When Competition Does Not Matter: Grassland Diversity and Community Composition

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abstract: We examined whether the intense root competition in a rough fescue grassland plant community in central Alberta, Canada, was important in structuring plant species diversity or community composition. We measured competition intensity across gradients of species richness, evenness, and community composition, using pairs of naturally occurring plants of 12 species. One plant in each pair was isolated from neighbors to measure competition; community structure and environmental conditions were also measured at each pair. We used structural equation modeling to examine how competition influenced community structure. Competition intensity was unrelated to species richness and community composition, but increased competition intensity was associated with a slight decline in evenness. Size-symmetric root competition was probably unimportant in structuring this plant community because there are no feedback mechanisms through which size-symmetric competition can magnify small initial differences and eventually lead to competitive exclusion. In plant communities with little shoot competition, competition and community structure should be unlinked regardless of competition intensity. In more productive systems, we propose that interactions between root and shoot competition may indirectly structure communities by altering the overall asymmetry of competition.

Keywords: competition, community structure, importance, intensity, root, shoot.

Competition for resources in limited supply is one of the key processes determining the growth, survival, and fecundity of individual plants, yet after nearly a century of research, the role of competition in structuring the diversity and composition of plant communities remains poorly understood (e.g., Clements et al. 1929; Goldberg and Barton 1992; Gurevitch et al. 1992; Grime 2001; Keddy 2001; Aarssen and Keogh 2002; Schenk 2006). Size-asymmetric competition for light plays an obvious role in structuring plant communities because larger plants can shade and competitively exclude smaller neighbors (Weiner 1986; Schwinning and Weiner 1998; Keddy 2001). In many communities, however, roots make up the majority of the plant biomass (Jackson et al. 1996; Mokany et al. 2006), and the dominant form of competition is belowground (Casper and Jackson 1997). Many studies have documented variation in root competition intensity along environmental and community gradients, but whether that variation is important to structuring plant community diversity or composition has rarely been examined (Welden and Slauson 1986; Cahill 2003; Rajaniemi et al. 2003; Schenk 2006).

The "intensity of competition" is defined as the degree to which competition for a limited resource reduces plant performance below the physiological maximum achievable in a given environment, and "importance" is the effect of competition relative to other environmental conditions (Welden and Slauson 1986). More broadly, competition can be considered important if variation in the intensity of competition is the cause of predictable variation in plant community structure. Even though Welden and Slauson (1986) were clear that the two measures of competition are not necessarily related, the assumption that intensity and importance are highly correlated pervades the literature (Grace 1991; Brooker et al. 2005).

A positive relationship between the intensity and importance of shoot competition is well established (e.g., Grime 2001; Keddy 2001), but a wide range of evidence suggests that root competition and community structure may be generally unlinked. Unlike shoot competition, there are few consistent relationships between the intensity of root competition and plant root biomass (e.g., Belcher et al. 1995; Peltzer et al. 1998; Cahill 1999; Cahill and Casper 2000; Lamb et al. 2007). Similarly, in rough fescue

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grasslands, there are few links between root biomass or competition intensity and diversity (Cahill 2003; Lamb 2008). These studies suggest that root competition may play only a small role in structuring plant community diversity and composition in many communities, but this hypothesis has never been comprehensively studied.

Plant community structure is generally under the control of complex networks of interaction among factors ranging from soil and environmental conditions to disturbance regimes, herbivory, productivity, litter, and standing-shoot biomass (e.g., Grace and Pugesek 1997; Gough and Grace 1999; Grace 1999; Grace and Jutila 1999; Aarssen 2004; Weiher et al. 2004; Clark et al. 2007; Lamb 2008). Some studies of the networks influencing community structure have made inferences about the role of shoot competition in structuring plant communities, but none have measured competition intensity directly. Grace and Jutila (1999), for example, found that aboveground biomass had negative effects on species richness in ungrazed but not grazed plots, suggesting that grazing had reduced the intensity of shoot competition. Explicitly incorporating competition into these networks of environmental and community factors is crucial for a full evaluation of the importance of competition in structuring plant communities.

In this study, we explore whether competition is an important factor controlling plant community diversity and composition in a rough fescue grassland by including competition intensity in a structural equation model (Shipley 2000; Grace 2006) relating diversity and composition to environmental conditions and plant community biomass. This community is an ideal one in which to examine these hypotheses because root competition has been shown to be the dominant form of competition in this community, and plant community structure changes along gradients of nitrogen and water availability, the two key limiting soil resources (Lamb et al. 2007; Lamb 2008). We place the results of this study into a more general framework by showing how the overall asymmetry of competition may be key to understanding how competition may structure the diversity and composition of plant communities.

