DIRECT AND INDIRECT CONTROL OF GRASSLAND COMMUNITY STRUCTURE BY LITTER, RESOURCES, AND BIOMASS

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Abstract. Multiple factors linked through complex networks of interaction including fertilization, aboveground biomass, and litter control the diversity of plant communities. The challenge of explaining plant diversity is to determine not only how each individual mechanism directly influences diversity, but how those mechanisms indirectly influence diversity through interactions with other mechanisms. This approach is well established in the study of plant species richness, but surprisingly little effort has been dedicated toward understanding the controls of community evenness, despite the recognition that this aspect of diversity can influence a variety of critical ecosystem functions. Similarly, studies of diversity have predominantly focused on the influence of shoot, rather than root, biomass, despite the fact that the majority of plant biomass is belowground in many natural communities. In this study, I examine the roles of belowground biomass, live aboveground biomass, litter, and light availability in controlling the species richness and evenness of a rough fescue grassland community using structural equation modeling. Litter was the primary mechanism structuring grassland diversity, with both richness and evenness declining with increasing litter cover. There were few relationships between shoot biomass, shading, and diversity, and more importantly, no relationship between root biomass and diversity. The lack of relationship between root biomass and species richness and evenness suggests that, even though root competition in grasslands is intense, belowground interactions may not play an important role in structuring community diversity or composition.

Key words: competition; diversity; evenness; fertilization; litter; root biomass; SEM; shoot biomass; species richness; structural equation modeling.

INTRODUCTION

Understanding the mechanisms that control plant diversity is a central goal of community ecology. Numerous studies have identified important influences on diversity ranging from soil and environmental conditions to disturbance regimes, herbivory, productivity, and standing biomass (e.g., Al-Mufti et al. 1977, Facelli and Pickett 1991, Foster and Gross 1998, Grace 1999, Xiong and Nilsson 1999, Gross et al. 2000, Grime 2001, Keddy 2001, Mittelbach et al. 2001, Rajaniemi 2003, Aarssen 2004, Crawley et al. 2005, Balvanera et al. 2006, Gillman and Wright 2006, Adler and Levine 2007). While much is known about the net effects that individual factors have on diversity, it is becoming clear that in most plant communities diversity is actually controlled by multiple factors linked through complex networks of interaction (Grace 1999). Thus the problem of explaining diversity is not one of identifying which of several competing explanations is most important in a particular community, but rather determining how each mechanism affects diversity both directly and indirectly.

This problem is challenging because interactions among mechanisms mean that most of the important variables measured in a field study will be intercorrelated. Some factors may be a part of causal relationships influencing diversity, while others can be without any importance beyond a correlation with a third factor that does have a causal influence on diversity (Grace 1999, 2006). There can even be hidden interactions where a factor with no net impact on diversity can be involved in multiple mechanisms with opposite effects on diversity (e.g., Grace and Jutila 1999).

A number of recent studies have taken a holistic approach to examine the controls on plant diversity in a range of communities including coastal wetlands, grasslands, and shrublands (Grace and Pugesek 1997, Gough and Grace 1999, Grace and Guntenspergen 1999, Grace and Jutila 1999, Grace et al. 2000, Weiher et al. 2004, Mancera et al. 2005, Grace and Keeley 2006). These studies used structural equation modeling (SEM) to explicitly evaluate the causal relationships among multiple interacting variables that together affect diversity (Shipley 2000, Grace 2006). A number of important generalities emerge from these studies. (1) Species richness was directly affected by either aboveground standing biomass or a variable highly correlated with biomass such as light interception by vegetation. Similar to the well-known hump-shaped species-rich-

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ness-biomass relationship (e.g., Al-Mufti et al. 1977, Gross et al. 2000, Grime 2001, Keddy 2001, Mittelbach et al. 2001, Rajaniemi 2003, Gillman and Wright 2006), in the SEM studies species richness was often found to peak at intermediate levels of shoot biomass. (2) Environmental conditions indirectly influence diversity through the effects of those conditions on standing biomass and directly through "species pool" effects (Gough et al. 1994, Grace and Pugesek 1997). Species pools become an important control of diversity along environmental gradients such as salinity where fewer species have evolved the traits necessary to establish on certain parts of the gradient. (3) Recent disturbances (e.g., herbivory, wave damage, fire) have few direct effects on species richness; rather disturbance influences diversity indirectly through the effects of disturbance on variables such as aboveground biomass.

