Relative herbivory tolerance and competitive ability in two dominant: subordinate pairs of perennial grasses in a native grassland

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Abstract

We evaluated herbivory tolerance and competitive ability within two dominant: subordinate pairs of C_4, perennial grasses at each of two sites to determine the contribution of these processes to herbivore-induced species replacement. Herbivory tolerance was assessed by cumulative regrowth from defoliated plants of each species and competitive ability was evaluated by relative uptake of a ^{15}N isotope placed into the soil between paired species in the field. Herbivory tolerance was similar for the dominant and subordinate species in both plant pairs and defoliation intensity had a greater influence on herbivory tolerance than did defoliation pattern. Both species within the *Sorghastrum nutans*: *Schizachyrium scoparium* pairs exhibited comparable nitrogen acquisition from a ^{15}N enriched pulse with or without defoliation. In contrast, *S. scoparium* acquired more ^{15}N than did its subordinate neighbor, *Bothriochloa laguroides* when this species pair was undefoliated. Uniform defoliation of this species pair at a defoliation intensity removing 70% of the shoot mass accentuated this response further demonstrating the greater competitive ability of the dominant compared to the subordinate species. Although the 90% defoliation intensity reduced nitrogen acquisition by the dominant relative to the subordinate species, *B. laguroides*, it did not reduce nitrogen acquisition by the dominant below that of the subordinate neighbor. The occurrence of similar herbivory tolerance among dominant and subordinate species indicates that selective herbivory suppressed the greater competitive ability, rather than the greater herbivory tolerance, of the dominant grasses in this experimental design. These data suggest that interspecific competitive ability may be of equal or greater importance than herbivory tolerance in mediating herbivore-induced species replacement in mesic grasslands and savannas.

Introduction

It has been well established that defoliation can influence plant performance and competitive ability to modify community composition and structure (Weiner 1993; Fahnestock and Knapp 1994; Silvertown et al. 1994; Bonser and Reader 1995). However, defoliation-competition interactions are not entirely predictable because both direct and indirect effects may be involved to produce positive, neutral or negative outcomes (Burger and Louda 1994; Mulder and Ruess 1998; Van der Wal et al. 2000). Mechanistic insight into defoliation-competition interactions is

limited because competition is often inferred indirectly from plant performance, rather than from the direct assessment of resource acquisition (Caldwell et al. 1985). Our understanding of the effects of defoliation on resource acquisition and competition is especially limited for native plants in field settings (Louda et al. 1990).

Herbivores often selectively consume plant species or species groups and thereby place them at a competitive disadvantage relative to undefoliated or more leniently defoliated neighbors by reducing their capacity to acquire resources (Caldwell et al. 1987; Louda et al. 1990). Selective grazing may be the pri-

mary process contributing to herbivore-induced shifts in species composition because it may suppress the competitive ability of late-seral dominant grasses relative to mid-seral subordinate grasses in mesic grasslands (Heitschmidt et al. 1990; O'Connor 1991; Brown and Stuth 1993; Anderson and Briske 1995; Ash and McIvor 1998). This pattern of compositional change has contributed to the hypothesis that herbivore-induced species replacement in grasslands and savannas is driven primarily by selective grazing, rather than by contrasting regrowth abilities (i.e., herbivory tolerance) among species (Anderson and Briske 1995; Moretto and Distel 1997). However, an alternative hypothesis predicts that the relative balance between herbivory tolerance and selective grazing among species contributes to herbivore-induced shifts in community composition (Augustine and McNaughton 1998). Herbivory tolerance is anticipated to be of equal or greater importance than selective herbivory in communities where palatable species retain dominance.

Both hypotheses assume that selective herbivory contributes to species replacement by shifting the competitive advantage from dominant to subordinate species, but they differ in the degree to which herbivory tolerance contributes to species dominance. The selective herbivory hypothesis implicitly assumes that herbivory tolerance is relatively similar between dominant and subordinate species (Anderson and Briske 1995) while the tolerance-selective herbivory hypothesis predicts that tolerance is greater in dominant than in subordinate grasses (Augustine and McNaughton 1998). Unfortunately, the estimation of herbivory tolerance is often confounded with competitive ability in defoliation investigations (Caldwell 1984). The relative expression of herbivory tolerance and competitive ability in dominant and subordinate species requires further investigation to effectively evaluate the selective herbivory and tolerance-selective herbivory hypotheses of herbivore-induced species replacement.

