1986 values to account for variation among plants at the initiation of the experiment. Absolute values for tiller density and basal area per plot did not differ significantly among dispersion treatments on this date ($P > 0.10$). Production from defoliated plants was estimated by determining the amount of biomass removed from each plant at each of four harvests throughout the year. Production from nondefoliated plants was estimated from a single harvest in October.

Variables were also measured on 12 tillers within each of the three treatments (two/plant in minimum dispersion, one/plant in intermediate dispersion and in alternating plants in maximum dispersion treatments) in mid-April, early June, mid-August and early October of both years. Leaf number, total leaf blade area and total dry weight were recorded for each tiller. Xylem pressure potential and leaf conductance to H_2O vapor were measured with a pressure chamber and steady-state diffusion porometer (Li-Cor 1600), respectively, on young, fully expanded leaf blades. Water relations data were collected from all treatments, within a 1-h interval, at mid-day.

The experiment was established as a 3 (dispersion treatments) × 2 (defoliation treatments) complete, ran-

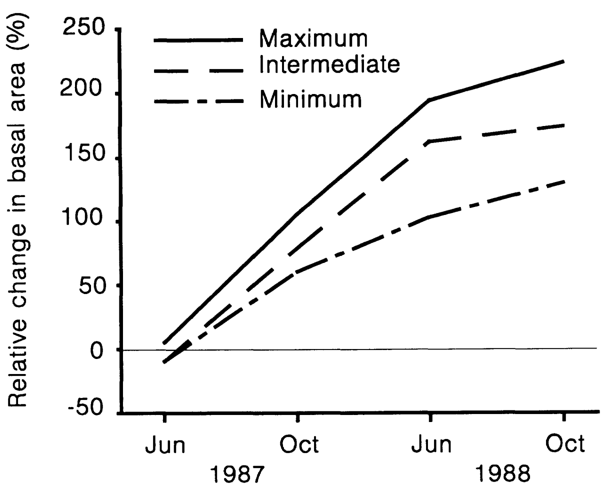

Fig. 3. Relative change in basal areas of *Schizachyrium scoparium* on a per plot basis during 1987 and 1988 as influenced by tiller dispersion (P < 0.001). Percentages are based on absolute values of 233, 289 and 257 cm^2 per plot for maximum, intermediate and minimum dispersion treatments, respectively, in September 1986.

dom factorial design with three replications (all plants within an individual plot). Water relations data were collected on an individual replication per day to limit the duration of the sampling period and thereby minimize diurnal variation in abiotic variables. These data were blocked by collection date to account for variation in daily environmental conditions. Analysis of variance procedures were used to test for factor level and treatment differences.

Results

Plant responses

The intermediate and maximum dispersion treatments exhibited greater increases in relative tiller densities per plot than the minimum dispersion treatment at all sampling dates ($P < 0.001$, Fig. 2a). Relative increases in tiller density per plot were 61, 56 and 6%, respectively, for maximum, intermediate and minimum dispersion at the end of the investigation (October 1988). Relative tiller densities in the intermediate and maximum dispersion treatments increased 125% in June 1988, but by the conclusion of the study, densities had decreased to values only 60% greater than those observed in September 1986. Relative tiller density in the minimum dispersion treatment increased 70% in June 1988, but then decreased to density values comparable to those at the start of the study. Tiller density decreased below the September 1986 value in only the minimum dispersion treatment in October 1987.

Defoliated plants initially responded with higher relative tiller densities (October 1987) than did the non-defoliated plants (Fig. 2b, $P = 0.016$). This trend was reversed in 1988 when relative tiller densities within the non-defoliated plants exceeded those of the defoliated plants by 50% on the last two sampling dates. Seasonal fluctuations in tiller density were observed within all treatments with the maximum occurring in the spring (June) and the minimum in the autumn (October). No significant defoliation by tiller dispersion interactions were observed ($P > 0.10$).

Dispersion treatments significantly influenced relative increases in basal area per plot (Fig. 3, $P < 0.001$). Mean relative basal area in the maximum, intermediate and minimum dispersion treatments increased 220, 170 and 130%, respectively, over the course of the investigation. A reduction in the relative rate of increase over time suggests that basal area expansion was beginning to diminish in response to resource limitations. Defoliation did not significantly affect the rate of basal area expansion or create a significant defoliation × basal area interaction ($P > 0.10$).