Methods

Field Site

The study area is in a 50-ha field at the University of Alberta Research Ranch near Kinsella, Alberta, Canada (53°05′N, 111°33′W), in the Aspen Parkland Ecoregion (Sims and Risser 2000). The study site is a savanna-type habitat containing a mixture of trembling aspen (*Populus tremuloides*) forest, wetlands, and rough fescue (*Festuca hallii*) prairie. This study was carried out in the largest section of the field (∼200 m × 350 m), where fescue prairie was the dominant plant community type. Plant biomass at the field site is limited by both nitrogen and water availability, and belowground competition is intense (Lamb 2007, 2008; Lamb et al. 2007). The site historically had been lightly grazed by cattle in the fall, but grazing was halted three years before the beginning of this experiment. Soils at the site are dominantly classified as thin orthic black chernozems, or grassland soils with thin organic-matter-enriched topsoil horizons, over glacial till (Howitt 1988; Soil Classification Working Group 1998).

Experimental Design

Total competition intensity, plant community biomass, diversity, species composition, and environmental variables were measured at 192 locations in the study field (table 1). Competition intensity was measured as the total effect of neighbors on the performance of an individual plant (Keddy 2001). Pairs of established plants of 12 species (*Achillea millefolium* L., *Artemisia frigida* Willd., *Artemisia ludoviciana* Nutt., *Carex stenophylla* Wohl., *Cerastium arvense* L., *Festuca hallii* (Vasey) Piper., *Galium boreale* L., *Geum triflorum* Pursh, and *Hesperostipa curtiseta* (A.S. Hitchc., *Poa pratensis* L., *Rosa arkansana* Porter, and *Solidago missouriensis* Nutt.) were used to measure competition intensity. These species account for more than 75% of total plant cover in this system (Lamb 2007). The use of established plants from multiple species differs from studies where competition intensity is measured by planting seedlings of a phytometer species (Keddy 2001). We chose this approach because the competition experienced by transplanted seedlings is a very poor indicator of the competition experienced by established perennial plants in this system (Lamb and Cahill 2006).

Twenty pairs of established plants of each species were identified between May 1 and May 7, 2004, for a total of 240 pairs. Plant pairs were selected by searching the ground for two plants of the same species that were of similar size and separated by ∼1 m. The pairs were distributed across the largest (∼200 m × 350 m) patch of fescue prairie at the study site on a variety of topographic positions, including south-facing slopes and level ground. Clumping in the distribution of pairs was unavoidable due to the presence of several small aspen stands in the field, but efforts were made to ensure that the pairs belonging to each species were as widely distributed as possible. To measure the intensity of competition, one plant in each pair was randomly selected for neighbor removal. The difference between the performance of the plant without competition (neighbors) and the plant with competition is a standard measure of competition intensity (Keddy 2001). Neighboring shoots were clipped in a 12–15-cm

Table 1: Observed variables included in the structural equation models

Variable	Mean (±SD)	Range	Description
Competition intensity	−.33 ± 1.09	−4.19–5.86	Log response ratio: $\ln RR = \ln(RGR_{AN}/RGR_{NN})$ (Cahill 1999; Hedges et al. 1999). Positive values indicate facilitation while increasingly negative values indicate increasing competition intensity. The lnRR assumes that competitive ability does not vary with plant size (Lamb et al. 2006), but the assumption was met since the relationships between RGR_{AN} and RGR_{NN} for each species were linear.
Species competitive ability	.08 ± .24	−.37–.41	The slope of a linear regression between RGR_{AN} and RGR_{NN} (Lamb et al. 2006). Increasing slopes indicate increasing competitive ability or species that achieved an increasing proportion of their potential growth (RGR_{NN}) when competing with neighbors. Negative slopes indicate facilitation.
Species richness	3.8 ± .36	3–4.58	Number of vascular plant species observed in .5 × .5-m quadrats in July 2004. Square-root transformed.
Species evenness	.84 ± .04	.71–.92	Pielou's *J* (Pielou 1969). Calculated from percent cover data. Not transformed.
Community composition	0 ± 1	−2.97–2.61	A single NMS ordination axis (McCune and Grace 2002) based on percent cover data and calculated using PC-Ord 4 (McCune and Mefford 1999). The axis represents a gradient from grassland dominated by *Poa pratensis* and *Galium boreal* to grassland dominated by *Hesperostipa curtiseta*. See the appendix in the online edition of the *American Naturalist* for details of the analysis.
Shoot biomass ($g\ m^{-2}$)	5.6 ± .29	4.73–6.35	Aboveground live biomass clipped from a .2 × .5-m quadrat. Ln transformed.
Root biomass ($g\ m^{-2}$)	6.88 ± .42	5.21–8.09	Root biomass washed from a 5.3-cm-diameter × 12-cm-deep core. Ln transformed.
Light interception	.83 ± .21	.21–1.38	Percentage of the total photosynthetically active radiation intercepted by aboveground live biomass and litter. Arcsine transformed.
Soil moisture (%)	.2 ± .03	.13–.29	Relative soil moisture (average of 4 measures at each plot). Arcsine transformed.
Topographic position	.67 ± .02	.55–.74	Topographic position as indicated by incident radiation. Calculated from slope and aspect following McCune and Keon (2002). Not transformed.
Total nitrogen (%)	.5 ± .13	.21–1.37	Total nitrogen in the upper 12 cm of the soil. Arcsine transformed.
Nitrogen treatment			0/1 indicates whether or not a plot received the nitrogen addition treatment.