A field experiment was conducted to evaluate herbivory tolerance and competitive ability within two pairs of dominant: subordinate C_4, perennial grasses that are abundant in the southern true prairie of central North America. Two defoliation intensities and two defoliation patterns were imposed on both species pairs to evaluate the influence of defoliation on herbivory tolerance and competitive ability. We tested the hypotheses that: 1) dominant and subordinate species possess similar herbivory tolerance, and 2) defo-

liation suppresses the competitive ability of dominant relative to subordinate species. Herbivory tolerance was assessed by cumulative regrowth from defoliated plants of each species throughout the growing season. Competitive ability was evaluated by placement of an ^{15}N isotope into the soil between species pairs and then determining the amount of ^{15}N isotope taken up by each species in response to various defoliation treatments. Greater knowledge of the relative contribution of herbivory tolerance and competitive ability among dominant and subordinate species will increase our mechanistic understanding of herbivore-induced patterns of species replacement in grasslands and savannas.

Study area

Research was conducted on the Texas A&M University campus in east-central Texas (30°35′ N; 96°21′ W; 150 m a.s.l.) within the southern true prairie of North America. The site is characterized as a tallgrass community with a mean annual net primary production of 3,500 kg ha^{-1} and had not been grazed by livestock or burned for at least 5 years prior to the investigation. The research was located on gently sloping (1 to 5%) upland soils (fine, montmorillonitic, thermic Vertic Albaqualfs) formed from alluvium deposited over coastal plains sediments. This upland soil series is characterized by an eroded fine sandy loam A horizon (0–17 cm in depth) and a dense clay B horizon (Hallmark et al. 1986). Mean monthly temperatures range from 11 °C in January to 29 °C in July. The frost-free period averages 270 days and extends from March, through November. Precipitation averages 993 mm annually and has a bimodal distribution, with maxima in the spring and autumn (Office of the Texas State Climatologist 1997). Precipitation during the first month of the investigation (June) was 81% greater than the long-term mean for that month (Office of the Texas State Climatologist 1997). A period of dry conditions occurred during the following two growth intervals (July–September) when precipitation was only 56% of the long-term mean. Abundant rainfall in October ended the dry period when precipitation was 28% greater than the long-term mean for that month.

Two sites within the study area were identified by topographic position and vegetation composition. Vegetation in a downslope position (referred to as site 1) was dominated by *Sorghastrum nutans* (L.) Nash.

and *Schizachyrium scoparium* (Michx.) Nash. var. *frequens* (C.E. Hubb) was an abundant subordinate species. The second site (site 2) was located in a up-slope position approximately 50 m from site 1. Vegetation in site 2 was dominated by *S. scoparium* and *Bothriochloa laguroides* was an abundant subordinate species. *Sorghastrum nutans* and *S. scoparium* achieve their greatest relative abundance in late-successional grasslands while *B. laguroides* generally achieves its greatest relative abundance in early to mid-successional grasslands (Diamond and Smeins 1985, 1988). *Bothriochloa laguroides* is known to replace the two dominants in communities subjected to long-term intensive herbivory by domestic cattle (Dyksterhuis 1946; Launchbaugh 1955). Taxonomic nomenclature of species follows Hatch et al. (1990).

Methods

Two patterns of defoliation were imposed at two intensities to evaluate the effect of defoliation on herbivory tolerance and competitive ability in two dominant: subordinate pairs of perennial grasses during 1997. Fifty replicate plant pairs consisting of two adjacent dominant: subordinate plants with approximately one plant diameter distance ($\sim$ 15 cm) between the two plant peripheries were selected in each of the two sites. Individual plants within a pair were of similar basal area (174.5 cm^2 ± 15.0; mean ± s.e).

