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Author(s): Val J. Anderson and David D. Briske

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HERBIVORE-INDUCED SPECIES REPLACEMENT IN GRASSLANDS: IS IT DRIVEN BY HERBIVORY TOLERANCE OR AVOIDANCE?¹

VAL J. ANDERSON

Department of Botany and Range Science, Brigham Young University, Provo, Utah 84602 USA

DAVID D. BRISKE²

Department of Rangeland Ecology and Management, Texas A&M University,
College Station, Texas 77843-2126 USA

Abstract. Herbivore-induced shifts in species composition have been documented from grasslands throughout the world, but the mechanism(s) of species replacement remains largely unexplored. An experiment was conducted in a transplant garden, on the campus of Texas A&M University, to test the hypothesis that greater herbivory tolerance of mid-seral species, rather than selective herbivory of a late-seral dominant, is the dominant mechanism contributing to species replacement in a mesic grassland. Individual plants of a dominant, late-seral, perennial grass, *Schizachyrium scoparium*, were grown in competition with conspecifics and two other perennial grasses (*Bothriochloa saccharoides* and *Stipa leucotricha*) known to increase in relative abundance in response to intensive grazing by domestic herbivores in the southern true prairie. Uniform defoliation of both *S. scoparium* and neighbors was imposed to test the relative expression of herbivory tolerance, while selective herbivory was imposed by defoliating *S. scoparium* plants, but not neighbors.

After four successive defoliations, mean annual shoot production and cumulative shoot production of *S. scoparium* plants were suppressed to a greater extent by conspecific neighbors than by either of the two mid-seral neighbors. Mean basal area of *S. scoparium* plants was not significantly suppressed by either intra- or interspecific neighbors; however, tiller number per plant was suppressed by *B. saccharoides*, but not by *S. leucotricha* or conspecific neighbors. Defoliation of *S. scoparium* plants, but not neighbors, negatively impacted the late-seral plants. Selective defoliation of *S. scoparium* plants significantly reduced tiller variables of mean mass, leaf blade area, and leaf number, but did not significantly reduce plant variables including mean basal area, tiller number, or annual shoot production. Defoliation of both *S. scoparium* plants and neighbors increased annual shoot production, mean basal area per plant, mean tiller leaf area, leaf number, tiller mass, stomatal conductance to H₂O vapor, and plant xylem pressure potential in comparison with *S. scoparium* plants grown with comparable, nondefoliated neighbors. An increase in both plant and tiller variables in defoliated *S. scoparium* plants grown with uniformly defoliated neighbors establishes that replacement of a late-seral dominant is not driven by a greater relative expression of herbivory tolerance of mid-seral species.

These results collectively suggest that the late-seral dominant, *S. scoparium*, possesses a greater competitive ability and a comparable or greater degree of herbivory tolerance than the mid-seral species that comprise the community. Therefore, the initial hypothesis was rejected. It can be inferred that the alternative mechanism, selective herbivory of the late-seral dominant, is the dominant mechanism contributing to species replacement. Herbivore-induced modifications of competitive interactions are most likely to drive species replacement in grasslands characterized by high and consistent resource availability. This may partially explain why condition and trend analysis was developed and initially implemented in the true and mixed prairie associations of North America and why it is widely used by rangeland managers in these grasslands.

Key words: competitive ability; grass–grazer interactions; grassland ecology; grazing resistance; herbivory; herbivory avoidance; herbivory tolerance; rangeland monitoring; *Schizachyrium scoparium*; selective herbivory.

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² Address correspondence to this author.

INTRODUCTION

Herbivore-induced shifts in species composition have been documented from grasslands throughout the world (Ellison 1960, Archer 1989, Bosch 1989, Noy-Meir et al. 1989, Westoby et al. 1989, Milton et al. 1994). Compositional changes most frequently involve the replacement of late-seral dominants by early or mid-seral species (Canfield 1957, Dyksterhuis 1958), while structural changes frequently involve the replacement of tallgrasses by mid- or shortgrasses (Arnold 1955, Mitchley 1988, Belsky 1992). If species replacement continues, a grassland community may become vulnerable to an ingress of ruderals and herbaceous and woody perennials, which support fewer domestic herbivores and may eventually decrease the production potential of the site (Ellison 1960, Archer and Smeins 1991, Milton et al. 1994).

This pattern of herbivore-induced species replacement has been observed with sufficient frequency and predictability that it has been adopted as the basis for monitoring the impact of domestic herbivores on grassland communities (Dyksterhuis 1949). Rangeland condition and trend analysis is used to determine the current ecological status and relative direction of community change in comparison with the composition and productivity of a comparably pristine site supporting a late-seral plant community (Pendleton 1989). Although the concept of rangeland condition and trend analysis has served as a basic tenet of rangeland management in the United States for over 40 yr, experimental verification of the mechanism(s) contributing to herbivore-induced species replacement has received remarkably little attention. This may partially account for the controversy regarding the validity of condition and trend analysis as an effective procedure for evaluating community dynamics in response to herbivory (Laycock 1989, Westoby et al. 1989, Johnson and Mayeux 1992).

Two major scenarios may be invoked to explain herbivore-induced species replacement. The first scenario involves a limited capacity of late-seral dominants to replace leaf area following herbivory, based on a lesser expression of tolerance mechanisms. Tolerance mechanisms increase the rate of leaf replacement through meristematic activity and several physiological processes including compensatory photosynthesis and increased carbon allocation to leaves (Briske 1991, Briske and Richards 1994). The second scenario involves selective herbivory of late-seral dominants based on a lesser expression of avoidance mechanisms. Avoidance mechanisms minimize the frequency and/or intensity of herbivory by reducing plant palatability and accessibility (Briske 1991). Species grazed less severely (i.e., avoidance mechanisms), capable of growing more rapidly following defoliation (i.e., tolerance mechanisms), or possessing a combination of these two mechanisms, realize a competitive advantage

within a community (Caldwell et al. 1981, Richards 1984, Polley and Detling 1988, Briske 1991). Although both mechanisms are known to occur, the relative contribution of these mechanisms to herbivore-induced species replacement is unknown in grassland communities.

