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Competitive ability of the bunchgrass *Schizachyrium scoparium* as affected by grazing history and defoliation

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Abstract

Herbivory by large animals is known to function as a selection pressure to increase herbivory resistance within plant populations by decreasing the frequency of genotypes possessing large, erect canopies. However, the increase in herbivory resistance of the remaining genotypes in the population may potentially involve a tradeoff with competitive ability. The perennial bunchgrass *Schizachyrium scoparium* was grown in a transplant garden to test the hypothesis that late successional plant populations with a history of grazing are at a competitive disadvantage relative to conspecific populations with no history of grazing in the presence of competition from mid-successional species. Plants with a history of grazing were found to possess a greater competitive ability than plants with no grazing history in the absence of herbivory. This unexpected response resulted from the capacity of plants with a history of grazing to recruit a greater number of smaller tillers than did plants with no grazing history. This response was only significant when plants with a history of grazing were nondefoliated and grown with the weakest of the mid-successional competitors, indicating that both defoliation and intense interspecific competition can mask the architectural expression of herbivore-induced selection. Individual tillers did not display any architectural differences between plants with contrasting grazing histories other than mean tiller weight. These data confirm that herbivory by domestic cattle may function as a selection pressure to induce architectural variation in grass populations within an ecological time frame (ca ≤25 yrs).

Nomenclature: Gould, F. W. 1975. The Grasses of Texas. Texas A&M Univ. Press, College Station, TX.

Introduction

Plants cope with herbivory by relying on various combinations of avoidance and tolerance mechanisms which collectively comprise their total resistance to herbivory. Avoidance mechanisms reduce the probability and severity of herbivory and are most frequently expressed as morphological or biochemical deterrents (Briske 1991). Tolerance mechanisms facilitate growth following herbivory and are conferred by a broad range of physiological processes (e.g., resource allocation patterns and resource acquisition rates). Herbivory avoidance is frequently assumed to convey an associated 'cost' which reduces plant growth in comparison with plants allocating fewer resources to avoidance mechanisms (Coley *et al.* 1985, Briggs & Schultz 1990, but see Simms & Rausher 1987, 1989). Costs of herbivory avoidance are most evident in cases where production of a secondary compound (i.e., biochemical avoidance mechanism) reduces growth or competitive ability in comparison with conspecifics which do not produce the compound or produce it in lesser quantities (Dirzo & Harper 1982; Coley 1986; Briggs & Schultz 1990). However, the costs associated with the possession of morphological avoidance mechanisms are less frequently considered (e.g., Björkman & Anderson 1990).

Long-term herbivory is known to select against genotypes possessing an erect canopy architecture in several populations of perennial grasses (Peterson 1962; Scott & Whalley 1984; Painter *et al.* 1989). The remaining genotypes in grazed populations frequently possess greater herbivory avoidance in the form of decumbent canopy architectures consisting of a greater number of small tillers with a reduced canopy area. These 'grazing morphs' effectively minimize the detrimental consequences of herbivory by reducing the amount of biomass removed by large herbivores and maintaining greater leaf area and meristematic tissue to facilitate subsequent growth (Alexander & Thompson 1982; Carman & Briske 1985; Jaramillo & Detling 1988). However, grazing morphs are frequently less competitive than the more erect genotypes in species populations in the absence of herbivory (Eagles 1983; Painter *et al.* 1989).

This investigation was conducted to test the hypothesis that populations of a late-successional species with a history of grazing are at a competitive disadvantage relative to conspecific populations with no grazing history in the presence of competition from mid-successional species. Selective herbivory of *Schizachyrium scoparium*, the climax dominant of the southern true prairie, by domestic herbivores increases the relative density of mid-successional species within neighborhoods of the climax dominant (Dyksterhuis 1946; Launchbaugh 1955). Therefore, the competitive ability of the climax dominant, relative to that of associated mid-successional species, is of direct consequence to population maintenance in the presence of herbivory as well as population recovery following the cessation of herbivory.

Study site, materials and methods

Plant material, transplant garden and abiotic variables

Schizachyrium scoparium var. *frequens* both with and without a recent history of grazing (ca ≤25 yrs), were grown in association with two grass species which replace *S. scoparium* in communities subjected to long-term intensive herbivory by domestic cattle (Dyksterhuis 1946; Launchbaugh 1955). The neighborhood species were *Bothriochloa saccharoides* and *Stipa leucotricha*, a C_4 and C_3 mid-grass, respectively (Gould 1975; Waller & Lewis 1979). Neighborhoods comprised of these species represent conditions of intermediate and severe herbivore-induced shifts in species composition, respectively (Dyksterhuis 1946; Launchbaugh 1955).