Defoliation patterns were: (1) defoliation of only the dominant species in a pair (selective) and (2) defoliation of both the dominant and subordinate species in a pair (uniform). A third pattern of defoliation, defoliation of the subordinate species only, was not evaluated because this pattern of defoliation is assumed to occur infrequently (Gillen et al. 1990; Brown and Stuth 1993) and the number of species pairs available at each site was limited. Defoliation intensities were (1) removal of 70% of canopy biomass; and (2) removal of 90% of canopy biomass. Defoliation heights corresponding to these intensities were determined at the beginning of the investigation (May 1997) by constructing height-weight relationships for each species. The 70% defoliation intensity was imposed by defoliating plants at 7.0 cm above the soil surface and plants receiving the 90% defoliation intensity were defoliated at 2.5 cm. These defoliation heights were imposed for all subsequent defoliations. These defoliation intensities were based on documented grazing intensities in this region and repre-

sented heavy to severe utilization by cattle (Brown and Stuth 1993). We assumed that the comparison of tolerance and competitive abilities among species would be more clearly distinguished at more severe defoliation intensities. Individual plants in the neighborhood surrounding the experimental plant pairs were not defoliated.

The experimental design consisted of 10 plant pairs randomly assigned to each of the following treatments: 1) undefoliated, 2) 70% biomass removal of the dominant species, 3) 90% biomass removal of the dominant species, 4) 70% biomass removal of both the dominant and subordinate species, and 5) 90% biomass removal of both the dominant and subordinate species. Tiller number per plant was measured at the beginning and end of the investigation (May 1997 and November 1997). Defoliations were imposed in the first week of both June and July and in mid-August. Shoot biomass following defoliation was collected above the height of defoliation at the end of each interval. Total plant shoot mass in defoliated plants and end of season shoot mass in undefoliated plants were collected in mid-October 1997. Tiller number per plant differed significantly between dominant and subordinate plants because of inherent size variation among species. Therefore, end of season tiller number per plant was analyzed as a percentage of the initial values.

Acquisition of ^{15}N from the soil equidistant between plants within an experimental pair was evaluated in five randomly selected pairs of the 10 experimental plant pairs in each defoliation treatment. Nitrogen isotope pulses consisted of 50 ml of a 100 mM ^{15}(NH$_4$)$_2$SO$_4$ solution containing 68.4 % ^{15}N excess and were injected into soils to a depth of 10 cm with a syringe at the beginning of the investigation (Derner and Briske 1998). Nitrogen was applied as NH$_4$ rather than NO$_3$ because it is the most abundant form of available nitrogen in these soils (Derner and Briske 1999a). Harvested biomass was dried at 60 °C for 48 h and ground to pass through a 40-mesh screen. Approximately 7.5 mg of biomass was placed in tin capsules and analyzed for ^{15}N atom % using a Carlo-Erba NA-1500 elemental analyzer interfaced with a VG-Isomass mass spectrometer (Isotope Services Inc., Los Alamos, NM, USA). Mean (n = 6) background ^{15}N atom % values (*S. nutans:* 0.3673 ± 0.0006, *S. scoparium*: 0.3709 ± 0.0019, *B. laguroides*: 0.3670 ± 0.0005) were subtracted from labeled samples of the respective species to determine ^{15}N atom % excess values (Boutton 1991). ^{15}N samples were

collected from undefoliated plants at the end of the season when aboveground biomass was harvested. Analysis of ^{15}N samples for defoliated plants was limited to the first growth interval (40 days) due to inadequate harvested shoot mass during the second and third intervals when precipitation was below average. Pools of ^{15}N were calculated by multiplying the shoot mass (g), shoot nitrogen % and ^{15}N atom % excess of harvested shoot tissues. Ratios of ^{15}N atom % excess and ^{15}N atom % excess pools for dominant: subordinate species pairs were used to identify the magnitude of nitrogen acquisition between the two species. Ratios greater than 1:1 indicate greater ^{15}N acquisition and allocation into shoot biomass by the dominant species.