The studies cited above provide a very firm foundation for understanding the mechanisms controlling plant diversity, but several key questions remain unanswered. Aboveground standing biomass is clearly an important influence on diversity, but in the SEM studies the effects of live shoot biomass were not separated from those of litter. This may be an important distinction because, in addition to shading, litter accumulation can have strong negative effects on diversity through mechanisms such as alteration of germination cues, direct physical interference, sheltering invertebrate seed predators, and encouraging pathogens (Carson and Peterson 1990, Facelli and Pickett 1991, Facelli 1994, Foster and Gross 1998, Xiong and Nilsson 1999). In addition, it is important to separate the direct effects of live biomass and litter from indirect effects due to shading. For example, Grace and Pugesek (1997) and Grace et al. (2000) found that the majority of the effects of biomass on diversity could be explained indirectly through the effects of biomass on light, providing strong evidence that competition for light was an important mechanism in those communities.

The roles of root biomass and root competition in driving diversity have not been addressed in a holistic framework. This gap is critical because in many plant communities roots make up the majority of the plant biomass (Jackson et al. 1996, Mokany et al. 2006), the dominant form of competition is often belowground (Casper and Jackson 1997), and root competition intensity can be correlated with neighbor root biomass (Cahill and Casper 2000). A positive bivariate relationship between diversity and root biomass has often been found in studies where diversity was experimentally manipulated (Balvanera et al. 2006), but the shape of the relationship between diversity and root biomass can be similar to the aboveground biomass-diversity relationship found in the same system (Liira and Zobel 2000). Since root and shoot biomass are closely linked in most systems (Cairns et al. 1997, Mokany et al. 2006), it is difficult to separate a causal relationship between root biomass and diversity from a simple correlation between root and shoot biomass.

Finally, structural equation modeling studies of the controls on diversity have focused entirely on species richness. Evenness is an equally important component of diversity that can be affected by changes in environmental conditions independently of species richness (Wilsey et al. 2005). The observed relationships between productivity or biomass and evenness can be quite variable (e.g., Wilsey and Potvin 2000, Mulder et al. 2004, Wilsey and Polley 2004), suggesting that much remains to be learned about this component of diversity. Plant community evenness is linked to a wide range of ecological functions including competition, productivity, and species richness. For example, low evenness indicates the dominance of a small number of species and, in the absence of severe herbivory or abiotic stress, can imply intense interspecific competition (Cotgreave and Harvey 1994, Keddy 2001). Low evenness also can indicate that there are species with very small population sizes in the community that may be at risk of local extinction (Wilsey and Polley 2004).

In this study, I examine how factors including resource availability, root biomass, shoot biomass, litter, and light availability control species richness and evenness in a grassland plant community. I quantify the effects of these factors and examine the networks of interaction among them using structural equation modeling (SEM).

METHODS

Field site

The study area is in a 50-ha field at the University of Alberta Research Ranch near Kinsella, Alberta, Canada (53°5′ 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) groves and rough fescue (Festuca hallii) prairie. Plant biomass at the field site can be limited by both nitrogen and water availability, and root competition is much more intense than shoot competition (Lamb et al. 2007). The study site included more productive Poa pratensis-dominated grasslands in wetter microsites and less productive Hesperostipa curtisetadominated grasslands in drier locations. The study site has an average of 14.1 ± 2.6 (mean \pm SD) species per 0.25-m² plot and mean aboveground standing biomass of 259.5 \pm 78.0 g/m² (E. G. Lamb, unpublished data). This site is very diverse relative to the range of species richness $(8.7-13.2 \text{ species/m}^2)$ across a long productivity gradient (45-600 g·m⁻²·yr⁻¹) in North American grasslands (Gross et al. 2000). The study site historically has been lightly grazed by cattle in the fall, but grazing was halted two years prior to the beginning of this experiment. The majority of soils at the site are 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