Entire plants of the climax dominant and two mid-successional species were excavated from a remnant true prairie community 45 km west of Texas A&M University near Caldwell, Texas (Goodnight Ranch). Plants with a history of minimal grazing were collected from a hay meadow which had been mowed once per year and protected from domestic livestock grazing prior to 1900. Plants with a history of grazing were collected from a comparable site located 5 km east of the hay meadow which had been intensively grazed by domestic cattle for approximately 25 yrs. Precipitation and temperature regimes for the sites are similar to those described for the transplant garden (see below).

The transplant garden was located at the Texas A&M University Native Plant and Animal Conservancy 2 km west of the Texas A&M main campus, College Station, Texas. Plants that did not survive the initial transplanting in January and February of 1986 were replaced in March. Natural precipitation was augmented with sprinkler irrigation during February and March to increase transplanting success. Periodic hand weeding within plots and tilling between plots minimized competition from non-experimental species.

Long-term (30 yr, 1951–1988) and actual precipitation received during the investigation were recorded at a weather station 2 km south of the transplant garden. Long-term average annual precipitation is 993 mm and is bimodally distributed with maxima in the spring and fall (NOAA 1986–1988). Total annual precipitation during 1986 and 1987 approximated the 30-year average, but distribution was proportionately greater than the norm during May through July of both years. Total annual (351.0 mm) and May through August precipitation (151.8 mm) in 1988 were 58 and 50% less than the 30-year average, respectively. The entire garden was irrigated during May and June 1988 with a total of 50 mm of water to ensure plant survival and maintain live biomass throughout the season. The 30-yr mean daily temperature is 20 °C with the minimum occurring in January (9.4 °C) and maximum in July (29.4 °C). Temperatures during the investigation did not deviate appreciably from the 30-year mean.

Plot configuration and defoliation treatments

Four individuals of *S. scoparium* were planted in each plot (indicator plants) with nine individuals of one of the two neighbor species. Each indicator plant was positioned in the center of four neighbors (approximately 21 cm from the center of a neighbor to the center of an indicator plant) to ensure the occurrence of intense interspecific competition. The neighbors were not confined on the plot periphery and individual plots were separated by a 2 m tilled border. The initial basal area for both the indicator plants and neighbors ranged between 50 and 70 cm^2.

Three patterns of plant defoliation were imposed to complete the experimental design. First, all plants within a plot (both indicator plants and their neighbors) were defoliated at a similar intensity to mimic nonselective herbivory. Second, indicator plants, but not neighbors were defoliated to mimic selective herbivory of the climax dominant. Third, plots in which neither the indicator plants nor neighbors were defoliated served as a control to evaluate responses to each of the defoliation treatments. Herbivory was simulated by removing approximately 70% of above-ground biomass (by weight) with hand clippers following each of four data collection periods per year (see below). Indicator plant height following defoliation was approximately 15 and 25 cm for vegetative and reproductive plants, respectively.

Data collection

Plant variables. Data were collected on two permanently marked indicator plants within each plot. All treatment combinations were replicated in four individual plots. Data for all variables were collected in mid-April, early June, mid-August, and early October of 1987 and 1988, except for tiller number and basal area which were estimated in June and October each year. Aboveground production of defoliated indicator plants was estimated by summing the amount of biomass removed at each of the four collection periods. Aboveground biomass harvested from indicator plants at the end of the growing season (October 1987 and 1988) yielded an estimate of total annual production so the production response of nondefoliated and defoliated indicator plants could be compared.

Tiller number per plant was estimated with a double sampling procedure (Javed & Bonham 1982). The direct measure was a count of all tillers on every fourth plant. The indirect measure was a count of tillers in one quarter of the basal area of each plant, after bisecting the basal area with two perpendicular rods. Plant basal area was estimated by a measure of plant circumference at the soil surface. Since indicator plant size was not completely uniform at the initiation of the experiment, tiller numbers and basal areas were analyzed on the basis of percent change from the initial values recorded in September 1986. Initial data collection occurred 8 months after transplanting and all plants were assumed to be well established.