Note: Scatterplots of the bivariate relationships among these variables can be found in the appendix in the online edition of the *American Naturalist*, and the complete raw data set is available in Lamb (2007). RGR_{AN} = relative growth rate with competition from neighbors. RGR_{NN} = relative growth rate without competition from neighbors.

radius, and the remnants were brushed with glyphosate herbicide (Roundup) to prevent regrowth. Herbicide was not allowed to touch the focal plant shoots, and it is unlikely that there were any effects of the herbicide on focal plant roots because glyphosate is highly immobile and rapidly degrades in soil (Sprankle et al. 1975). Given the low average standing shoot biomass (259 g m^{-2} ± 78 SD; Lamb 2007) at this site, the 12–15-cm radius was sufficient to prevent shading by neighboring plants. Root and rhizome connections around both focal plants in each pair were severed in the same radius to a depth of 15 cm. Roots and rhizomes were severed around both the control and clipped focal plants to control for any negative effects of the severing treatments on the focal plants. Decomposition of the severed roots probably had little effect on the performance of the focal plants (McLellan et al. 1995). To reduce root reestablishment by neighbors, shoot regrowth within the clipped zone was reclipped at 2-week intervals throughout the experiment. Root severing was not repeated, to avoid disrupting focal plant root foraging patterns. This design results in a reduction, rather than elimination, of root competition. Given that root competition in this system is an order of magnitude stronger than shoot competition (Lamb et al. 2007), any improvements in plant performance in the neighbor-removal treatment can be attributed to root competition. Finally, an experimental fertilization treatment was applied to increase the range of plant biomass and competition intensity in this study because soil nitrogen is one of the major limiting resources in rough fescue grassland (Lamb 2007, 2008), and fertilization can alter the intensity of root competition (Lamb et al. 2007). Half of the pairs from each species were randomly selected to receive 5.4 g m^{-2} NH_4-NO_3, half applied on May 15 and half on June 30). This rate of fertilization was much higher than background nitrogen levels in this system (ammonium levels range between 0.2 and 1 g m^{-2}; B. Attaeian, J. F. Cahill, and S. X. Chang, unpublished data). Fertilizer was applied to both the focal plants and to the surrounding vegetation.

The aboveground biomass of each focal plant was harvested when other plants of the same species in the fields had begun to senesce. *Cerastium* was harvested on July 9 (58 growing days); *Carex*, *Festuca*, and *Galium* were harvested on August 12 (92 days); *Achillea*, *Hesperostipa*, and *Poa* were harvested on August 13 (93 days); *Artemisia ludoviciana*, *Solidago*, *Rosa*, and *Geum* were harvested on August 31 (121 days); and *Artemisia frigida* was harvested on September 8 (129 days). Forty-eight pairs were excluded because one of the focal plants had died or experienced severe herbivory (estimated loss of more than 10% of total leaf area), leaving 192 pairs (100 control and 92 with nitrogen added).

Environmental and community variables were measured at each sampling location in mid-July, the period when live shoot biomass peaks in fescue grasslands (Coupe 2003). The percent cover of all vascular plant species was recorded by eye in a 0.5 × 0.5-m quadrat centered on the control (unclipped) focal plant. Standing shoot biomass (g m^{-2}) was measured by clipping all standing biomass in a 20 × 50-cm quadrat placed between the control and clipped focal plants. Care was taken to ensure that the clipping did not disturb any plants within 50 cm of the control plant. Root biomass (g m^{-2}) was measured by washing the roots from a 5.3-cm diameter root core taken from the center of the plot used to measure shoot biomass and to a depth of 12 cm. Soil percentage of total nitrogen was measured in soil sieved from the root biomass samples. The sieved soil was dried and ground, and a subsample was analyzed using a Leco FP-428 N-Determinator (Leco, St. Joseph, MI). Relative soil moisture was sampled at four locations around the focal plants (~50 cm away from the control plant in each direction) using a Hydrosense moisture probe (Campbell Scientific, Logan, UT). Photosynthetically active radiation was measured once above the plant canopy and immediately after at the soil surface using an Accu-Par light meter (Decagon, Pullman, WA).