Tiller dispersion did not significantly affect annual aboveground production per plot ($P > 0.10$), although

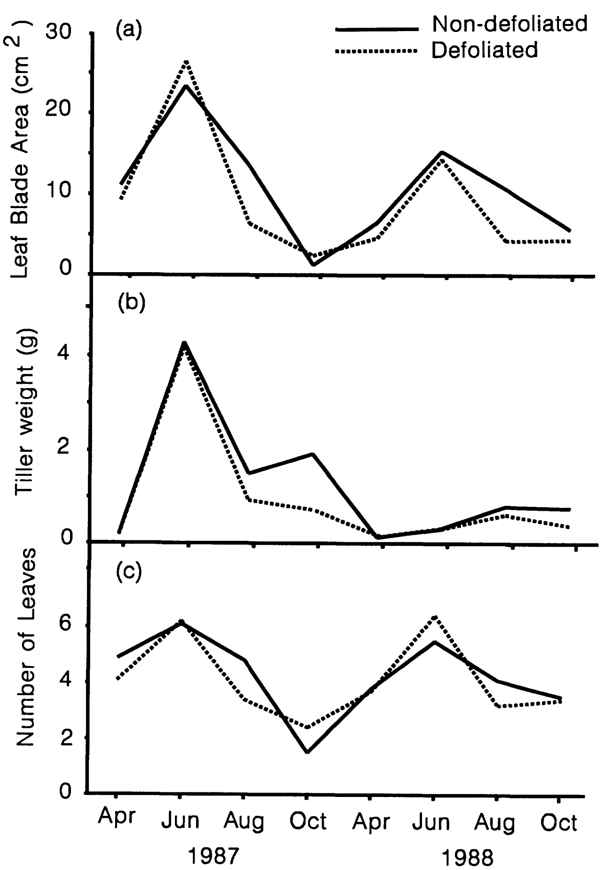

Fig. 4. (a) Leaf blade area per tiller ($P < 0.001$), (b) tiller weight ($P < 0.001$) and (c) leaf number per tiller ($P < 0.001$) of defoliated and nondefoliated *Schizachyrium scoparium* plants in 1987 and 1988.

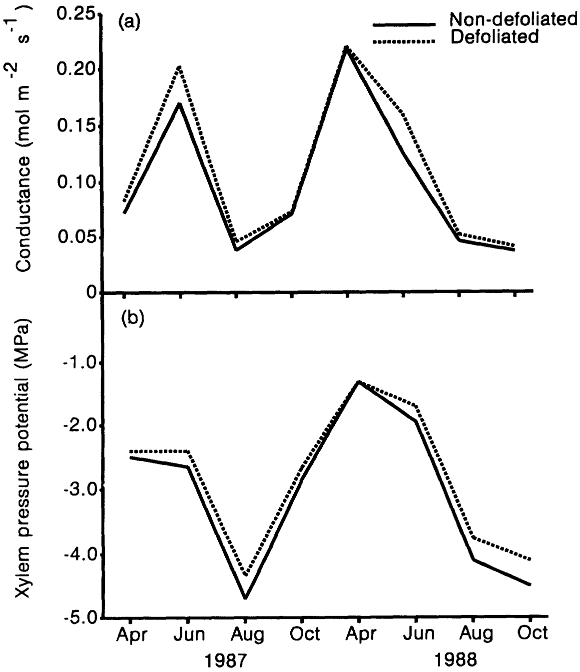

Fig. 5. (a) Leaf conductance (P = 0.038) and (b) xylem pressure potential (P = 0.002) of the youngest fully expanded leaf blade of defoliated and nondefoliated *Schizachyrium scoparium* plants in 1987 and 1988.

maximum and intermediate dispersion treatments tended to produce more biomass than did the minimum dispersion treatment (321, 436 and 297 g per plot for nondefoliated plants and 376, 391 and 298 g per plot for defoliated plants, respectively). Defoliation did not significantly affect total annual production (352 and 355 g per plot, P > 0.10).

Tiller responses

Morphometric variables of individual tillers including leaf number, blade area and tiller weight, were not significantly affected by tiller dispersion treatments (P > 0.01). However, a significant season × defoliation interaction was observed for each of the variables. Defoliated tillers exhibited lower leaf blade areas and tiller weights than the nondefoliated tillers in August (Fig. 4a, P < 0.001 and b, P < 0.001). Defoliated tillers possessed fewer leaves than nondefoliated tillers in August of both years (Fig. 4c, P < 0.001), but the ranking was reversed in October 1987 and June 1988.

Tiller dispersion treatments did not significantly affect leaf stomatal conductance or xylem pressure potential (P > 0.10). However, both stomatal conductance and xylem pressure potential were most favorable in defoliated plants (Fig. 5a, P = 0.038 and b, P = 0.002). Tiller water status was most favorable in April and June with water deficits increasing as the summer progressed.