Tiller variables. Eight tillers were harvested from each treatment, one from each of the two monitored indicator plants in each of four treatment replications, during each of the four data collection periods per year. Total leaf blade area, number of leaves, and total aboveground dry weight were measured for each of the tillers. Leaf number per tiller was determined by counting all blades with greater than two cm^2 of live blade area. Leaf blade area was estimated by removing all blades from individual tillers and placing them through a leaf area meter. Weights were determined after tillers were dried in a forced air oven at 60 °C. Number and length of internodes comprising maximum height (stem base to top of inflorescence) and component weights (blade, sheath, culm, and inflorescence) of individual tillers were measured in October 1987 and August 1988 to evaluate tiller architecture in plants with contrasting grazing histories.

Statistical analysis

This experiment was established as a 2 (levels of grazing history) x 2 (levels of competitors) x 2 (levels of indicator plant defoliation) x 2 (levels of competitor defoliation) incomplete factorial design. One potential factor combination, defoliation of neighbors, but not the climax dominant, was assumed to occur infrequently in the field and was omitted from the experimental design. Since the design was incomplete, two balanced submodels were analyzed with analysis of variance to test for factor level and treatment differences.

Results

Plant responses

A significant neighborhood x grazing history interaction occurred for annual aboveground production per plant (Fig. 1, P = .03). Indicator plants with a history of grazing yielded 56% more annual production in nondefoliated *Stipa* neighborhoods than did plants with no grazing history. However, plants with contrasting grazing histories yielded comparable production in nondefoliated *Bothriochloa* neighborhoods.

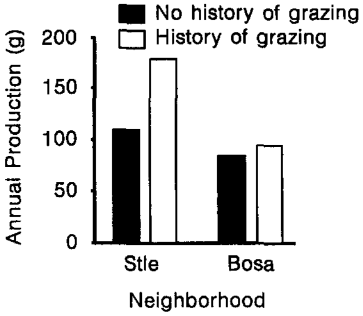

Fig. 1. Mean total annual aboveground production of *S. scoparium* plants during 1987 and 1988 as influenced by grazing history and neighborhood composition (Stle = *S. leucotricha*, Bosa = *B. saccharoides*, P = .03).

Mean annual aboveground production following indicator plant defoliation was not signifi-

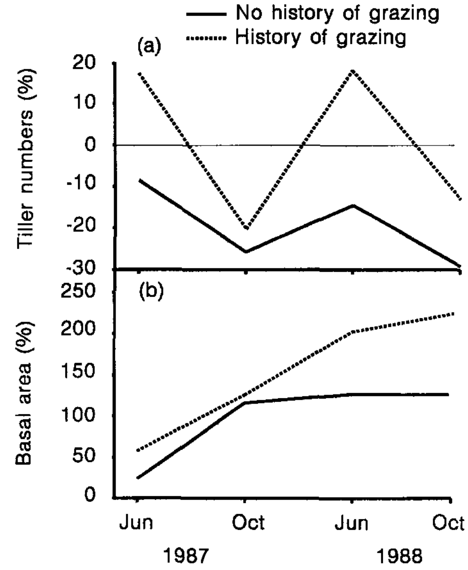

Fig. 2. Relative change in (a) tiller numbers (P = .03) and (b) basal areas (P = .07) of *S. scoparium* plants during 1987 and 1988 in reference to September 1986 values as influenced by history of grazing. Tiller numbers and basal areas were 101 and 92, and 67 and 75 cm^2 for plants with and without a history of grazing, respectively, in September 1986.

cantly affected by grazing history or neighborhood defoliation (P > .10). However, mean annual production following indicator plant defoliation was 72% greater for plants in *Stipa* than in *Bothriochloa* neighborhoods (42.9 and 24.9 g, respectively, P = .004) indicating that *Bothriochloa* was the more competitive neighbor.

Plants with a history of grazing consistently expressed greater relative increases in tiller numbers and basal areas than plants with no history of grazing (Fig. 2a, P = .03 and b, P = .07). These two variables were not significantly affected by either neighborhood or indicator plant defoliation (P > .10). Tiller numbers per plant fluctuated seasonally with maximum numbers occurring in June. Tiller numbers in plants with a grazing history exceeded those with no grazing history by 28 and 34%, respectively, in June of 1987 and 1988. Tiller numbers in plants with no grazing history were 26 and 30% lower in October of 1987 and 1988, respectively, than initial values recorded in September 1986. Mean basal area progressively increased to a value 200% greater than the initial value recorded in September 1986 in plants with a history of grazing. Mean basal area leveled off at the end of the first year and only increased to a value 100% greater than the September 1986 value in plants with no history of grazing (Fig. 2b).

Tiller responses

Morphometric variables of individual tillers collected at the end of each growing season revealed no significant differences between plants with contrasting grazing histories (Table 1, P > .10). However, plants with a history of grazing tended to have shorter internodes, lower culm weights, lower inflorescence weights, and shorter tillers than plants with no grazing history.