Statistical Analysis

Mixed-effects models were used to examine directly the bivariate relationships between competition intensity and species richness, evenness, and community. If competition is an important factor structuring this community, then significant bivariate relationships should be expected. In each analysis, the fit of a model with a linear relationship was compared with the fit of a null model with only an intercept and a quadratic model using the “lmer” function in the R package (R Development Core Team 2006). “Species” was included as a random term in each of these models.

The importance of competition is defined as the effect of competition relative to other environmental conditions (Welden and Slauson 1986). We used structural equation modeling (SEM) with observed variables (path modeling) to place the relationships between competition intensity and community structure within a wide suite of environmental conditions known to influence both competition intensity and community structure in fescue grassland (Lamb 2007, 2008; Lamb et al. 2007). SEM allows the network of direct and indirect theoretical causal relationships between variables to be specified as well as reciprocal effects where two variables each exert a causal influence on the other (Shipley 2000; Grace 2006). Structural equation modeling is particularly well suited to experimental studies where a suite of intercorrelated variables may be affected by an experimental treatment (Grace 2006). The primary goals of these analyses were to (1) evaluate the effects of competition intensity on measures of community structure, including species richness, evenness, and composition, and (2) to place the relationship between competition intensity and community structure within the overall network of interactions controlling community structure in rough fescue grassland. SEM can be used in either a confirmatory or exploratory mode (Grace 2006). In a confirmatory application, the model is specified based on prior theoretical knowledge and is tested to determine whether the model adequately fits the data. In an exploratory application, such as this study, the initial theoretical model may be altered to improve the fit between model and data.

Path models were developed to relate species richness, evenness, and community composition to competition intensity, neighborhood biomass, and environmental conditions. The initial path-model structure is shown in figure 1, and the variables are described in table 1. Figures showing the bivariate relationships among variables are shown in the appendix in the online edition of the *American*

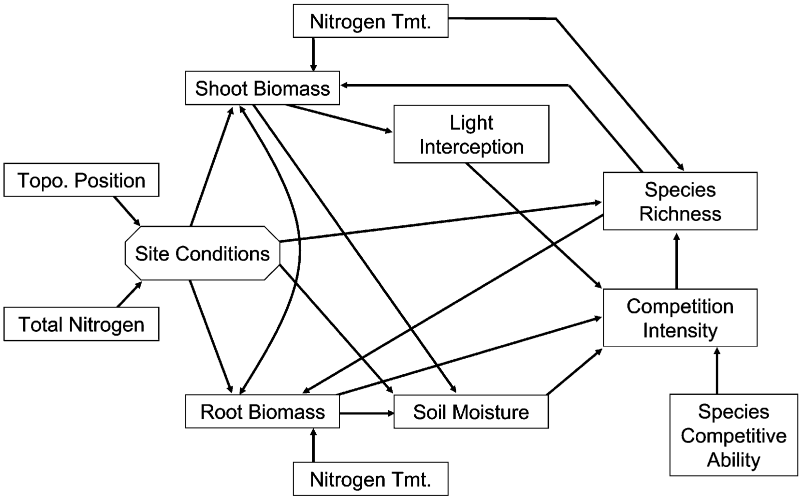


Figure 1: Initial structural equation model.

Naturalist, and the raw data are available in an article by Lamb (2007). We chose to model richness, evenness, and composition separately because a single SEM including all three variables would be overly complex. We chose not to use the three descriptors of community structure as indicators of a latent community structure variable because they were only weakly correlated with each other (richness vs. eveness: $r = 0.207$, $P = .003$; richness vs. composition: $r = -0.058$, $P = .427$; evenness vs. composition: $r = 0.066$, $P = .359$). Finally, apart from a mathematical dependency between richness and evenness (Pielou 1969), there is little theory to guide the description of the causal relationships among the three variables. We chose to model the observed variables directly rather than using the observed variables as indicators for latent variables because the resulting model would have had only a single indicator variable per latent. Two environmental variables (topographic position and soil total nitrogen) served as indicators for a composite variable summarizing site conditions. The composite variable was included to simplify the model structure (Grace 2006; Grace and Bollen, forthcoming).

