

# Shoot, but not root, competition reduces community diversity in experimental mesocosms

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## Summary

1. We used a mesocosm experiment to determine how both the intensity and relative importance of root and shoot competition, and their interactions, influence the structure of plant communities. Experimental communities of nine grassland plant species were planted under different levels of soil fertility. Root, shoot, and total competition intensity and relative importance, along with plant community structure (evenness) were measured in each mesocosm. Structural equation modelling was used to separate the direct and indirect influences of root, shoot and total competition on species evenness.

2. Increasing shoot competition intensity and importance reduced plant community evenness, while increases in root competition intensity and importance had no direct effects on evenness. Root competition intensity and importance indirectly reduced plant community evenness because increased root competition intensity increased shoot competition intensity.

3. We propose that the separate influences of shoot competition and root–shoot competition interactions on community structure can be integrated through a new state variable: the total size-asymmetry of competition. We propose that there is a direct relationship between the overall size-asymmetry of competition and the influence of competition on plant community structure.

4. *Synthesis.* This study provides the first experimental evidence that, even though there are no direct links between the intensity or relative importance of root competition and plant community structure, root competition may indirectly structure communities through root–shoot competition interactions. Integrating root and shoot competition as competitive size-asymmetry can explain why intense root competition can be unimportant for community structure, while relatively less intense shoot competition and root–shoot competition interactions can have strong effects on plant community composition and diversity.

**Key-words:** community ecology, competition, evenness, facilitation, intensity vs. importance, mesocosm, structural equation modelling (SEM)

## Introduction

Most coexisting plant species utilize a small number of essential resources from roughly the same locations at roughly the same time as their neighbours. As a result, there is substantial opportunity for resource competition among plants, a finding that is commonly observed in the field (Goldberg & Barton 1992; Gurevitch *et al.* 1992; Grime 2001; Keddy 2001). These simple observations stand in contrast to the competitive exclusion principle (Hardin 1960), and a central paradigm in

community ecology: that competition will cause a selective loss of species from a community (Newman 1973; Carson & Pickett 1990; Goldberg & Miller 1990; Huston & DeAngelis 1994; Grime 2001; Keddy 2001).

Competition among plants is more complicated than in many animals, with plants competing simultaneously above- and below-ground for different resources (Casper & Jackson 1997; Keddy 2001). Size-asymmetric competition for light creates positive feedback where larger individuals are able to overtop smaller individuals, capturing a disproportionate fraction of the available light, growing faster and taller than their smaller neighbours and causing even greater size disparities among individuals. Such feedback can ultimately

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lead to the competitive exclusion of smaller plants and species (Weiner 1986; Keddy 2001). Root competition, however, is size-symmetric with a plant's access to soil nutrients proportional to the size of its root system. Without a feedback mechanism to magnify size differences, the impact of competition will be proportional for all plants in the community (Weiner 1986; Schwinning & Weiner 1998; Cahill & Casper 2000; von Wettberg & Weiner 2003). Root competition results in less skewed size hierarchies than shoot competition (Wyszomirski *et al.* 1999), and increases in the strength of root competition are thus not expected to affect diversity as severely as increases in shoot competition (Newman 1973). Even though the effects of root and shoot competition on individual plants are well understood, little is known about the differential effects of the two forms of competition at the community level. Recent evidence indicates that even though intense root competition may greatly reduce individual plant growth, competition may not be important because it has little impact on community structure (Lamb & Cahill 2008). No studies, however, has directly examined both the *intensity* of root and shoot competition and the *importance* of the two forms of competition in structuring plant community diversity.

If there is a desire to link competitive interactions to impacts on community structure, it is critical to examine both the intensity and importance of competition. The distinction between the two is a longstanding issue in plant ecology (Welden & Slauson 1986; Brooker & Kikvidze 2008). Plant ecologists generally measure the intensity of competition but are most interested in whether or not that competition is important. Competition intensity is the degree to which competition reduces plant performance below the physiological maximum achievable in a given environment, while importance is the impact of competition on plant performance relative to the impact of other environmental conditions (Welden & Slauson 1986; Brooker *et al.* 2005). More broadly, competition can be important if variation in intensity can be shown to cause predictable variation in an aspect of plant community structure (Lamb & Cahill 2008). Even though intensity and importance are not necessarily related (Welden & Slauson 1986), many authors have pointed out that the assumption that that intensity is equivalent to importance remains widespread (Grace 1991; Brooker *et al.* 2005; Brooker & Kikvidze 2008). Since different forms of competition may have different impacts on community structure, the most important issue is not simply to determine how intensity and importance are related, but rather to directly determine how competition influences community structure.

Recent evidence from field experiments has shown that root competition can cause a tenfold reduction in plant growth but have little impact on plant community diversity or composition (Cahill 2003; Lamb *et al.* 2007; Lamb & Cahill 2008). These results suggest that competition is likely to be unimportant in structuring diversity in low-statured communities such as dry grasslands, even though competition may strongly influence productivity within these systems. However, communities such as productive old fields often have both intense root and shoot competition (e.g. Cahill

1999), and it is important to understand the conditions under which competition may become both intense and important to community structure.

Lamb & Cahill (2008) proposed that, even though symmetric root competition may not directly influence plant community structure, root–shoot competition interactions may provide an indirect mechanism through which root competition could structure communities. Root–shoot competition interactions occur when one component of competition affects a plant's ability to compete for the other component. For example, root competition may reduce shoot growth and thus affect a plant's ability to compete for light (Cahill 1999). Root–shoot competition interactions have been shown to occur in a wide array of species and communities (Wilson 1988; Cahill 1999, 2002a), but little is known about the community-level consequences of such interactions. In this study we created mesocosms in which we measured root, shoot, and total competition intensity and relative importance along with community structure. This design allowed us to use structural equation modelling (SEM) to evaluate how root and shoot competition, and root–shoot competition interactions influence plant community structure.