This investigation was conducted to test the hypothesis that greater herbivory tolerance of mid-seral species, rather than selective herbivory of a late-seral dominant, is the dominant mechanism regulating species replacement in grazed communities. The experimental approach involved the establishment of individual plants of a late-seral dominant, *Schizachyrium scoparium* (Diamond and Smeins 1988), with conspecific neighbors and neighbors of two perennial grasses (*Bothriochloa saccharoides* and *Stipa leucotricha*) that are known to replace it in communities subjected to long-term intensive herbivory by domestic cattle (Fig. 1; Dyksterhuis 1946, Launchbaugh 1955). The contribution of herbivory tolerance was investigated by defoliating both target plants and neighbors with an equivalent frequency and intensity to approximate the occurrence of uniform herbivory among species. In this treatment, the outcome of competitive interactions between species pairs would be influenced by the rate at which plants replaced leaf area removed by defoliation (i.e., relative expression of tolerance mechanisms). The contribution of selective herbivory was investigated by defoliating a late-seral dominant, but not associated neighbors. In this treatment, the outcome of competitive interactions between species pairs would be influenced by the greater relative leaf area of the mid-seral species. Species pairs in which neither the late-seral dominant nor neighbors were defoliated served as a control to evaluate performance of the late-seral plants to defoliation treatments.

We recognize that disproportionate defoliation of late- and mid-seral species is a simplistic depiction of selective herbivory that does not identify or accurately approximate the relative expression of avoidance mechanisms that occur among plant species in natural settings (e.g., Heitschmidt et al. 1990, Brown and Stuth 1993). However, it does provide an experimental design to evaluate selective herbivory that would otherwise be extremely difficult to implement in the field with grazing animals. Consequently, we chose to test the herbivory tolerance hypothesis because it could be most definitively evaluated within this experimental design. Greater insight into the mechanisms regulating herbivore-induced species replacement will enable ecologists and rangeland managers to more effectively interpret and anticipate population and community dynamics in grazed grasslands.

METHODS

Plant material, transplant garden, and abiotic variables

Schizachyrium scoparium (Michx.) Nash var. *frequens* (Hubb.) Gould, a late-seral dominant of the

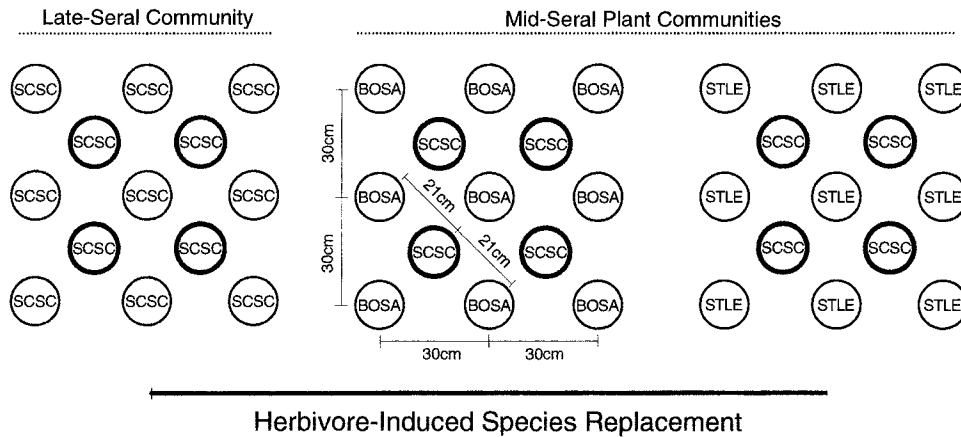


FIG. 1. Illustration of the experimental plots established to investigate the response of *Schizachyrium scoparium* target plants (bold circles), to competition by neighbors (standard circles) known to increase in relative abundance at various stages of herbivore-induced species replacement in the southern true prairie. Tolerance to herbivory was evaluated by monitoring the response of target plants when both the target plants and neighbors were subjected to an equivalent intensity of defoliation while herbivory avoidance was evaluated by defoliating only target plants, but not neighbors. Data were collected on two of the four target plants located within the center of each plot 12 mo after initial plant establishment. Species abbreviations are: *Stipa leucotricha* = STLE, *Bothriochloa saccharoides* = BOSA, and *Schizachyrium scoparium* = SCSC.

southern true prairie (Diamond and Smeins 1988), was grown in association with conspecific neighbors and neighbors of two perennial grasses that are known to replace it in communities subjected to long-term intensive herbivory by domestic cattle (Dyksterhuis 1946, Launchbaugh 1955). The three neighbors were *Schizachyrium scoparium* var. *frequens*, *Bothriochloa saccharoides* (Sw.) Rydb., and *Stipa leucotricha* Trin. & Rupr. (nomenclature follows Gould 1975). The competitive interactions provided by these three neighbors approximate those experienced by *S. scoparium* under conditions of minimal and intermediate degrees of herbivore-induced shifts in species composition (Dyksterhuis 1946, Launchbaugh 1955). Both *S. scoparium* and *B. saccharoides* are midgrasses and possess the C_4 photosynthetic pathway while *S. leucotricha* is a C_3 midgrass (Waller and Lewis 1979, Hicks et al. 1990).