I manipulated three essential resources (nitrogen, water, and light) in this study to establish strong gradients of community biomass and diversity. Natural diversity gradients occur at the site, but measuring the community biomass and diversity responses to resource manipulations provides much more specific information on the mechanisms controlling diversity than simply observing the unmanipulated relationships (Keddy 2001, Grace 2006). Twenty-two blocks distributed through both the Poa pratensis- and Hesperostipa curtisetadominated grasslands, each containing six 1.5×1.5 m plots separated by 1 m wide buffers were established in May 2003. Control, nitrogen, water, nitrogen + water, shade, and nitrogen + shade treatments were randomly assigned to plots in each block. Logistical constraints limited the water and shade treatments to only two plots each per block, so no plots including both shade and water treatments were applied. Nitrogen and water were manipulated because both resources can be limiting to plant growth in this system (Lamb et al. 2007), and they have contrasting effects on species richness in other systems (Stevens et al. 2006). Reducing light using shade cloth does not alter the red : far-red ratio, and thus is not entirely equivalent to shading by neighboring plants, but other researchers have successfully used it to simulate the effects of shading without also manipulating soil nutrients (Rajaniemi 2002). In low-statured plant communities where shading by plants is limited even at high productivity, shade treatments are a practical method to impose light limitation without also influencing root competition.

In the nitrogen treatments, granular ammonium nitrate fertilizer was applied in May and late June from 2003 through 2005. Each fertilizer application delivered 2.72 g/m² nitrogen for a total nitrogen application of 5.44 $g \cdot m^{-2} \cdot yr^{-1}$. Water was added weekly from mid May through late September at rates equivalent to a 50% addition to long-term average rainfall. Rainfall varies through the growing season, so plots received the equivalent of 5 mm of rain per week in May, 10.5 mm in June, 9.5 mm in July, 7.5 mm in August, and 4.5 mm in September for a total of 139 mm each growing season. This represented a 54% increase over natural rainfall (256 mm) during the same period in 2003, 48% (290 mm) in 2004, and 52% (265 mm) in 2005. Precipitation was measured at the Viking, Alberta weather station (53°16' N, 111°46' W; data available online).² Light levels were reduced using shade cloth stretched over 1.8×1.8 m wooden frames \sim 30 cm above the ground. The shade cloth reduced light reaching the top of the vegetation by $73\% \pm 4\%$ (mean \pm SD). Relative soil moisture levels were significantly higher ($F_{1,105} = 37.68$, P < 0.001) in the watered plots, but the shade treatments had no effect on relative soil moisture ($F_{1,105} = 0.46$, P = 0.499).

Plant community composition (percent cover of all vascular species) was visually estimated at the beginning of the experiment in May 2003 and in mid-July from 2003 to 2005 in permanently marked 0.5×0.5 m quadrats in each plot. Biomass was measured in mid-July in 2003 and 2005. Live shoot biomass (g/m^2) and litter biomass (g/m²) were measured by removing all live and dead biomass from a 0.1×1 m quadrat in each plot. Live and dead materials were later sorted in the lab. Root biomass (g/m^2) was estimated by washing the roots from 5.3 cm diameter root cores taken to a depth of 12 cm in each plot. Light interception (percentage of ambient light intercepted by both vegetation and the shade cloth, if present) was measured using an Accu-Par light meter (Decagon, Pullman Washington, USA). Species richness was measured as the number of species present in each permanent quadrat. Evenness was calculated from the cover data using the "odds measure of evenness" (Simpson's D' - 1)/(species richness - 1) (Kvålseth 1991).

Statistical analysis

Examining the bivariate relationships between variables is an important precursor to structural equation modeling (SEM) because it allows potentially nonlinear relationships to be identified (Grace 2006). The bivariate relationships between species richness and evenness and shoot, root, and litter biomass were explored using generalized linear mixed models with experimental block as the random term. In each analysis, the fit of a model with a linear relationship was compared to the fit of a model with a quadratic relationship. The lmer function in the R Package (Bates 2005, R Development Core Team 2006) was used for these analyses. Species richness was modeled using a Poisson distribution, while a normal distribution was used for evenness.

Structural equation modeling (SEM) using observed variables (path modeling) was used to examine the relationships between species richness and biomass (Shipley 2000, Grace 2006). SEM is most often applied to survey data, but is equally appropriate for experiments (Grace 2006). Univariate analyses such as ANOVA can only quantify the net effects of an experimental treatment on a response variable, while SEM allows the net effects of an experimental treatment to be partitioned into direct effects and indirect effects that occur through other aspects of the system under study. The primary drawback of SEM is that the results are dependent on correctly specifying the theoretical causal relationships between variables prior to analysis (Shipley 2000, Grace 2006). I chose to model the observed variables directly, rather than using the observed variables as indicators of latent variables because the latter model would have had only a single indicator per latent variable. SEM can be used in either

² (http://climate.weatheroffice.ec.gc.ca)

a confirmatory or exploratory mode (Grace 2006). In a confirmatory application, the model is specified based on prior theoretical knowledge and then tested to determine whether the model adequately fits the data. In an exploratory application, such as used in this paper, the initial theoretical model is altered based on modification indices to improve the fit between model and data.