In the initial model, site conditions were presumed to directly affect shoot and root biomass, soil moisture, and community structure because less exposed locations with higher soil organic matter are likely to support more plant biomass and a plant community dominated by different species than more exposed slopes (Lamb 2007). The nitrogen treatment was presumed to directly affect root and shoot biomass because plant biomass can be nitrogen limited in this system (Lamb 2007). Nitrogen addition is also known to indirectly affect plant community structure through effects on biomass and litter (Lamb 2008). Shoot biomass directly influenced light interception, while both root and shoot biomass affected soil moisture. Both root and shoot biomass affected moisture because increased root length and leaf area can increase transpiration rates. Competition intensity was a function of species competitive ability, soil moisture, light interception, and root biomass. Species competitive ability was included to control for differences in competitive ability between the 12 species used in this study. The path from light interception to competition intensity represented competition for light, the paths from soil moisture to competition intensity represented competition for water, and the path from root biomass to competition intensity represented competition for nitrogen. Since available nitrogen was not measured directly, we included the path from root biomass to competition as a surrogate. Finally, paths from community structure to above- and belowground biomass were included because those variables can be a function of the species present in the community (Aarssen 2004).

This initial model configuration differs from most other structural equation models that have related environmental conditions to community biomass and diversity. Those models included direct paths from biomass, light interception, and soil resources to diversity. The strength of these paths was generally interpreted as representing the effects of competition on community structure. Those paths are not necessary in our model, however, because competition intensity is directly included.

Each bivariate relationship represented by an arrow in the initial path model was examined using generalized linear models to identify potentially nonlinear relationships. In each analysis, the fit of a model with a linear relationship was compared with the fit of a model with a quadratic relationship using the "glm" function in the R package (R Development Core Team 2006). No potentially nonlinear relationships were found.

The structural equation models were fit using M-plus 4.1 (Muthén and Muthén 2006). Competition intensity was nested within species using the "TYPE = TWOLEVEL" option with a species-level covariate (average competitive ability) affecting only competition intensity. TYPE = TWOLEVEL creates a model where species competitive ability is treated as a random term rather than a fixed effect (hierarchical model). The χ^2 test of model fit was used to determine whether the fit between model and data was adequate ($P > .05$). The χ^2 test of model fit is recommended since a nonsignificant result is a strong indication of an adequate fit between model and data (Grace 2006).