Plants of the late-seral dominant and two mid-seral species were excavated from a remnant true prairie community near Caldwell, Texas (Goodnight Ranch). The site is located 45 km west of Texas A&M University and has been mowed periodically for hay, but has not been grazed by livestock, since ≈ 1900 . Soils are deep, moderately well drained with minimal permeability and are classified as fine montmorillonitic, thermic, Udic Pellustert (Miller 1987). Precipitation and temperature patterns are similar to those described for the transplant garden.

The transplant garden was located on the Texas A&M University Native Plant and Animal Conservancy 2 km west of the main campus, College Station, Texas ($30^{\circ}38' N$, $96^{\circ}21' W$). Soils in the garden possessed a sandy loam A horizon <25 cm in depth underlain by a dense B horizon with limited permeability. Soils are classified as fine, montmorillonitic, thermic, vertic ochraqualfs (USDA 1958). Plants that did not survive

the initial transplanting in January and February of 1986 were replaced in March. Sprinkler irrigation was used to augment natural precipitation during February and March to increase transplanting success. Periodic hand weeding within plots and tilling between plots ensured that competition from nonexperimental species was minimal.

Long-term (30 yr, 1951–1988) average annual precipitation at the site is 993 mm and is bimodally distributed with maxima in the spring and autumn (NOAA 1986–1988). Total annual precipitation during 1986 and 1987, recorded at a weather station 2 km south of the transplant garden, approximated the 30-yr average, but May-through-July precipitation exceeded the long-term average in both years. However, in 1988, total annual (351.0 mm) and May-through-August precipitation (151.8 mm) 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 ensure plant survival and maintain live biomass throughout the season. The 30-yr mean daily temperature is $20.0^{\circ}C$, with the minimum occurring in January (9.4°) and the maximum in July (29.4°). Temperatures during the investigation did not deviate appreciably from the 30-yr mean.

Plot configuration and defoliation treatments

In each plot, four individuals of *S. scoparium* designated as target plants, were planted with nine plants of one of three neighbors (Fig. 1). Each target plant was positioned in the center of four neighbors, ≈ 21 cm from the center of the neighbors. The neighbors were not confined on the plot periphery and individual plots were separated by a 2-m tilled border. Initial basal

areas for both target plants and neighbors ranged between 50 and 70 cm².

Defoliation treatments were imposed on these species combinations to evaluate the relative contributions of herbivory tolerance and selective herbivory of the target plants by defoliating both target plants and neighbors equally and by defoliating only the target plants while leaving the neighbors intact, respectively. Approximately 70% of aboveground biomass was removed with hand clippers in mid-April, early June, mid-August, and early October to simulate a moderate intensity of herbivory by domestic cattle (Gillen et al. 1990, Derner et al. 1994). Height of the target plants following defoliation was \approx 15 and 25 cm for vegetative and reproductive plants, respectively. To ensure that comparable defoliation intensities were imposed among species of various heights, height-mass relationships were established for vegetative, culmed, and reproductive tillers of each species as phenological development progressed throughout the season. These relationships were constructed by dividing individual tillers into 5-cm increments, weighing each increment, and then regressing tiller height against tiller mass on an incremental basis.

Data collection

Plant variables.—Tiller number and basal area per plant, cumulative seasonal shoot production from defoliated plants, and end-of-season shoot production from undefoliated plants were collected on two *S. scoparium* target plants within each plot. Cumulative seasonal shoot production was collected for defoliated plants in mid-April, early June, mid-August, and early October and end-of-season shoot production was collected for undefoliated plants in early October of 1987 and 1988. These data enabled us to compare shoot production of defoliated plants with those of undefoliated plants. Tiller number and basal area of individual plants were estimated in June and October each year. All treatment combinations were replicated in four individual plots.

Tiller number per plant was estimated with a double sampling procedure (Javed and Bonham 1982). On every fourth plant, a complete count of all tillers was made. However, on all others, a count was made in only one-quarter of the basal area of each target plant, after the basal area was bisected with two perpendicular rods. Plant basal area was estimated by a measure of plant circumference at the soil surface. Since the size of target plants 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 values initially recorded in September 1986. Data collection began 8 mo after the initial transplanting. A large increase in plant basal area and vertical root growth in excess of 80 cm (V. J. Anderson and D. D. Briske, unpublished data) indicated that all plants had become established at this time.

Tiller variables.—Eight tillers were harvested from each treatment, one from each of the two monitored target plants in each of the four treatment replications, during each of the four data collection periods each year. Total leaf blade area, number of leaves, and total tiller dry mass were estimated for each of the tillers collected. Leaf number per tiller was determined by counting all blades with a minimal live blade area >2 cm². Leaf blade area was estimated by removing all blades from individual tillers and placing them through a leaf area meter. Tiller masses were determined after drying in a forced air oven at 60°C.

Xylem pressure potential was measured, with a pressure chamber, on young, fully expanded leaf blades. Leaf conductance was also estimated on young, fully expanded leaf blades with a steady state porometer fitted with a narrow aperture (1 cm²). Both variables were collected on eight tillers per treatment combination (two from each of the four replicate plots). During 1987, water relations data were collected twice daily, once in the morning (0700–0800) and again in the afternoon (1200–1300) at each of the four collection periods to identify the minimum and maximum values for these variables. The 1987 data contained limited variability so xylem pressure potential and stomatal conductance data were collected only once per day in 1988. This collection was made within a 1-h interval at midday to minimize confounding by diurnal fluctuations in atmospheric variables. Two target plants, in one of the four replicate plots, were sampled each day during a 4-d sampling period for all treatment combinations.