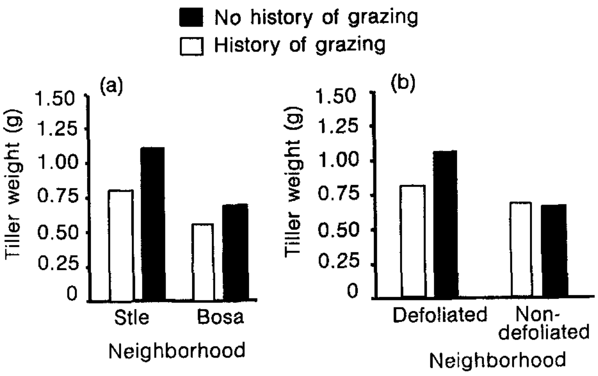

Fig. 3. Mean tiller weights of *S. scoparium* plants during 1987 and 1988 as influenced by (a) grazing history and neighborhood composition (Stle = *S. leucotricha*, Bosa = *B. saccharoides*, P = .01) and (b) grazing history and neighborhood defoliation (P = .02).

No significant main effects were observed for grazing history, neighborhood composition, neighborhood defoliation or indicator plant defoliation for the tiller variables of leaf blade area, leaf number, or aboveground weight (P > .10). However, significant two-way interactions were observed for grazing history × neighborhood composition and for grazing history × neighborhood defoliation for tiller weight (Fig. 3a, P = .02 and b, P = .03, respectively). Mean tiller

Table 1. Mean morphometric variables for reproductive tillers of *S. scoparium* plants with contrasting grazing histories in October 1987 and August 1988. None of the variables were significantly affected by grazing history (P > 0.10)

	October 1987		August 1988	
	History of grazing	No history of grazing	History of grazing	No history of grazing
Blade weight (g)	0.04	0.04	0.20	0.23
Sheath weight (g)	0.09	0.09	0.35	0.41
Blade:Sheath ratio	0.66	0.60	0.87	0.91
Culm weight (g)	0.30	0.41	0.32	0.62
Inflorescence weight (g)	0.33	0.36	0.17	0.90
Internode length (cm)	5.6	5.9	4.8	6.0
Tiller height (cm)	50.4	56.4	49.0	53.9

weight in plants with a history of grazing was 23 and 27% less than in plants with no grazing history in nondefoliated and defoliated *Stipa* neighborhoods, respectively. Mean tiller weights were not significantly different in plants with contrasting grazing histories in either nondefoliated or defoliated *Bothriochloa* neighborhoods.

Discussion

The hypothesis that *S. scoparium* plants with a history of grazing are at a competitive disadvantage in the presence of competition from mid-successional species relative to plants with no grazing history was rejected. Plant and tiller variables of indicator plants with a history of grazing were equal to or greater than those of indicator plants with no history of grazing with the single exception of individual tiller weight. Unexpectedly, plants with a history of grazing yielded greater annual production in *Stipa* neighborhoods than plants with no history of grazing when neither indicator plants nor neighbors were defoliated (Fig. 1). However, both the severe competition in *Bothriochloa* neighborhoods and indicator plant defoliation, regardless of neighborhood composition, minimized annual production differences between plants with contrasting grazing histories.

Greater annual production in nondefoliated plants with a history of grazing than in plants with no grazing history initially appears contradictory to the anticipated effect of long-term selection by herbivores (Eagles 1983; Painter *et al.* 1989). However, greater plant production resulted from greater tiller recruitment per plant even though mean tiller weight was lower than in plants with no grazing history (Figs. 2a and 3a and b). The occurrence of a large number of small tillers conforms to the canopy architecture documented for grazing morphs (Mahmoud *et al.* 1975; Detling & Painter 1983; Painter *et al.* 1989). Greater tiller numbers per plant have previously been observed to compensate for lower individual tiller weights in *S. scoparium* plants with long-term grazing histories (Carman & Briske 1985). Greater tiller numbers per plant also contributed to the greater mean basal area per plant because most tiller recruitment occurs on the plant periphery in the bunchgrass growth form (Fig. 2b, Butler & Briske 1988; Olson & Richards 1988).