Statistical analysis

Herbivory tolerance of the dominant species was assessed by cumulative shoot mass from defoliated plants and by the total number of tillers per plant at the end of the season. The main effects of defoliation pattern and intensity and their interaction were tested using a factorial ANOVA (treatments 2–5). Data were analyzed with GLM procedures (SAS Institute Inc. 1990) using residual error terms to test the main factors and factor interactions and Tukey's HSD test for all multiple pairwise comparison of significant main factors (P < 0.05). Defoliated plant tiller number was compared to the undefoliated control (treatment 1) using a Dunnett's comparison (SAS Institute Inc. 1990). If defoliation intensity and pattern did not significantly affect tiller number and shoot mass we would not reject the hypothesis that herbivory tolerance was similar between dominant and subordinate species (hypothesis 1).

Two sets of variables were used to assess relative competitive abilities between dominant and subordinate species. These variables were ^{15}N acquisition in response to defoliation and the response of undefoliated subordinate species to dominant species defoliation at each site. We tested the effect of defoliation intensity on ^{15}N isotope acquisition among uniformly defoliated plant pairs (treatments 1, 4 and 5) by using least-squares means (LSMEANS; stderr, SAS Institute Inc. (1990)). Individual tests were performed to determine if the ^{15}N atom % excess and pools of ^{15}N atom % excess ratios (dominant: subordinate species) were significantly different from 1:1 among undefoliated plant pairs and pairs defoliated at 70 and 90%. Ratios of ^{15}N atom % excess and pools of ^{15}N atom

% excess for dominant: neighbor species pairs were log transformed prior to analysis to normalize residuals. Means and standard errors were reported after back-transformation. The response of undefoliated subordinate species to dominant species defoliation was assessed with tiller number per plant, end of season canopy biomass, ^{15}N atom % excess, and pools of ^{15}N atom % excess at each site. We used t-tests to test for treatment differences (treatments 1, 2 and 3) for these variables. If defoliation intensity and pattern did not significantly affect ^{15}N acquisition of the dominant and the response of undefoliated subordinate species to dominant species defoliation, we would reject the hypothesis that competitive ability of dominant species would be suppressed by defoliation relative to subordinate species (hypothesis 2).

Results

Tiller number per plant for the dominant species was substantially reduced following defoliation at both defoliation intensities in comparison with undefoliated plants (Figure 1a and b). In site 1, both defoliation pattern (uniform vs. selective) and defoliation intensity (70 vs. 90%) were significant factors reducing tiller number per plant (F = 10.05, P = 0.003 and F = 18.71, P = 0.0001, respectively), (Figure 1a). Tiller number decreased significantly as defoliation intensity increased from 70 to 90% and when defoliation was imposed selectively to the dominant, *S. nutans*, compared to uniformly defoliated plant pairs. In site 2, tiller number per plant for the dominant species, *S. scoparium*, decreased significantly as defoliation intensity increased from 70% to 90% (F = 20.90, P = 0.0001), but tiller number was not affected by defoliation pattern (Figure 1b). The interaction between defoliation pattern and intensity for dominant species tiller number per plant was not significant in either site. Defoliation significantly reduced tiller number per plant for subordinate species at both sites as defoliation intensity increased from 70% to 90% (Figure 1c and d). The 90% defoliation intensity reduced tiller number per plant to < 10% of the pre-defoliation values for both *S. scoparium* and *B. laguroides*, while *S. nutans* maintained higher values at both defoliation intensities.