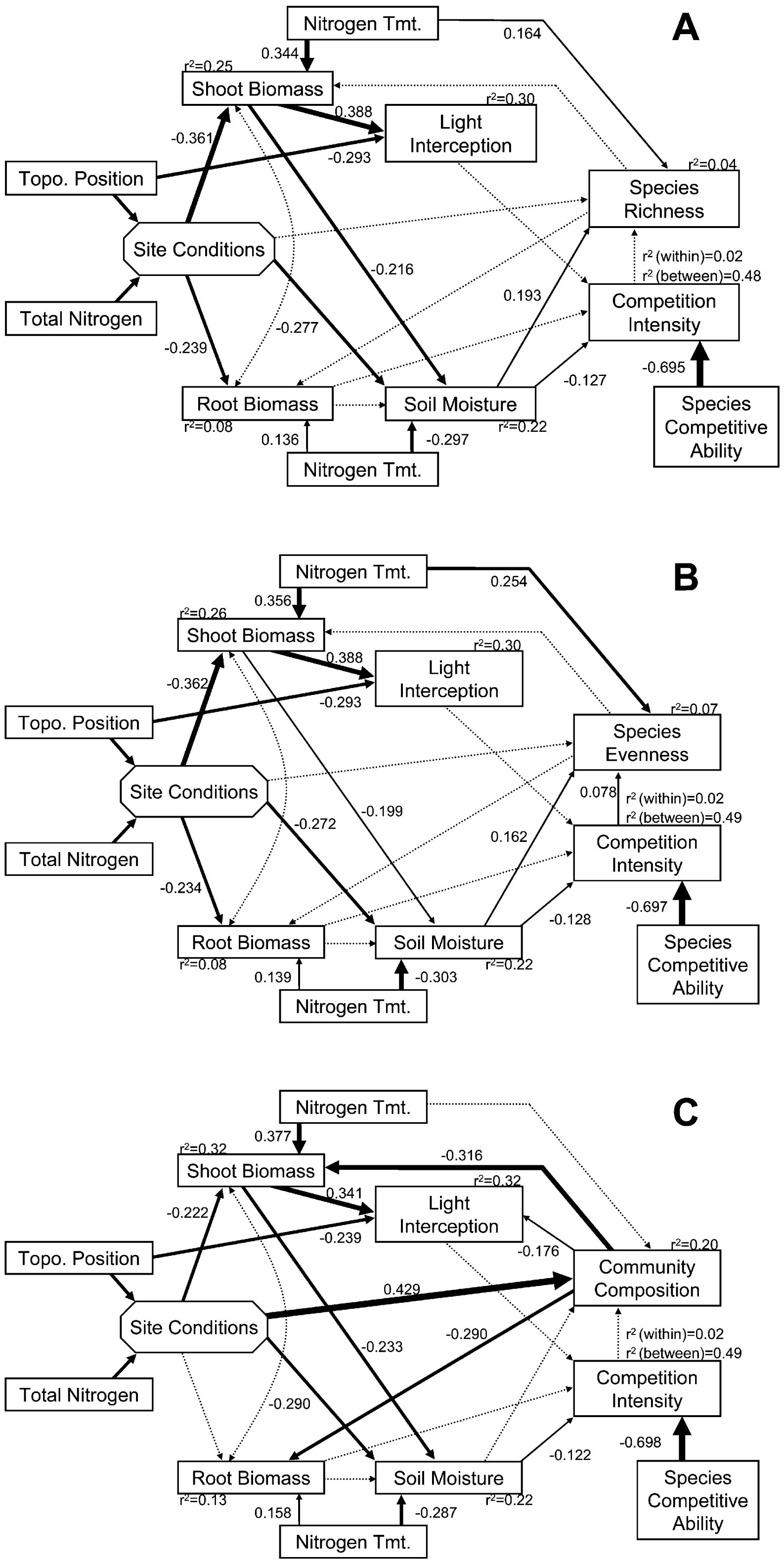
The fit between the initial species richness model and data was not adequate ($\chi^2 = 86.111$, df = 16, $P < .001$). Modification indexes suggested the inclusion of a direct path from topographic position to light interception, a path from nitrogen treatment to soil moisture, and a path from soil moisture to species richness. The fit of the modified model was adequate ($\chi^2 = 14.402$, df = 12, $P = .276$). The initial evenness and composition models were based on the modified species richness model. Both of these models failed to converge. Error messages indicated that the problem was due to the starting values for the path from total nitrogen to the site composite variable. Fixing this parameter to the value of that path in the species richness model allowed convergence. The fit of the evenness model was adequate ($\chi^2 = 9.406$, df = 13, $P = .742$), but the fit of the composition model was not adequate ($\chi^2 = 28.237$, df = 13, $P < .008$). The addition of a path from community composition to light interception resulted in a model with adequate fit ($\chi^2 = 16.266$, df = 12, $P = .179$). Path coefficient significance was evaluated by dividing each coefficient by its standard error. The resulting value follows a t distribution, allowing P values to be calculated. Given the exploratory nature of these analyses, coefficients with $P < .100$ were considered significant. Nonsignificant paths were retained in the final model. Many of the path coefficients changed between the three models. These changes occurred because the community structure variables had varying influences on root and shoot biomass, which in turn affected the coefficients of other variables with paths to root and shoot biomass.

An important caveat on these analyses is that the number of parameters in the models exceeded the number of species on which competitive ability was measured. This situation can lead to unreliable estimates for the standard errors of model parameters (Muthén and Muthén 2006). To ensure that these potentially unreliable estimates did not affect our interpretation, we reran the final models without the species-level covariate of competitive ability. The fit of all three reduced models was adequate, and variation in the standard errors between models resulted in only one change in the paths deemed significant. The path from competition intensity to evenness was significant in the full model ($t = 1.962$, df = 192, $P = .051$) but not in the reduced model ($t = 1.642$, df = 192, $P = .102$). Since the P value for the path in the reduced model was very close to the cutoff value for significance ($P = .100$), we chose to accept the significant result of the full model. The standard errors reported in this article are from the full models.

Results

Competition intensity ranged from severe competitive suppression to strong facilitation (table 1). There were no significant bivariate relationships between competition intensity and species richness ($\chi^2 = 0.000$, df = 1, $P = 1.000$), evenness ($\chi^2 = 0.569$, df = 1, $P = .451$), or community composition ($\chi^2 = 0.769$, df = 1, $P = .380$). The final structural equation models for species richness ($\chi^2 = 14.402$, df = 13, $P = .276$), evenness ($\chi^2 = 9.406$, df = 13, $P = .742$), and community composition ($\chi^2 = 16.266$, df = 12, $P = .179$) adequately fit these data (fig. 2). The full model results are included in the appendix. Competition intensity was strongly influenced by phytometer species identity, and it declined with increased soil moisture but was not dependent on any other variables. Competition intensity did not affect species richness or community composition, but an increase in competition intensity was weakly associated with a decline in evenness. Environmental conditions strongly controlled shoot and to a lesser extent root biomass, and a combination of environmental conditions and plant biomass exerted strong control on light interception and soil moisture. Both species richness and evenness were positively influenced by the nitrogen addition treatment and higher soil moisture but were otherwise not significantly related to other parameters. Plant community composition, however, was tightly linked to both environmental conditions

Figure 2: Structural equation model results for species richness (*A*), species evenness (*B*), and plant community composition (*C*). Standardized path coefficients are shown in the figure, and r^2 values are listed for each dependent variable. The variance explained for competition intensity is separated into that due to species competitive ability (between) and that due to the other variables in the model (within). Paths that were not significant ($P \geq .10$) are indicated by dotted arrows.