Statistical analyses

This experiment was designed as a 3 (neighbors) \times 2 (target plant defoliation treatments) \times 2 (neighbor defoliation treatments) incomplete factorial design. One factor combination, defoliation of neighbors but not the late-seral dominant, was assumed to occur infrequently under natural conditions (Gillen et al. 1990, Brown and Stuth 1993) and was omitted from the experimental design. Since the design was incomplete, two balanced submodels were analyzed using basic analysis of variance techniques to determine factor level and treatment differences. In cases where elements unique to the individual submodels (target plant and neighbor defoliation) were not significant, the data were pooled. Data were blocked by collection date for water relations variables because only a portion of the experimental plots were sampled on a given day.

RESULTS

Plant responses

S. scoparium target plants grown in the *Bothriochloa* and *Stipa* neighborhoods produced 170 and 290% more shoot biomass, respectively, than did target plants grown in a *Schizachyrium* neighborhood (Fig. 2a, $P <$

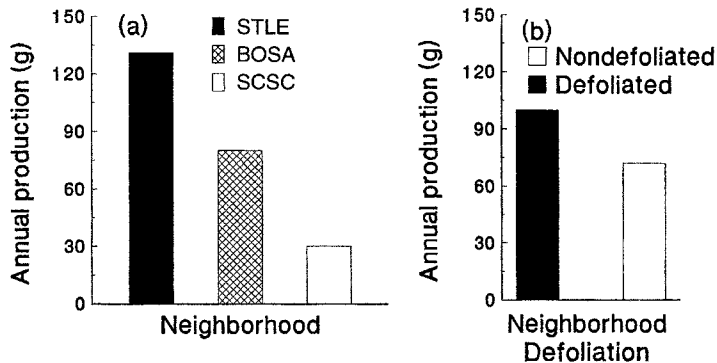


FIG. 2. Mean annual production for *S. scoparium* target plants, recorded in October of 1987 and 1988, in response to (a) neighborhood composition ($P < 0.001$) and (b) neighborhood defoliation ($P = 0.002$). Species abbreviations as in Fig. 1.

0.001). Target plant defoliation, in the absence of neighborhood defoliation, did not significantly affect shoot production ($P > 0.10$). Defoliated target plants in defoliated neighborhoods yielded 25% greater shoot biomass annually than did defoliated target plants grown in nondefoliated neighborhoods (Fig. 2b, $P = 0.002$). Target plant defoliation, with or without neighborhood defoliation, did not suppress production of shoot biomass as much as species composition of the neighborhood.

Mean cumulative shoot production of target plants during the four harvest dates within a growing season showed a comparable response to shoot production of nondefoliated target plants harvested at the end of the season. Target plants produced a mean of 43, 22, and 10 g of shoot biomass following four defoliations per year in *Stipa*, *Bothriochloa*, and *Schizachyrium* neighborhoods, respectively ($P < 0.001$). Defoliated target plants yielded a mean of 18 and 33 g of shoot biomass following four defoliations per year when grown in nondefoliated and defoliated neighborhoods, respectively ($P = 0.013$).

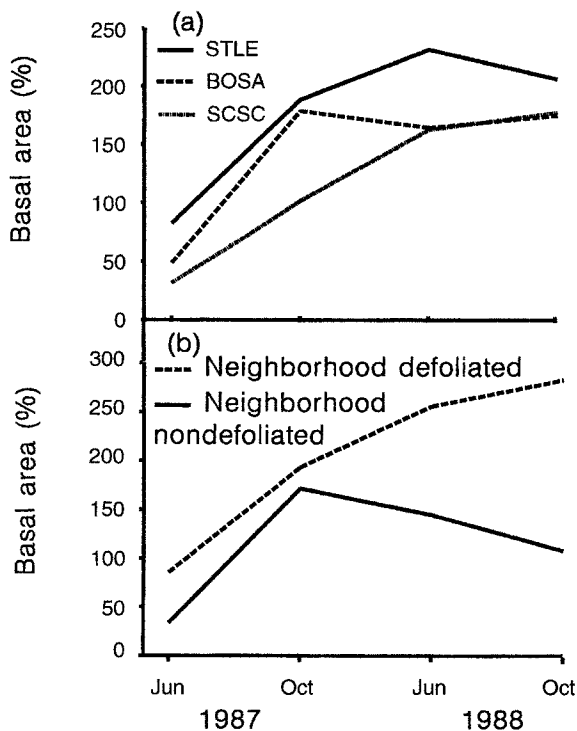


FIG. 3. Mean relative basal areas for *S. scoparium* target plants, recorded in June and October of 1987 and 1988, in response to (a) neighborhood composition ($P > 0.10$) and (b) neighborhood defoliation ($P = 0.023$). Basal area values represent the percentage change from the values recorded in September 1986, which were 82, 66, and 31 cm² in *Stipa leucotricha* (STLE), *Bothriochloa saccharoides* (BOSA) and *Schizachyrium scoparium* (SCSC) neighborhoods, respectively, and 54 and 64 cm² in defoliated and nondefoliated neighborhoods, respectively.

At the end of the investigation, mean absolute basal area of target plants was 180, 120, and 65 cm² in *Stipa*, *Bothriochloa*, and *Schizachyrium* neighborhoods, respectively. However, mean relative basal area of target plants increased $\approx 200\%$ regardless of neighborhood composition (Fig. 3a, $P > 0.1$). Therefore, the absolute differences in target plant basal area occurred during the establishment phase of the investigation, prior to September 1986. The initial increase in mean relative basal area was greater for target plants grown with *Bothriochloa* and *Stipa* neighbors than with conspecifics. Target plant defoliation, in the absence of neighbor defoliation, did not significantly affect basal area expansion ($P > 0.10$). Defoliation of target plants and their associated neighbors increased mean basal area of target plants 175% compared with target plants grown with nondefoliated neighbors (Fig. 3b, $P = 0.023$). Mean basal area increased comparably in target plants grown with defoliated or undefoliated neighbors in 1987, but mean basal area of target plants was 160% greater in defoliated neighborhoods in 1988.