Path models were developed to relate both species richness and evenness to neighborhood biomass, litter, and light conditions. The continuous variables included in the models are described in Appendix A, including a figure showing the initial model setup. The experimental nitrogen, water, and shade treatments were entered as dummy variables (0,1). Since quadratic relationships better described the relationships between biomass and richness and biomass and evenness than linear models (see Results), shoot, root, and litter biomass were lntransformed to improve the fit of the linear relationships. Following transformation, quadratic relationships still better described the relationships between shoot and root biomass and species richness (shoot, $\chi_1^2 = 5.48$, P =0.019; root, $\chi_1^2 = 8.45$, P = 0.004), but not between evenness and litter biomass ($\chi_1^2 = 3.55$, P = 0.059). While the relationships between shoot and root biomass remained nonlinear, inspection of the transformed relationships (Appendix A) shows that, in each case, the dominant pattern was for a linear increase across the range of biomass sampled in this study. For this reason, I chose to model the nonlinear relationships as if they were linear.

The initial species richness model (Appendix A) included direct paths from shoot and root biomass, litter biomass, and light interception to richness. A direct path from pretreatment richness measured in May 2003 was included to control for the initial conditions in each plot. Light interception received direct paths from shoot biomass, litter biomass, and shade. Shoot, root, and litter biomass and species richness all received direct paths from the experimental treatments. Litter biomass received both a direct path from shoot biomass and a path from initial ground cover in May 2003. Initial ground cover was included to account for pretreatment differences in litter accumulation. The only experimental treatment with a direct path to light interception was shading, since it was assumed that the effects of water and nitrogen on light interception could be accounted for by their effects on aboveground biomass and litter. I chose not to include direct paths from species richness to above and belowground biomass, even though diversity is not necessarily only a consequence of environmental and community characteristics, but can also be a cause of those community characteristics (Aarssen 1997, Weiher et al. 2004). Initial analyses indicated that including the reciprocal relationships between plant biomass and species richness could interfere with fully solving the structural equation model. I chose to focus on the paths from biomass to species richness in this study because those paths represented the effects of root and shoot competition on species richness.

The models were fit using M-plus 4.1 (Muthén and Muthén 2006). Experimental blocks were included as a random factor using the "TYPE=COMPLEX" option. The χ^2 test of model fit was used to determine whether the fit between model and data was adequate (P > 0.05). Of the numerous tests of model fit available, the χ^2 is recommended since a nonsignificant result is a strong indication of an adequate fit between model and data (Grace 2006:130). Each path coefficient was divided by its standard error to assess significance. The resulting value follows a *t* distribution, allowing *P* values to be calculated. Given the exploratory nature of these analyses, coefficients with P < 0.100 were considered significant. Nonsignificant paths were retained in the final model (Grace 2006).

The initial species richness model did not have an adequate fit ($\chi_{12}^2 = 32.48$, P = 0.001). The modification indices indicated that paths from nitrogen and water to light interception should be added. The path from water to light interception can be justified because regularly pouring water onto the plots could have altered the physical arrangement of shoots and litter, increasing light interception. The justification for the path from nitrogen to light is less clear, but clearly the net effects of the experimental nitrogen treatment on light interception were not completely accounted for by shoot biomass and litter. The fit of the modified model was adequate ($\chi_{10}^2 = 14.98$, P = 0.133).

The initial evenness model included all of the paths added to the final richness model. I retained the additional paths involving light interception since that part of the model was unchanged by the substitution of evenness for richness. The fit of this model was not adequate ($\chi_{10}^2 = 18.35$, P = 0.049). Modification indices suggested the addition of a path from initial litter cover to light interception. The fit of this modified model was adequate ($\chi_9^2 = 12.75$, P = 0.174), however there is little theoretical justification for the path from initial litter to light interception. Given that there were no changes in the significance and extremely small changes in magnitude of the path coefficients involving evenness between the initial and modified models, I chose to accept the initial model.