End of season shoot mass for the dominant species was significantly reduced in site 1 as defoliation intensity increased from 70% to 90% (F = 13.70, P = 0.0019), but this was not the case for site 2 (Figure
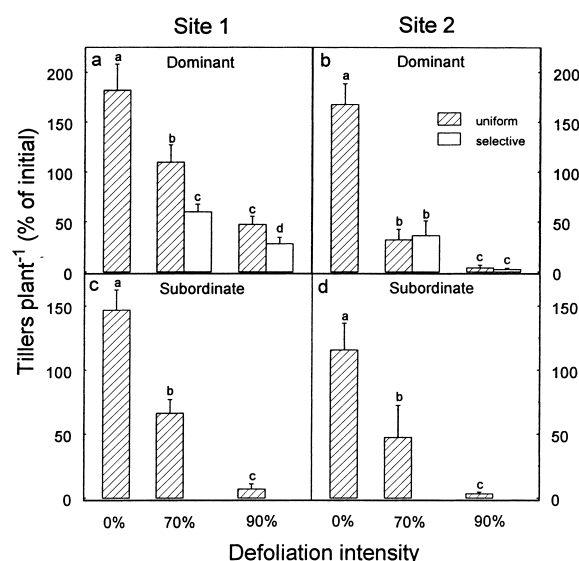
Figure 1. Mean (± SE; n = 10) percent tillers plant^{-1} for dominant and subordinate species in undefoliated plant pairs and in response to defoliation pattern and intensity in each site following three defoliations: a) dominant species in site 1, *Sorghastrum nutans*, b) dominant species in site 2, *Schizachyrium scoparium*, c) subordinate species in site 1, *Schizachyrium scoparium*, d) subordinate species in site 2, *Bothriochloa laguroides*. Defoliation patterns were defoliation of both dominant and subordinate species (uniform) and defoliation of only the dominant species (selective). Defoliation intensities were undefoliated and removal of 70% and 90% of the plant canopy mass. See methods section for initial absolute values. Different letters above bars indicate significant (P < 0.05) differences among defoliation treatments within a species.

2a and b). The significant reduction in biomass observed in site 1 was evident by the end of the first growth interval (P = 0.003; data not shown). Neither the pattern of defoliation nor the interaction between defoliation pattern and intensity significantly affected end of season shoot mass for the dominant species in either site. Defoliation intensity did not significantly affect shoot mass of the subordinate species at either site (Figure 2 c and d).

End of season shoot mass was not significantly different between undefoliated dominant and subordinate species at the end of the investigation (Table 1). Undefoliated subordinate species did not respond significantly to dominant species defoliation at either defoliation intensity in either site. Total harvested shoot mass, percent shoot nitrogen, ^{15}N atom % excess and ^{15}N excess pools in undefoliated subordinate species were similar regardless of the defoliation intensity imposed on the dominant species.

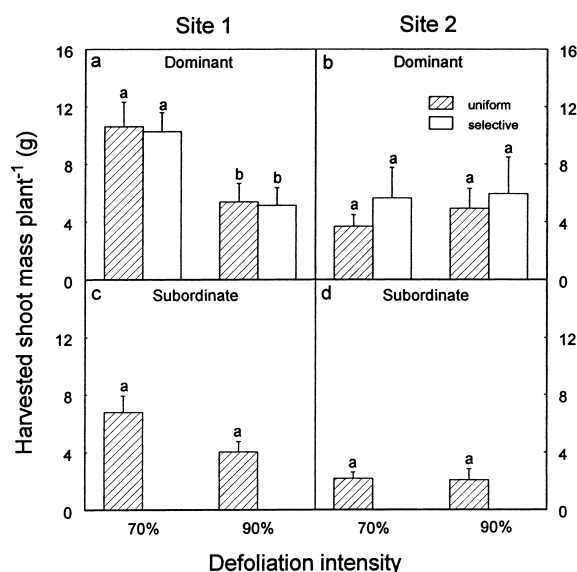*Figure 2.* Mean (± SE; n = 5) total aboveground biomass for dominant (a and b) and subordinate (c and d) species in response to defoliation pattern and intensity following three defoliations. Dominant and subordinate species are identified in Figure 1. Defoliation patterns were defoliation of both dominant and subordinate species (uniform), and defoliation of only the dominant species (selective). Defoliation intensities were undefoliated and removal of 70% and 90% of the plant canopy mass. Different letters above bars indicate significant (P < 0.05) differences among defoliation treatments within a species.

Dominant: subordinate species ratios of ^{15}N atom % excess and ^{15}N excess pools in undefoliated plant pairs indicated greater acquisition of the ^{15}N pulse by the dominant than the subordinate species at the end of the season at both sites (Table 1). However, the ratio of ^{15}N atom % excess significantly exceed a 1:1 ratio in only site 2 (P = 0.0289).