Discussion

Tiller dispersion did not significantly affect aboveground production in either defoliated or nondefoliated populations. Consequently, the hypothesis that a population characterized by a high density of small plants confers greater herbivory tolerance than a population composed of a low density of large plants was rejected. The spatial arrangement of tillers in populations of the bunchgrass *S. scoparium* was inconsequential in mediating plant responses to herbivory within the range of plant sizes and tiller densities utilized in this investigation. A more severe defoliation regime may have magnified differences among dispersion treatments. Plant production and tiller weights were not significantly affected by the defoliation regime imposed.

Bunchgrass populations with greater tiller dispersion expressed proportionately greater increases in tiller recruitment and basal area (Figs 2a, b and 3). Greater increases in tiller density and basal area were presumably mediated through a mechanism regulating tiller recruitment, as opposed to the efficiency of resource acquisition, because comparable levels of aboveground production occurred over the range of tiller dispersion treatments evaluated. Proportionately greater tiller recruitment has been documented on the periphery, as opposed to the interior, of two perennial bunchgrasses, *S. scoparium* (Butler and Briske 1988) and *Agropyron desertorum* (Olson and Richards 1988a). The mechanism associated with this response is unknown, but radiation quality has been implicated (Deregibus et al. 1985, Simon and Lemaire 1987). Consequently, greater plant periphery in populations with intermediate and maximum tiller dispersion may have increased the opportunity for tiller recruitment. Rapid tiller recruitment on the plant periphery also accounts for proportionally greater increases in basal area.

Relative tiller density responded differently to defoliation between years of the investigation. Defoliated plants recruited a greater number of tillers than nondefoliated plants in 1987 regardless of the degree of tiller dispersion. However, in 1988 nondefoliated plants showed relative increases in tiller density 50% greater than those of defoliated plants (Fig. 2b). This response cannot be entirely attributed to the limited precipitation received during 1988 (50% of the long-term norm; Fig. 1), because both defoliated and nondefoliated plants made the greatest relative increases in tiller density between October 1987 and June 1988 (Fig. 2b). Defoliated plants, which expressed lower relative increases in tiller density, had more favorable xylem pressure potentials and stomatal conductance values than nondefoliated plants during portions of 1988 (Fig. 5a and b). In addition, leaf number and weight of defoliated tillers were comparable to those of nondefoliated tillers on most sampling dates in 1988 (Fig. 4a–c). However, leaf blade area was reduced substantially by defoliation in 1988.

Reduced tiller recruitment in defoliated populations during the second year of the study supports the conclusion of Ellison (1960) that grazing generally inhibits tillering in grasses over the long-term. Although defoliation may stimulate tillering by alleviating apical dominance in the short-term, the repeated removal of photosynthetic area eventually minimizes the availability of resources for tiller growth. This interpretation is supported by the observation that neither *S. scoparium* nor *Agropyron desertorum,* a grazing-tolerant perennial bunchgrass, displayed increased tiller recruitment after 2 yr of livestock grazing (Butler and Briske 1988, Olson and Richards 1988b). However, short-term increases in tiller recruitment have been observed in both *S. scoparium* (Jameson and Huss 1959, Vogel and Bjugstad 1968) and *A. desertorum* (Olsen and Richards 1988c) when defoliation coincided with reproductive culm elongation.

Tiller dispersion did not influence variables associated with individual tillers to as great an extent as variables at the plant level. Neither morphometric variables nor water relations were significantly affected (Fig. 4a–c). However, defoliated tillers possessed a more favorable water status than did nondefoliated tillers (Fig. 5a and b). Defoliation apparently decreased leaf area sufficiently to reduce total transpiration (Fig. 5a), thereby enhancing xylem pressure potentials and stomatal conductance of the remaining leaf area (McNaughton 1983, but see Nowak and Caldwell 1984, Wraith et al. 1987). Alternatively, defoliation may have limited the rate at which plants were able to access water within the deeper portions of the soil profile by restricting root development (Richards 1984). However, a defoliation-induced postponement of soil water absorption may be of limited ecological value because the efficiency of water use may decrease as vapor pressure deficits increase with a progression of the growing season and defoliation may increase water availability for neighboring species defoliated less severely (Caldwell et al. 1983, Wraith et al. 1987).

Although the spatial distribution of tillers did not influence aboveground production after defoliation (i.e., herbivory tolerance), it represents only one aspect of herbivore-mediated modifications in population structure. Herbivory also modifies plant size class distribution and alters absolute tiller density in the various species populations which comprise the community (e.g., Sala et al. 1986, Butler and Briske 1988). Consequently, small plants will be placed at a competitive disadvantage with neighboring large plants (e.g., Liddle et al. 1982, Fowler 1986). Similarly, populations possessing greatest tiller densities may potentially acquire the greatest proportion of available resources within the community (e.g. Caldwell et al. 1987, Soriano et al. 1987). The population attributes of plant size class distribution and absolute tiller density appear to be of greater significance to herbivory tolerance than tiller dispersion in perennial bunchgrass populations.

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