Mean relative tiller number of target plants were significantly greater when grown in *Stipa* and *Schizachyrium* neighborhoods than in a *Bothriochloa* neighborhood (Fig. 4, $P = 0.009$). Mean relative tiller number of target plants declined progressively throughout the experiment in a *Bothriochloa* neighborhood. Tiller number per target plant fluctuated seasonally with minimum tiller numbers occurring in autumn and maximum numbers occurring in spring. A significant decrease in mean relative tiller number of target plants occurred in all neighborhoods during the autumn of

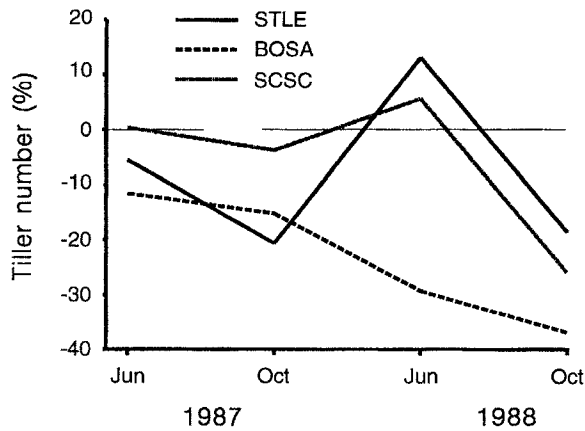


FIG. 4. Mean relative tiller numbers for *S. scoparium* target plants, recorded in June and October of 1987 and 1988, in response to neighborhood composition ($P = 0.009$). Tiller numbers represent the percentage change from the values recorded in September 1986, which were 101, 84, and 63 in *Stipa leucotricha* (STLE), *Bothriochloa saccharoides* (BOSA), and *Schizachyrium scoparium* (SCSC) neighborhoods, respectively.

1988, in response to a regional drought. Precipitation for May–August 1988 was only 50% of the long-term norm. Neither target plant defoliation nor defoliation of both target plants and neighbors had a significant effect on relative tiller number of target plants ($P > 0.10$).

Tiller responses

Mean leaf blade area, leaf number per tiller, and tiller mass of target plants displayed a significant interaction between neighborhood composition and neighborhood defoliation, although neither main effect was significant (Fig. 5a, $P = 0.02$; Fig. 5b, $P = 0.02$; Fig. 5c, $P < 0.001$). Target plants grown in a nondefoliated *Schizachyrium* neighborhood had lower mean leaf blade areas and leaf numbers than those grown in a *Bothriochloa* neighborhood. However, when both target plants and neighbors were defoliated, mean leaf blade area and leaf number were greatest for target plants grown in a *Bothriochloa* neighborhood compared with target plants grown in *Stipa* and *Schizachyrium* neighborhoods. Mean tiller mass was lowest in target plants grown in a nondefoliated *Bothriochloa* neighborhood, compared with the two other neighborhoods. Mean tiller masses were 61 and 74% greater in target plants grown in defoliated *Stipa* and *Bothriochloa* neighborhoods, respectively, compared with those grown in a defoliated *Schizachyrium* neighborhood. Target plant defoliation in a *Schizachyrium* neighborhood did not significantly affect mean tiller mass of target plants ($P > 0.05$).

Mean leaf blade area, leaf number per tiller, and tiller mass of target plants displayed a significant neighborhood composition \times target plant defoliation interaction, although neither main effect was significant

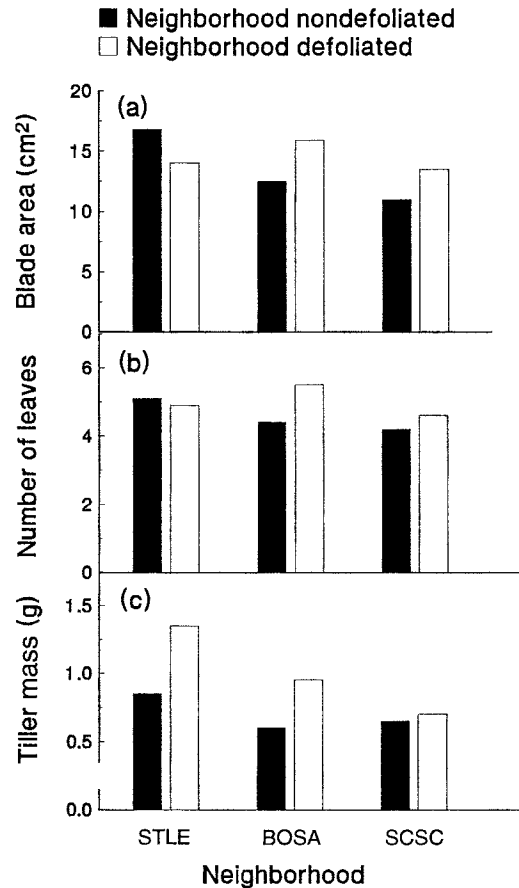


FIG. 5. (a) Mean leaf blade area per tiller ($P = 0.017$), (b) number of leaves per tiller ($P = 0.022$) and (c) tiller masses ($P < 0.001$) for *S. scoparium* target plants, recorded four times in 1987 and 1988, in response to neighborhood composition and neighborhood defoliation. Species abbreviations as in Fig. 1.