Within uniformly defoliated plant pairs, shoot mass, ^{15}N atom % excess, and ^{15}N % excess pools were generally greater for the dominant species than the adjacent subordinate species (Table 2). However, the ratio of ^{15}N atom % excess and ^{15}N excess pools for dominant: subordinate species in site 1 were not significantly greater than 1:1 when they were uniformly defoliated at either 70 or 90%. In site 2, the ^{15}N atom % excess ratios were significantly greater than 1:1 following uniform defoliation at 70% intensity (P = 0.0104), while ^{15}N excess pool ratios were significantly greater at both the 70 and 90% intensities (P = 0.0332 and P = 0.0513, respectively). ^{15}N atom % excess and ^{15}N excess pools did not differ significantly between selectively defoliated domi-

Table 1. Mean (SE) shoot mass (g), shoot nitrogen (%), ^{15}N atom % excess (%), and ^{15}N atom % excess pool (mg) for dominant species in undefoliated dominant: subordinate plant pairs and for subordinate species at three intensities of selective dominant plant defoliation in two sites. Dominant and subordinate species in site 1 are *Sorghastrum nutans* and *Schizachyrium scoparium*, respectively. Dominant and subordinate species in site 2 are *Schizachyrium scoparium* and *Bothriochloa laguroides*, respectively. Ratios are ^{15}N atom % excess and ^{15}N atom % excess pools for dominant: subordinate species in undefoliated pairs. Sample sizes were as follows: tillers plant^{-1} and shoot mass (n = 10); and shoot nitrogen (%), ^{15}N atom % excess and ^{15}N atom % excess pools (n = 5). Asterisk indicates ratios that are significantly (P < 0.05) different from 1:1.

Site	Species	Dominant plant defoliation intensity	Shoot mass (g)	Shoot nitrogen (%)	^{15}N atom % excess (%)	^{15}N atom % excess pool (mg)	^{15}N atom % excess ratio	^{15}N atom % pool ratio
Site 1	Dominant	0%	32.30 (8.94)	0.42 (0.03)	2.81 (0.51)	3.14 (1.08)	1.45 (0.30)	1.45 (0.40)
	Subordinate	0%	28.46 (5.95)	0.47 (0.03)	2.42 (0.73)	2.44 (0.62)		
		70%	23.18 (4.63)	0.49 (0.02)	2.93 (1.27)	2.50 (0.66)		
		90%	33.24 (6.00)	0.47 (0.04)	3.35 (0.86)	4.25 (0.92)		
Site 2	Dominant	0%	42.17 (10.33)	0.52 (0.06)	3.24 (0.25)	5.78 (1.21)	3.41 (1.54)*	3.49 (1.99)
	Subordinate	0%	50.09 (8.43)	0.50 (0.03)	1.73 (0.56)	3.94 (1.34)		
		70%	67.20 (10.09)	0.47 (0.02)	1.43 (0.14)	4.01 (0.62)		
		90%	49.83 (6.20)	0.52 (0.04)	1.43 (0.39)	4.44 (1.23)		

Table 2. Mean (SE; n = 5) shoot mass (g), shoot nitrogen (%), ^{15}N atom % excess (%), ^{15}N atom % excess pool (mg) and ratios of ^{15}N atom % excess and ^{15}N atom % excess pools for dominant: subordinate species in pairs after the first growth interval (40 days) following two intensities of uniform defoliation at two sites. Dominant and subordinate species are identified in Table 1. Shoot mass and percentage shoot nitrogen were used to calculate ^{15}N atom % excess pools. Asterisks indicate ratios that are significantly (P < 0.05) different from 1:1.