A plant composed of numerous, small tillers presumably functions as a herbivory avoidance mechanism to minimize the probability and intensity of defoliation by large herbivores (Westoby 1980; Carman & Briske 1985; Jaramillo & Detling 1988). The accessability of shoot biomass to cattle decreases with increasing proximity to the soil surface because of the limited prehensile abilities of these herbivores (Stobbs 1973; Chacon & Stobbs 1976). Therefore, shorter tillers will have less biomass removed and greater amounts of photosynthetic and meristematic tissue will remain to promote growth following herbivory. Conversely, plants composed of fewer, larger tillers with a greater total leaf area will presumably increase competitive ability in environments supporting dense plant canopies (Grime 1977; Alexander & Thompson 1982).

The capacity for tiller recruitment was the most pronounced morphological distinction between plants with contrasting grazing histories (Fig. 2a). Tiller number per plant and the associated variable of basal area per plant showed a significant grazing history effect for all treatments (neighborhood composition, neighborhood defoliation, and indicator plant defoliation) (Fig. 2a and b). Herbivory can potentially influence tiller recruitment by affecting substrate availability for axillary bud growth, the degree of bud inhibition (i.e., apical dominance), the number of viable buds, and microclimatic conditions for tiller growth. Current information suggests that a reduction in bud inhibition, rather than greater bud number or bud viability, is the most probable mechanism contributing to greater tiller recruitment in plants with a history of grazing (Mueller & Richards 1986; Busso *et al.*, 1989). Unfortunately, the precise function of this mechanism is unknown.

It is difficult to assess why architectural variables of individual reproductive tillers did not differ significantly between plants with contrasting grazing histories (Table 1), especially in light of the pronounced response of tiller recruitment and tiller weight (Figs. 2a and 3). The first and most direct possibility is that even though architectural variables were ranked as anticipated between plants with contrasting grazing histories, extreme inter-tiller variability within populations may have masked the differences between populations ($P > .10$). Wide variation has been documented in several architectural variables among *S. scoparium* genotypes within a single seed source (Carman 1985). A second possibility is that architectural differences between the two populations may have been lost after 36 months in the transplant garden without defoliation even though significant differences may have been present at the time of plant collection. Several investigators have observed a loss of or reduction in architectural variation between plants with contrasting grazing histories in the absence of defoliation (Peterson 1962; Quinn & Miller 1967; Painter *et al.* 1989). Limited insight into how herbivory induces architectural variation within populations makes it difficult to evaluate the potential alternatives. Even though grazing morphs appear to be the result of genetic selection by intensive herbivory (Scott & Whalley 1984; Jaramillo & Detling 1988; Painter *et al.* 1989), the relative contributions of stable genetic variation and phenotypic plasticity are not clearly understood (Peterson 1962; Quinn & Miller 1967; Painter *et al.* 1989).

These data substantiate the findings of Peterson (1962) and Carman and Briske (1985) which indicate that herbivory by domestic cattle may function as a selection pressure to induce architectural variation in perennial grass populations in an ecological time frame (ca ≤ 25 yrs; period grazing had been imposed on the hay meadow population). Previous investigators have not documented population variation to occur in response to herbivory by domestic cattle within comparable time periods (Quinn & Miller 1967; Etherington 1984). Selection has also been demonstrated to occur within relatively short time periods (10–15 yrs) in two perennial grasses subjected to herbivory by prairie dogs (*Cynomys ludovicianus*) in the mixed prairie of North America (Detling & Painter 1983; Jaramillo & Detling 1988; Painter *et al.* 1989). However, herbivore-induced selection on prairie dog colonies would undoubtedly be more severe than that of herbivory by cattle because prairie dogs frequently defoliate plants very near the soil surface and wild ungulates preferentially graze these areas as well (Coppock *et al.* 1983a and b). Herbivory by sheep, which is potentially more intensive than that of cattle based on their prehensile abilities (Hofmann 1988), has also been documented to induce architectural variation in perennial grass populations (Mahmoud *et al.* 1975; Etherington 1984; Scott & Whalley 1984).

A reduction in mean tiller weight was the only variable to suggest that herbivore-induced selection conferred an associated cost to plants with a history of grazing. However, lower mean tiller weight was offset by greater tiller recruitment, in plants with a history of grazing. Plants with a history of grazing displayed equivalent or greater annual production, tiller recruitment, and basal area expansion than plants with no history of grazing. Comparable or greater performance by plants with a history of grazing indicates that the increase in relative density of mid-successional species within the neighborhood of the climax dominant, *S. scoparium*, following long-term severe herbivory in the southern true prairie, is not a consequence of a reduction in competitive ability in response to herbivore-induced population selection. The alternative hypothesis to be examined indicates that selective herbivory of the climax dominant, relative to that of the mid-successional species, is the predominant mechanism governing species replacement in this tallgrass prairie community.

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