(Fig. 6a, $P < 0.001$; Fig. 6b, $P < 0.010$; Fig. 6c, $P < 0.001$). Mean leaf blade area and leaf number per tiller were greater for nondefoliated target plants grown in *Schizachyrium* and *Bothriochloa* neighborhoods than for their defoliated counterparts. Mean leaf blade area and leaf number per tiller were similar for target plants grown in a *Stipa* neighborhood regardless of whether or not target plants were defoliated. When target plants were not defoliated, mean tiller mass was 100% greater for target plants grown in a *Stipa* neighborhood than for those grown in a *Schizachyrium* neighborhood. When both target plants and neighbors were defoliated, mean tiller mass increased 56% in both *Stipa* and *Bothriochloa* neighborhoods while the effect was minimal in a *Schizachyrium* neighborhood.

Stomatal conductance to H_2O vapor for target plants displayed a significant neighborhood composition \times neighborhood defoliation interaction ($P = 0.002$), although neither main effect was significant (Fig. 7a, $P > 0.10$). In nondefoliated neighborhoods, stomatal conductance was greatest for target plants grown in a *Stipa*

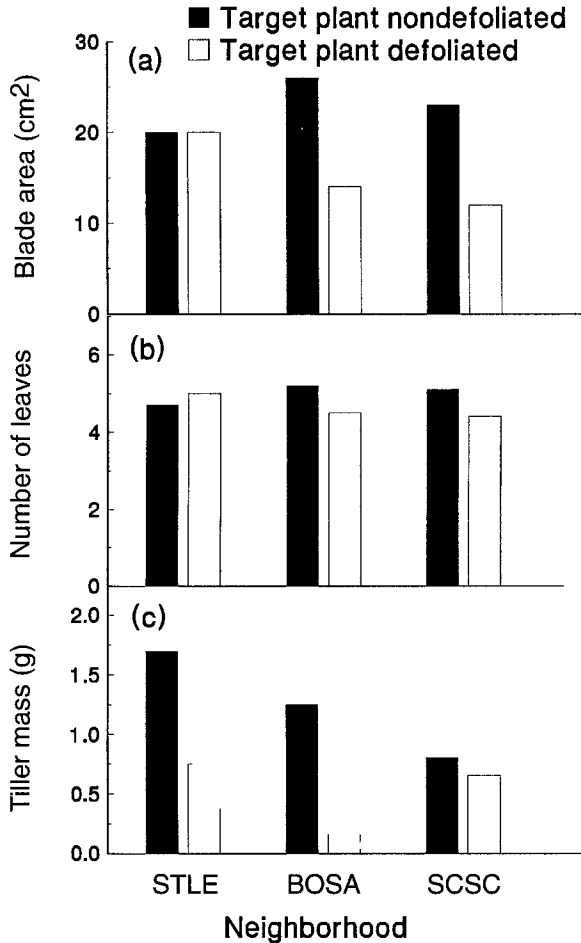


FIG. 6. (a) Mean leaf blade area per tiller ($P < 0.001$), (b) number of leaves per tiller ($P = 0.010$), and (c) tiller masses ($P < 0.001$) for *S. scoparium* target plants, recorded four times in 1987 and 1988, in response to neighborhood composition and target plant defoliation. Species abbreviations as in Fig. 1.

neighborhood in June 1987, but was similar to those grown in the other two neighborhoods through the remainder of the study. In defoliated neighborhoods, stomatal conductance was greatest for target plants grown in a *Schizachyrium* neighborhood and lowest in a *Stipa* neighborhood at the time of peak biomass production, in June of both years (Fig. 7b).

Xylem pressure potential of target plants was not significantly affected by either neighborhood composition or neighborhood defoliation and the interaction between these two treatments was not significant (Fig. 8a, $P > 0.10$). However, xylem pressure potentials were significantly more favorable when target plants and neighbors were defoliated than when they were not defoliated (Fig. 8b, $P = 0.03$). This response was most evident during the drought of 1988. Both xylem pressure potential and stomatal conductance fluctuated seasonally, with the most favorable water status occurring in June and then decreasing as the season progressed.

Xylem pressure potential was most negative in target plants possessing the greatest stomatal conductance, as anticipated (Fig. 7a).

DISCUSSION

Ecological implications

These data collectively indicate that, in our experimental system, a late-seral dominant, *S. scoparium*, possessed a greater competitive ability and at least a comparable degree of herbivory tolerance in comparison with two mid-seral species, *B. saccharoides* and *S. leucotricha*. Therefore, the hypothesis indicating that greater herbivory tolerance of mid-seral species, rather than selective herbivory of a late-seral dominant, is the primary mechanism contributing to herbivore-induced species replacement must be rejected. The alternative hypothesis of selective herbivory can be inferred to be the dominant mechanism contributing to species replacement in communities comprised of these species populations. However, these conclusions must be cautiously applied to other populations of *S. scoparium* based on the occurrence of extensive genetic variation within its broad distributional range (Gould 1975) and the potential for grazing history to modify both phenotypic expression and competitive ability (Carman and Briske 1985, Briske and Anderson 1992, Painter et al. 1993). It should also be recognized that this experimental approach only allowed an assessment of the relative contribution of selective herbivory and herbivory tolerance because plants were spatially arranged in the garden to manifest a treatment effect, rather than