Site	Defoliation intensity	Species	Shoot mass (g)	Shoot nitrogen (%)	^{15}N atom % excess	^{15}N atom % excess pool (mg)	^{15}N atom % excess ratio	^{15}N atom % pool ratio
Site 1	70%	Dominant	8.60 (1.20)	0.99 (0.05)	6.91 (1.05)	5.99 (1.27)	1.99 (0.48)	3.42 (0.80)
		Subordinate	5.73 (1 .13)	0.97 (0.04)	3.84 (0.56)	2.10 (0.49)		
	90%	Dominant	4.58 (1.27)	0.93 (0.03)	8.59 (1.83)	4.26 (1.59)	2.28 (1.02)	3.47 (2.27)
		Subordinate	3.89 (0.70)	0.99 (0.07)	5.80 (1.57)	1.95 (6.45)		
Site 2	70%	Dominant	3.29 (0.76)	1.19 (0.03)	6.60 (1.98)	2.71 (0.94)	3.64 (1.03)*	5.03 (1.64)*
		Subordinate	1.93 (0.34)	1.54 (0.05)	1.93 (0.36)	0.51 (0.05)		
	90%	Dominant	4.85 (1.38)	1.38 (0.10)	4.48 (1.75)	2.62 (1.47)	1.50 (0.41)	6.22 (3.46)*
		Subordinate	1.81 (0.56)	1.52 (0.16)	2.95 (0.72)	0.78 (0.32)		

nants and dominants in the uniform defoliation treatments in either site (data not shown).

Discussion

These data indicate that herbivory tolerance was similar for dominant and subordinate species and that defoliation intensity had a greater influence on herbivory tolerance than did defoliation pattern. However, both defoliation intensity and pattern had a significant effect on tiller number per plant for *S. nutans* at site 1, but only defoliation intensity significantly affected this variable for *S. scoparium* at site 2. Shoot mass per plant was significantly affected by defolia-

tion intensity, but not pattern, for only *S. nutans* at site 1. Therefore, we failed to reject hypothesis one stating that dominant and subordinate grasses possess similar herbivory tolerance.

These data further demonstrate that the effect of defoliation on competitive ability was influenced by the intensity of interspecific competition within species pairs and perhaps by resource availability between the two sites. Selective defoliation of the dominant species did not significantly affect ^{15}N acquisition of either the dominant or the undefoliated subordinate neighbor at either site. However, uniform defoliation of the dominant: subordinate pairs produced a greater ^{15}N atom % excess in the dominant than subordinate species at the 70% defoliation inten-

sity at site 2. The 90% defoliation intensity produced a ^{15}N atom % excess ratio that did not significantly differ from 1:1, but ^{15}N atom % excess pools remained greater for the dominant compared to the subordinate neighbor. Therefore, we failed to reject hypothesis two stating that defoliation suppresses the competitive ability of dominant relative to subordinate species.

Dominant species exhibited pronounced reductions in tiller number per plant following defoliation compared to undefoliated plants in both sites, but undefoliated subordinate species were generally unresponsive to defoliation of the dominant species. Intense defoliation has previously been documented to substantially reduce tiller number in both dominant species (Vogel and Bjugstad 1968; Butler and Briske 1988). The large reduction in canopy mass of the dominant species following these severe defoliation intensities very likely decreased acquisition of both above- and belowground resources relative to undefoliated subordinate species (e.g. Caldwell et al. (1987)). However, selective defoliation of an individual dominant may have had a minimal influence on total diffuse competition experienced by subordinate plants in this investigation because plants adjacent to the dominant: subordinate pair were not defoliated (Tilman 1989; Wallace and Macko 1993). The size of grazed patches has previously been demonstrated to have an important effect on defoliation-competition interactions in plant communities (Semmartin and Oesterheld 1996). We anticipate that plant performance may have been enhanced in both the dominant and subordinate species, if a greater number of plants had been defoliated in the neighborhood in this investigation (e.g. Mueggler (1972)). In addition, below normal precipitation during the second half of the growing season, as well as the spring and summer of the previous year, very likely reduced plant growth and nitrogen acquisition in all species.