An important caveat for these analyses is that the number of parameters in the models exceeds the number of blocks in the experiment. 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 my interpretation, I re-ran the final models in this study without the blocking variable. Variation in the standard errors between the blocked and non-blocked models resulted in no changes in the paths that were deemed significant. Since this issue did not affect my overall interpretation of the models, I chose to ignore it. The



FIG. 1. Bivariate relationships between shoot, root, and litter biomass and species richness and evenness. Regression lines for significant (P < 0.05) linear and nonlinear relationships are shown.

standard errors reported in this paper are from the blocked models.

RESULTS

Species richness-biomass relationships

Quadratic models better described the relationships between species richness and shoot and root biomass than linear models (shoot, $\chi_1^2 = 6.02$, P = 0.014; root, χ_1^2 = 6.28, P = 0.012) (Fig. 1). When the outlying point with root biomass of 3223 g/m² was removed the quadratic model was not significantly better ($\chi_1^2 = 1.02, P = 0.312$). The species richness-biomass relationships in rough fescue grasslands are likely hump shaped, though the dominant pattern over the range of biomass values sampled in this study is for a linear increase in richness with increasing biomass. There was a negative linear relationship between species richness and litter biomass, since the quadratic model was not significantly better than the linear model ($\chi_1^2 = 0.87$, P = 0.352; Fig. 1). While all of these relationships were significantly better than a null model with only an intercept (shoot, $\chi^2_2 =$ 575.67, P < 0.001; root, $\chi_2^2 = 570.83$, P < 0.001; litter, χ_1^2 = 578.04, P < 0.001), the R^2 values were low, ranging from 0.09 for root biomass to 0.16 for litter biomass.

Evenness-biomass relationships

There were no significant relationships between evenness and shoot or root biomass as quadratic models were no better than null models including only an intercept (shoot, $\chi_2^2 = 0.00$, P = 1.000; root, $\chi_2^2 = 2.16$, P =0.340). A quadratic model better described the relationship between evenness and litter biomass than a linear model (litter, $\chi_1^2 = 13.50$, P < 0.001; Fig. 1). The significant quadratic model between litter biomass and evenness does not appear to represent a hump-shaped relationship. Instead, the underlying pattern appears to be no relationship below $\sim 300 \text{ g/m}^2$ litter biomass, but a negative linear relationship above 300 g/m². The quadratic relationship between evenness and litter was significantly better than a null model including only an intercept ($\chi_2^2 = 7.45$, P = 0.024).

Structural equation models

The fit between the modified structural equation models and data were adequate for species richness $(\chi_{10}^2 = 14.98, P = 0.133)$ but not for evenness $(\chi_{10}^2 = 18.35,$ P = 0.049; Fig. 2). I chose accept this model, however, because the modifications required to achieve adequate fit were not plausible, and there were only very minor differences in the magnitude of the path coefficients involving evenness between the initial and modified models. These models explained 42.2% of the variation in species richness and 16.6% of the variation in evenness. Un-standardized path coefficients, t test results, and total direct and indirect effects are summarized in Appendix B. Increased litter cover was strongly associated with declines in both species richness and evenness in this system (Fig. 2). Even though there were significant bivariate relationships between biomass and species richness, shoot biomass had only an indirect negative effect on richness (-0.069) through the effects of shoot biomass on litter. Shoot biomass had a slightly stronger indirect effect (-0.095) on evenness through litter (Appendix B). All three experimental treatments had indirect negative effects on both species richness and evenness, primarily through the effects of the resource manipulations on litter biomass. The direct negative



FIG. 2. Final structural equation models for (a) species richness and (b) evenness. Nonsignificant paths are indicated by dotted arrows. The thickness of the solid arrows reflects the magnitude of the standardized SEM coefficients. Standardized coefficients are listed beside each significant path.

effects of both nitrogen and shade on species richness were compounded by these indirect negative effects. Nitrogen had direct positive effects on evenness that were largely counterbalanced by negative indirect effects through litter.

DISCUSSION

Litter was clearly the primary factor controlling species richness and evenness in rough fescue grassland;

the resource treatments affected diversity largely through their effects on litter cover. Litter can have strong negative effects on species richness in grasslands through many mechanisms including shading, alteration of germination cues, direct physical interference, sheltering invertebrate seed predators, and encouraging pathogens (Carson and Peterson 1990, Facelli and Pickett 1991, Facelli 1994, Foster and Gross 1998, Xiong and Nilsson 1999). The lack of an indirect pathway from litter to species richness through light interception suggests that the effects of litter were largely due to mechanisms other than shading.