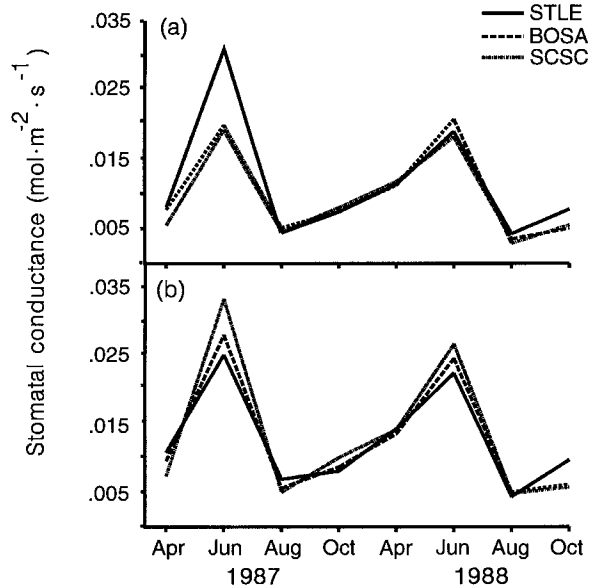


FIG. 7. Mean leaf conductance to H₂O vapor for *S. scoparium* target plants, recorded four times in 1987 and 1988, in response to (a) neighborhood composition ($P > 0.10$) and (b) neighborhood defoliation ($P = 0.002$). Species abbreviations as in Fig. 1.

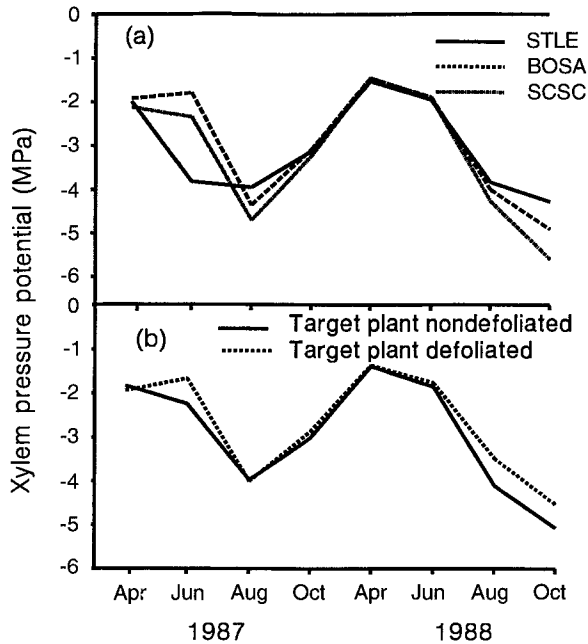


FIG. 8. Xylem pressure potentials for *S. scoparium* target plants, recorded four times in 1987 and 1988, in response to (a) neighborhood composition ($P > 0.10$) and (b) target plant defoliation ($P = 0.034$). Species abbreviations as in Fig. 1.

to approximate plant spatial arrangement in natural settings.

Neighborhood defoliation coincident with that of *S. scoparium* plants increased plant basal area, annual shoot production, and all tiller variables in most treatment combinations compared with late-seral plants grown in comparable nondefoliated neighborhoods (Figs. 2b, 3b, and 5a, b, c). These data do not directly demonstrate that a late-seral dominant possesses greater herbivory tolerance than mid-seral species because growth of the late-seral plants was not greater when grown with uniformly defoliated mid-seral neighbors relative to conspecific neighbors. However, an increase in both plant and tiller variables in defoliated *S. scoparium* plants grown with uniformly defoliated *B. saccharoides* and *S. leucotricha* neighbors establishes that species replacement is not driven by greater herbivory tolerance of the mid-seral species relative to the late-seral dominant.

Greater competitive ability of *S. scoparium*, as demonstrated by greater shoot production when plants were grown with interspecific, rather than intraspecific neighbors, was anticipated based on its position within the sere and the assumption that a strong competitive ability is an important attribute of abundant species (Keddy 1989, but see Duralia and Reader 1993). Weaker competitive abilities of the mid-seral species indicate that an increase in the proportion of these species within the neighborhood of *S. scoparium* would decrease the intensity of competition experienced by the late-seral dominant relative to conspecific neighbors. There-

fore, a herbivore-induced shift in species composition toward a greater relative abundance of mid-seral species would retard, rather than promote, species replacement under conditions of uniform herbivory among species. However, competition from mid-seral species could potentially be intensified if plant density and individual plant basal area increased in response to severe, long-term herbivory (Butler and Briske 1988, Briske and Anderson 1990).

The alternative hypothesis suggests that selective herbivory is required to reduce competitive ability of a late-seral dominant before mid-seral species are able to increase in size or abundance. Defoliation of *S. scoparium* plants, in the absence of neighbor defoliation, did suppress mean tiller mass, leaf blade area, and leaf number (Fig. 6a, b, c). Although the defoliation regime imposed was insufficient to reduce the plant variables of basal area, tiller number, and shoot production within a 2-yr period, the negative response of individual tiller variables suggests that plant variables may have been adversely affected if this defoliation regime had been continued. These data illustrate the potential of selective herbivory to modify competitive interactions and influence species composition (Mueggler 1972, Tripathi and Gupta 1980, Caldwell et al. 1985, 1987, Moloney 1990).

The potential occurrence of selective herbivory is supported by an apparent dietary preference of domestic herbivores for late-seral dominants in grasslands (Gammon and Roberts 1978, Gillen et al. 1990, Heitschmidt et al. 1990) and the lesser relative expression of avoidance mechanisms by late-seral dominants relative to mid-seral species. For example, tiller recruitment in *B. saccharoides* occurs by horizontal growth of axillary buds through the subtending leaf sheaths of the parental tiller. This pattern of tiller development increases the angle of tiller exertion and tiller proximity to the soil surface and potentially minimizes the intensity of herbivory (Alexander and Thompson 1982, Detling and Painter 1983, Carman and Briske 1985). Important avoidance mechanisms in *S. leucotricha* include a relatively small stature (less than one-half the total height of either *B. saccharoides* or *S. scoparium*) and sharpened calli of the caryopses (Gould 1975).