Selective defoliation of *S. nutans* reduced herbivory tolerance compared to uniform defoliation of the dominant: subordinate species pair on the basis of tiller number per plant. In contrast, selective defoliation of *S. scoparium* in site 2 did not modify herbivory tolerance compared to uniform defoliation of the dominant: subordinate species pair, including *B. laguroides*. Contrasting herbivory tolerance between the two dominant species following uniform defoliation inclusive of the subordinate neighbor is very likely a function of unique competitive intensities associated with different species pairs. *S. nutans* and *S.*

scoparium in the downslope site were apparently more equitable competitors than were *S. scoparium* and *B. laguroides* in the upslope site. These unique competitive interactions correspond with the designation of *S. nutans* and *S. scoparium* as late-seral species and *B. laguroides* as a mid-seral species (Diamond and Smeins 1985, 1988). This interpretation is consistent with the hypothesis that late-seral species have a greater competitive ability than mid-seral species (Wilson and Keddy 1986; Tilman and Wedin 1991; Peltzer et al. 1998).

The interpretation that unique competitive interactions between species pairs modified herbivory tolerance is also supported by the patterns of ^{15}N acquisition. Similar ratios of ^{15}N atom % excess for undefoliated dominant: subordinate species indicated that the dominant species were generally more effective in absorbing nitrogen from the soil than their subordinate neighbors, However, the ratio did not significantly differ from 1:1 in the *S. nutans*: *S. scoparium* pairs at either defoliation intensity indicating that both species acquired similar amounts of nitrogen when they were uniformly defoliated.

In contrast, the dominant on site 2, *S. scoparium*, acquired a greater amount of ^{15}N compared to the subordinate species, *B. laguroides*, in both undefoliated species pairs and in species pairs that were uniformly defoliated at the 70% intensity. Greater ^{15}N acquisition by *S. scoparium* demonstrates that the competitive ability of the dominant was greater than that of the subordinate species during a critical period of rapid growth. *S. scoparium* has previously been demonstrated to possess a greater rate of nitrogen absorption per unit root mass compared to an associated C_4 perennial grass, *Andropogon gerardii*, that is a dominant in tallgrass prairie (Derner and Briske 1999b). The most severe defoliation intensity reduced the competitive ability of *S. scoparium* relative to that of *B. laguroides* as indicated by a decrease in the ratio of ^{15}N atom % excess between these species so that it did not significantly differ from 1:1. However, severe uniform defoliation did not provide the subordinate species with a competitive advantage because ^{15}N acquisition by *S. scoparium* was not reduced below that of its subordinate neighbor as indicated by a ^{15}N atom % excess pool ratio that remained significantly greater than 1:1. These data highlight the importance of competitive ability, in addition to tolerance, in determining the outcome of defoliation-competition interactions (e.g. Mueggler (1972); Caldwell et al. (1987)).

Severe defoliation reduced both herbivory tolerance and competitive ability in the dominant species within the species pairs, but neither value was reduced below that of the subordinate species. The occurrence of similar herbivory tolerance among dominant and subordinate species indicates that selective herbivory is the critical process contributing to species replacement in mesic grasslands. However, selective herbivory suppressed the greater competitive ability, rather than the greater herbivory tolerance, of the dominant grasses in this experimental design. These results further demonstrate that interspecific competitive ability is of equal or greater importance than herbivory tolerance in regulating herbivore mediation of species composition (Calwell et al. 1985; Wallace and Macko 1993; Moretto and Distel 1997; Reader and Bonser 1998). However, both herbivory tolerance and competitive ability are species specific processes that will very likely show unique responses to various defoliation intensities and patterns. Additional comparative investigations are required before generalizations regarding the herbivory tolerance and competitive ability of dominant and subordinate species can be developed.

Greater competitive ability and similar herbivory tolerance of *S. nutans* and *S. scoparium* compared to subordinate grasses establishes these species as dominants in this grassland. Yet, both of these dominant species can be replaced by several mid-seral species, including *B. laguroides*, following intensive long-term herbivory (Dyksterhuis 1946; Launchbaugh 1955). This implies that chronic selective herbivory is required to suppress competitive ability and, to a lesser extent, herbivory tolerance of the dominant species to shift the competitive advantage to the subordinate species. The intensity of herbivory at which the competitive advantage shifts from dominant to subordinate species represents a herbivory resistance threshold (Briske 1996) that must be surpassed prior to the occurrence of compositional changes in plant communities.

Acknowledgements

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