A
Nitrogen Tmt.
0.164
0.344
r²=0.25
Shoot Biomass
0.388
r²=0.30
Light Interception
-0.361
-0.293
r²=0.04
Topo. Position
Species Richness
Site Conditions
-0.216
r² (within)=0.02
r² (between)=0.48
0.193
Competition Intensity
Total Nitrogen
-0.277
-0.239
-0.127
-0.695
Root Biomass
Soil Moisture
Species Competitive Ability
r²=0.08
r²=0.22
0.136
-0.297
Nitrogen Tmt.
B
Nitrogen Tmt.
0.254
0.356
r²=0.26
Shoot Biomass
0.388
r²=0.30
Light Interception
-0.362
-0.293
r²=0.07
Topo. Position
Species Evenness
Site Conditions
0.078
r² (within)=0.02
r² (between)=0.49
-0.272
-0.199
0.162
Competition Intensity
Total Nitrogen
-0.234
-0.697
-0.128
Root Biomass
Soil Moisture
Species Competitive Ability
r²=0.08
r²=0.22
0.139
-0.303
Nitrogen Tmt.
C
Nitrogen Tmt.
0.377
-0.316
r²=0.32
Shoot Biomass
r²=0.32
0.341
Light Interception
-0.222
-0.239
-0.176
r²=0.20
Topo. Position
Community Composition
0.429
Site Conditions
-0.233
-0.290
r² (within)=0.02
r² (between)=0.49
Competition Intensity
Total Nitrogen
-0.290
-0.122
-0.698
Root Biomass
Soil Moisture
Species Competitive Ability
r²=0.13
r²=0.22
0.158
-0.287
Nitrogen Tmt.

and plant biomass. The r^2 values for the dependent variables (fig. 2) were very low, indicating that the most important factors controlling community structure in this system were missing from these models.

Discussion

Root Competition and Plant Community Structure

The intensity of competition in rough fescue grassland was unrelated to species richness and composition, but more intense competition was weakly associated with reduced evenness. Competition in this community is primarily belowground (Lamb et al. 2007), so these results raise serious questions about the role of competition in structuring low-stature plant communities such as dry grasslands, deserts, and alpine and arctic tundra. There is no doubt that root competition is intense in such communities (e.g., Casper and Jackson 1997; Peltzer et al. 1998; Keddy 2001; Cahill 2003; Mitchell 2006; Lamb et al. 2007), but if that competition has no predictable consequences for plant community structure, then it is not important (Welden and Slauson 1986). Our finding that root competition appears to be largely unimportant for plant community structure is consistent with the lack of consistent relationships between root biomass and root competition intensity (e.g., Belcher et al. 1995; Peltzer et al. 1998; Cahill 1999, 2002; Lamb et al. 2007). Our findings are also consistent with the lack of relationships between diversity and both root competition intensity (Cahill 2003) and root biomass (Lamb 2008).

The only significant effect of competition on community structure was for a slight decline in evenness associated with increased competition intensity. This pattern is consistent with the view that, in the absence of severe abiotic stresses or increased predation, an increase in evenness indicates a reduction in the intensity of competition for a limiting resource (Cotgreave and Harvey 1994; Keddy 2001). A long-term increase in the dominance of certain species with more intense competition could lead to changes in species richness and community composition. However, given the extremely small magnitude of the competition—evenness path (0.078) and the low explanatory power of this model ($r^2 = 0.070$)—it is unlikely that this mechanism is of great importance in structuring rough fescue grasslands.

Why should intense root competition, capable of reducing individual plant performance by an order of magnitude or more (Lamb et al. 2007), have so little impact on plant community structure? Root competition is generally thought to be size symmetric (e.g., Weiner 1986; Schwinning and Weiner 1998; Cahill and Casper 2000; von Wettberg and Weiner 2003). In size-asymmetric competition, such as for light, competitive exclusion occurs because a slight advantage in size allows the larger plant to capture a disproportionate fraction of the available light. This advantage leads to positive feedback where the larger plant can grow faster and gain an even greater proportion of the resource pool (Weiner 1986; Keddy 2001). In contrast, there are no feedback mechanisms in size-symmetric root competition that can magnify small initial differences. Without a feedback mechanism, all of the plants competing symmetrically for a limiting resource experience proportionally similar reductions in performance rather than the selective exclusion of certain species or individuals.