The observation that the most competitive, and perhaps the most tolerant, species is eventually replaced by intensive herbivory suggests that tolerance mechanisms may only be capable of maintaining the competitive superiority of this species under conditions of frequent, moderate herbivory and/or infrequent, intensive herbivory (Voigt and Weaver 1951, Branson and Weaver 1953, Launchbaugh 1955). Chronic, intensive herbivory of a late-seral dominant apparently exceeds the ability of tolerance mechanisms to rapidly replace leaf area and a reduction in competitive ability results (e.g., Hodgkinson et al. 1989). When intensive herbivory minimizes the contribution of tolerance mecha-

nisms of a late-seral dominant, mid-seral plants with a greater relative expression of avoidance mechanisms potentially attain a competitive advantage. This scenario assumes that the most competitive species, the late-seral dominants, possesses the lowest relative expression of avoidance mechanisms. Perhaps competitive ability and avoidance mechanisms are inversely related as is assumed to be the case for plant growth and the production of secondary compounds (Coley et al. 1985, Briggs and Schultz 1990, but see Simms and Rauscher 1987, 1989). However, the "costs" associated with the production of morphological avoidance mechanisms, as opposed to biochemical mechanisms, are less clearly defined (e.g., Björkman and Anderson 1990, Briske and Anderson 1992). The expression of greater competitive ability and comparable herbivory tolerance by *S. scoparium* relative to the mid-seral species suggests that a trade-off does not exist between these two attributes within this species (Tilman 1988: 238).

Managerial applications

The inference that selective herbivory is the dominant mechanism contributing to herbivore-induced species replacement in mesic grasslands has important implications to grassland management and conservation. Replacement of a late-seral dominant in intensively grazed grasslands may have been misinterpreted as a consequence of a lesser expression of herbivory tolerance, rather than herbivory avoidance, in relation to associated mid-seral species. If a late-seral dominant is perceived as being relatively intolerant of herbivory, the only viable management strategy to maintain its dominance is to reduce the intensity of herbivory. Alternatively, if selective herbivory of a late-seral dominant is considered to be the dominant mechanism inducing species replacement, then managerial decisions to regulate the uniformity of herbivory among species may also be implemented to maintain dominance of late-seral species. Intensive herbivory of mid-seral species when the relative expression of avoidance mechanisms is lowest, including the period of maximum vegetative plant height (Arnold 1955, Belsky 1992) and prior to reproductive culm development (Willms et al. 1980, Ganskopp et al. 1992), can potentially reduce, although not eliminate, selective herbivory among grass species (Briske and Heitschmidt 1991, Brown and Stuth 1993).

The inference that selective herbivory is the dominant mechanism of species replacement within communities dominated by *S. scoparium* is supported by observations that intensive herbivory is required to shift community dominance from late-seral to mid-seral species. Mid-seral species in the San Antonio prairie of east-central Texas (Launchbaugh 1955), true prairie of eastern Nebraska (Voigt and Weaver 1951), and mixed prairie of west-central Nebraska (Branson and Weaver 1953) only increased after intensive herbivory

substantially reduced the abundance of *S. scoparium*. This suggests that threshold levels of population degradation of *S. scoparium* potentially precede large-scale changes in species composition (Archer 1989, Friedel 1991, Laycock 1991). Concomitant decreases in individual plant basal area and increases in plant density have previously been recognized as potential indicators of degradation in *S. scoparium* populations (Butler and Briske 1988). If threshold levels were identified within the species replacement process, they could potentially signal rangeland managers of impending compositional changes prior to their occurrence. Grazing management practices could then be modified to reverse or ameliorate large-scale shifts in community composition.

Xylem pressure potential and stomatal conductance of *S. scoparium* plants were not modified sufficiently by neighborhood composition or defoliation to be a reliable indicator of herbivore-induced competitive interactions (Figs. 7a, b and 8a, b). *S. scoparium* plants apparently adjusted to conditions of lower soil water availability in the most competitive neighborhoods by reducing leaf area per plant rather than by restricting leaf conductance or transpiration (Nobel 1981, Wraith et al. 1987). The low mean leaf blade area per tiller in *S. scoparium* plants grown in a conspecific neighborhood substantiates this argument (Figs. 5a and 6a). A reduction in total leaf area of *S. scoparium* plants apparently reduced total transpiration per plant sufficiently in the most competitive neighborhoods to maintain comparable xylem pressure potentials and leaf conductances with those plants grown in the least competitive neighborhoods. Defoliation presumably increased xylem pressure potentials by reducing transpirational area and the rate of soil water depletion (Toft et al. 1987, Wraith et al. 1987, Briske and Anderson 1990).

Herbivore-induced modifications of competitive interactions are most likely to regulate species replacement in mesic grasslands that respond to disturbance by relative shifts in species abundance rather than by regional, episodic events of plant mortality and recruitment (see Huston and Smith 1987, Milchunas et al. 1988, O'Connor 1991, Milchunas and Lauenroth 1993). The regulatory influence of herbivory on persistent competitive interactions is very likely diminished and overridden by abiotic variables in environments characterized by limited and unpredictable resource availability (e.g., Wilson and Keddy 1986). This may partially explain why condition and trend analysis was developed and initially implemented in the true and mixed prairie associations of North America (Dyksterhuis 1946, 1949) and why it is currently accepted and implemented in these grasslands (Laycock 1991). Herbivore-induced species replacement may more accurately be evaluated by an alternative procedure that is less dependent upon persistent competitive interactions (e.g., state-and-transition model, Westoby et al.

1989) in communities characterized by low and unpredictable resource availability.

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