The only major effects of the resource manipulations that could not be accounted for by litter were direct negative effects of nitrogen addition and shading on species richness and a positive effect of nitrogen on evenness. Environmental conditions can influence diversity directly by altering the "species pool," or the number of species that have evolved the traits necessary to establish on certain parts of the gradient (Gough et al. 1994, Grace and Pugesek 1997). The small number of grassland species likely able to tolerate the low light levels under the shade cloth may explain some of the direct effects of shading on species richness. Nitrogen addition can increase the intensity of root competition in rough fescue grassland independent of the effects of nitrogen on root biomass (Lamb et al. 2007), but how a change in the intensity of size-symmetric root competition could lead to competitive exclusion is not clear. The lack of direct nitrogen effects on above and belowground biomass were also surprising given that rough fescue grasslands can be strongly nitrogen limited (Lamb et al. 2007). Nitrogen increased shoot biomass in the first year of the experiment ($F_{1.99} = 15.98$, P <0.001), but in 2005 a nitrogen by shade interaction $(F_{1,104} = 22.32, P < 0.001)$ indicated that, while nitrogen addition increased shoot biomass in the unshaded plots, it reduced biomass in the shade treatments. The very large litter biomass that accumulated under the shade covers likely explains the nitrogen by shade interaction.

In contrast to the abundant evidence that litter and shoot biomass are important drivers of species richness, the relationship between biomass and evenness can be much more variable (e.g., Wilsey and Potvin 2000, Mulder et al. 2004, Wilsey and Polley 2004). Negative productivity-evenness relationships may arise because large, competitively dominant, species can both reduce evenness and increase overall community productivity (Cotgreave and Harvey 1994, Nijs and Roy 2000). The weak negative indirect effects of shoot biomass on evenness in this study occurred through litter biomass and light interception. The reductions in evenness associated with increased litter biomass and light interception suggest that a shift from symmetric root competition to asymmetric competition for light may have occurred at high levels of aboveground biomass and litter in this community (Cahill 1999, 2002). When shoot biomass is <300 g/m², shoot competition is negligible in this community (Lamb et al. 2007), however, light interception in unshaded plots with biomass >600 g/m² was 80% \pm 0.1% (mean \pm SD). In those plots, low-statured plants would receive only 240-360 μ mol m⁻² s⁻¹ in full sunlight (1200–1800 μ mol·m⁻²·s⁻¹), well below the photosynthetic saturation point of most plants (Fitter and Hay 2002). The 73% reduction in light by the shade cloth would have had similar effects on light availability. It is also of note that

the peak of the quadratic regressions relating both species richness and evenness to shoot biomass were at approximately 700 g/m^{-2} . Even if competition for light is occurring at some locations in this community, with only 20% of plots having biomass $>700 \text{ g/m}^2$ (Fig. 1) and all but one of those plots having received either water or nitrogen addition, it is likely that light competition is of minor importance in this community. The decline in evenness with increasing litter could also be interpreted as a consequence of competition. Plants can use litter as a competitive tool to suppress neighbors through a number of mechanisms. For example, the litter of a dominant species can discourage the establishment of competitors by altering nutrient cycling (Clark et al. 2005). Similarly, if a species is able to avoid mechanical interference from its own litter it may be at a competitive advantage (Facelli and Pickett 1991). The second explanation may be important in this system since *Poa pratensis*, the species with the largest increases in cover under conditions of high biomass, high litter, and low light, was also responsible for much of the litter production (E. G. Lamb, personal observation). Poa is able to push leaves through a dense mat of litter since it has much more plasticity in leaf traits such as leaf size and specific leaf area than other species at the study site (S. Kembel, personal communication).

There were few strong links between biomass and species richness or evenness in the structural equation models The univariate relationships between richness and biomass are in agreement with numerous studies showing strong relationships between biomass and species richness (e.g., Mittelbach et al. 2001, Balvanera et al. 2006, Gillman and Wright 2006), so why should there be such weak relationships in the structural equation models? The weak relationships between shoot biomass and species richness and evenness can be explained by the minor role of shoot competition in rough fescue grasslands. However, given the intense root competition (Lamb et al. 2007), the lack of relationship between root biomass and species richness and evenness is surprising. Such a strong belowground process should have consequences for plant community diversity (e.g., Grime 2001, Rajaniemi 2002, 2003, Schenk 2006), though Cahill (2003) showed that the strength of root competition was not affected by neighborhood diversity. I am aware of no similar structural equation-based studies that have explicitly included root biomass in their analysis. Thus this study provides some of the only comprehensive evidence from a natural community for a lack of relationship between root biomass and species richness and evenness.