This study provides direct experimental support for the inferences made in previous studies that size-symmetric root competition among established adult plants is unlikely to strongly affect plant community structure (Cahill 2003, Lamb et al. 2007; Lamb 2008). This study does not, however, provide any information on the effects that root competition from established plants may have on seedling germination and establishment. The regeneration niche can be a strong filter determining which species from the regional species pool can establish in a community (Grubb 1977). Seedling and adult plants can also have very different competitive abilities (Lamb and Cahill 2006), leaving open the possibility that the dynamics of competition may be very different in the aftermath of a disturbance. Root competition may prevent some species from entering the community, even if, as adults, they are strong competitors. Finally, small-scale variation in the spatial distribution of competition intensity may leave refuges of low competition intensity that allow poor competitors to establish (Cahill and Casper 2002; Hölscher et al. 2002). The effects of root competition from established plants on the regeneration niche and whether those effects on establishment success are important for plant community structure need further evaluation.

The Asymmetry of Competition and Plant Community Structure

Both this study and that of Cahill (2003) have shown that intense root competition can have little impact on community structure, but instances where root competition was important for community structure have been observed (Rajaniemi et al. 2003). Rajaniemi et al. (2003) found that root competition had no effect on diversity in unfertilized artificial communities but a negative effect in fertilized treatments. Productivity, light interception by vegetation, and presumably shoot competition intensity increased with fertilization in that study, suggesting that root competition may become important in communities where both root and shoot competition are strong.

We propose here that, while root competition alone may be generally unimportant for plant community structure, root competition may indirectly structure plant communities through interactions between root and shoot competition. Root and shoot competition are not independent, because each plant is a single integrated organism, and the intensity of root competition can determine whether or not a plant is able to reach the canopy to succeed in shoot competition (Cahill 1999, 2002). Symmetric root competition may indirectly influence community structure if it affects the outcome of size-asymmetric shoot competition. The overall asymmetry of the competition a plant experiences, a function of both the intensity of shoot competition and the strength of root-shoot competition interactions, may thus provide a mechanism to integrate the effects of both root and shoot competition on plant community structure.

Mechanisms Controlling Plant Community Structure in Rough Fescue Grasslands

The structural equation models in this study leave the mechanisms structuring rough fescue grasslands unexplained. Structural equation models routinely return r^2 values between 0.24 and 0.60 for species richness and evenness (e.g., Grace and Pugesek 1997; Grace 1999; Grace and Jutila 1999; Weiher et al. 2004; Lamb 2008). This study is a conspicuous exception (species richness: $r^2 = 0.040$; evenness: $r^2 = 0.070$; community composition: $r^2 = 0.197$), indicating that important explanatory variables were missing from the model. The r^2 for community composition was higher largely because site conditions determined the extent of the two major grassland communities at the site. Grassland dominated by *Poa pratensis* were found on flatter sites and north-facing slopes, while *Hesperostipa curtiseta*–dominated grasslands were common on south-facing slopes.

Factors not included in the models that could be important in structuring this community include site history, herbivory, seed limitation, and random (neutral) patterns. Site history is probably important because there was a strong positive effect of initial species richness on final species richness following a 3-year nitrogen, water, and shade manipulation experiment (Lamb 2008). There may be significant stochastic or neutral elements to the structure of this community at the small scale (0.5 × 0.5-m plots) measured in this study (Adler et al. 2007). Insect herbivores are probably unimportant, because a long-term insect-suppression experiment resulted in few changes in plant community structure (Coupe 2003); a long-term study examining the influence of native and introduced vertebrate herbivores in this community is currently under way. Other potentially important processes that were unmeasured or imperfectly measured include the role of litter, disturbance, and seed limitation (Facelli and Pickett 1991; Turnbull et al. 2000; Lamb 2008).

Conclusion

This study demonstrates that root competition is unlikely to play an important role in structuring plant community diversity or composition in rough fescue grassland. It is surprising that an ecological process that has such a severe impact on individual plants should have so little effect on overall community structure. We propose that by integrating root and shoot competition intensity into the overall symmetry of competition, we can predict when competition is likely to be important in structuring plant communities. Root competition may not be directly important to structuring plant communities, but root competition can be indirectly important if interactions between root and shoot competition determine which plants can succeed in shoot competition.

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