Studies where diversity has been experimentally manipulated generally have found positive bivariate relationships between diversity and root biomass (Balvanera et al. 2006), but it is not clear whether root biomass actually influences diversity or if it is simply a spurious correlation. Community root and shoot biomass are positively correlated for allometric reasons (e.g., Cairns et al. 1997, Liira and Zobel 2000, Mokany et al. 2006), and thus a significant shoot-biomassdiversity relationship could be accompanied by a similar root-biomass-diversity relationship in the absence of any important belowground processes. The hypothesis that any root-biomass-diversity relationships are simply a result of this correlation is supported by the similarity of the shapes of the root and shoot-biomass-diversity relationships in both this study and Liira and Zobel (2000). The evidence from studies of experimental plant communities with varying diversity is less clear. Some studies have found significantly different shoot and rootbiomass-diversity relationships (e.g., Spehn et al. 2000, He et al. 2002) while others have found matching above and belowground patterns (e.g., He et al. 2005, Lanta and Lepš 2006).

Several explanations could account for the lack of relationship between belowground biomass and species richness and evenness. (1) There may be no relationship between root biomass and shoot diversity because plant rooting systems generally cover much larger areas than canopies (Jackson et al. 1996). Thus the scale at which root biomass affects diversity may be very different from the scale at which aboveground diversity is generally measured. (2) There may be a relationship between root biomass and root community richness or evenness but, until advances in molecular methods make the direct measurement of root diversity practical (e.g., Moore and Field 2005), this possibility is likely to remain unresolved. (3) There may be important root-productivityspecies-richness or evenness relationships that are obscured because standing root biomass samples include both live and dead roots and can be a poor indicator of actual rates of root productivity and turnover (Dahlman and Kucera 1965, Steinaker and Wilson 2005). (4) The belowground-biomass-species-richness or evenness relationships may be obscured by the large proportion of belowground biomass in grasslands that is allocated to organs such as thick roots and rhizomes dedicated to functions other than resource capture (Pucheta et al. 2004). There is some evidence that this may be the case, as Spehn et al. (2000) found no relationship between diversity and total root biomass in an experimental plant community, but fine root biomass was positively correlated with diversity. (5) There may simply be no ecological mechanism through which root biomass can structure species richness or diversity. Root competition is frequently cited as an important mechanism structuring diversity (Rajaniemi et al. 2003, Schenk 2006), but root competition intensity may be saturated at all levels of root biomass found in this system (Cahill 2003, Lamb et al. 2007). Cahill and Casper (2000) found that root competition saturated at $\sim 300 \text{ g/m}^2$ in a productive old field; root biomass in the present study ranged between 308 and 3222 g/m². Competitive exclusion by root competition cannot occur along gradients of root biomass without variation in competition intensity along the same gradient. Given the extreme variability in the 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), perhaps it should not be surprising that there are so few links between diversity and root biomass.

The lack of biomass effects in this study contrasts with other SEM analyses that found significant relationships between standing aboveground biomass or cover and species richness (Grace and Pugesek 1997, Gough and Grace 1999, Grace and Guntenspergen 1999, Grace and Jutila 1999, Grace et al. 2000, Weiher et al. 2004, Mancera et al. 2005, Grace and Keeley 2006), but in those studies live shoot biomass and litter were not considered separately. Finally, I found that initial species richness and evenness remained important, indicating that, similar to other studies (Grace and Guntenspergen 1999), plot history is an important determinant of current community structure. SEMs of species richness generally have much more explanatory power than univariate relationships (Grace 2006).

In summary, litter dynamics appear to be the primary mechanism structuring species richness and evenness in rough fescue grasslands. The lack of strong relationships between aboveground biomass and light interception and richness and evenness reflects the importance of litter in this system. More importantly, the lack of relationship between root biomass and species richness and evenness suggests that, even though root competition in grasslands is intense, belowground interactions may not play an important role in structuring grassland plant communities.

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APPENDIX A

Description of the variables included in the structural equation model and figures showing the transformed relationships between species richness, evenness, and root, shoot, and litter biomass, and the initial structural equation model (*Ecological Archives* E089-011-A1).

APPENDIX B

Full model results including direct and indirect effects and unstandardized path coefficients (Ecological Archives E089-011-A2).