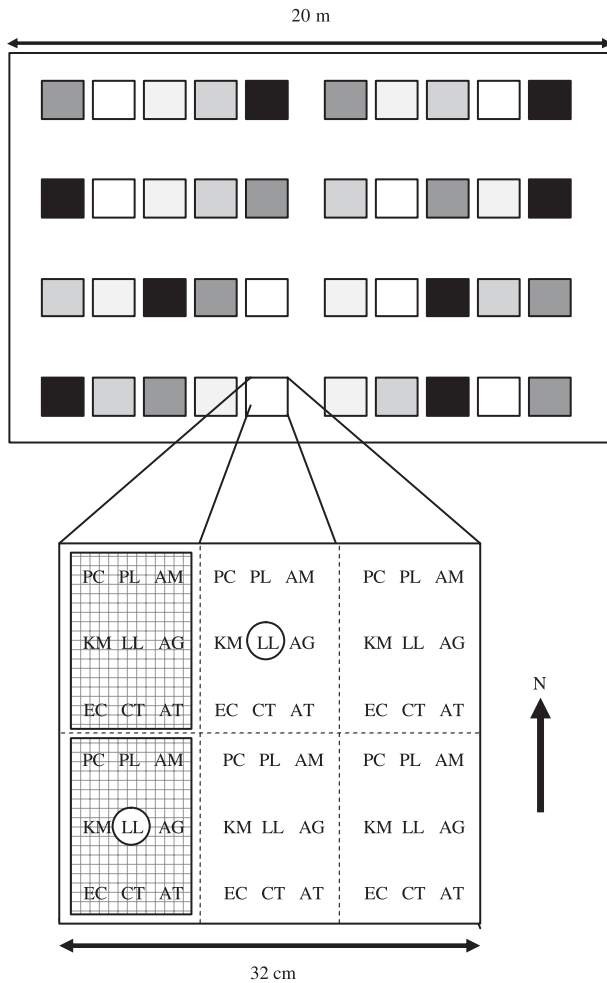
## Methods

### EXPERIMENTAL DESIGN

Forty mesocosms were arranged in a randomized block design (eight blocks of five mesocosms; Fig. 1). Each mesocosm consisted of a plant community of nine species in commercial bus-tubs (29 × 32 cm) filled with 15 cm of soil (1 : 2 topsoil : sand). Within each block, tubs were randomly assigned to one of the five fertilization treatments (0, 4, 8, 16 or 32 g m<sup>-2</sup> NPK in the form of Osmocote® 14–14–14 slow release pellets). Pellets were placed on the soil surface and mixed by hand until homogeneously distributed. Blocks were placed within a 20 × 20 m area on the roof of the University of Alberta Biotron in Edmonton, Alberta, Canada, experienced ambient climatic conditions, and were watered daily (holes in each tub allowed drainage).

Six seedlings of each of nine species (Table 1) were transplanted into each mesocosm on 10 June 2002. The seedlings of each species were randomly selected from a pool of similar seedlings (started in trays at the same time), thus eliminating any systematic size-bias at the beginning of each experiment. Each mesocosm was divided into six equally-sized planting units, with a seedling of each species present once in each planting unit (Fig. 1). To minimize confounding effects of neighbourhood structure on competition, the location of each species within a planting unit was randomly determined at the block level, except for *Linum lewisii* (see below), such that eight planting arrangements were used. *Linum lewisii* served as the focal species for the competition measures, and was always placed in the centre of each planting. All mesocosms started with identical species richness, evenness, composition and similar size structure.

Species were selected based upon a variety of criteria, including seed availability, potential for rapid growth allowing detection of growth differences in a single growing season, and a goal to have the overall species mixture include graminoids and forbs. We did not try to replicate any particular community, and these species do not naturally co-occur. Importantly, there is nothing in the hypothesis of interest which should be restricted to natural, or synthetic, plant communities. *Linum lewisii* was chosen as the focal species because



**Fig. 1.** Experimental layout and planting scheme. Mesocosms were arranged in eight blocks of five mesocosms each assigned a fertilization treatment (indicated by tub colour, increasing fertilization from white-black). Mesocosms were divided into six planting cells (indicated by dashed lines), and the arrangement of species, root exclusion tubes (circles), and netting (grid) were randomized at the block level.

a pilot study indicated it demonstrated effects of competition (Cahill, unpublished data), its growth form is generally upright facilitating the use of the shoot tie-backs (see below) to reduce shading, and it is not large and thus unlikely to be harmed by growing in root exclusion tubes (see below). Seeds were stratified, sown into flats filled with potting soil, and placed outside. Transplantation occurred after all species had grown several true leaves.

**COMPETITION TREATMENTS**

One *L. lewisii* individual was subjected to each of the four competition treatments (all neighbours, AN; no neighbours, NN; shoots of neighbours, SN; roots of neighbours, RN) in each mesocosm. The competition treatments (root exclusion tubes and netting; *sensu* Cahill 1999) were imposed on the four most westerly *L. lewisii* individuals within a mesocosm (Fig. 1). Treatment assignments were randomly determined at the block level. Root exclusion tubes consisted of a 5-cm diameter × 15 cm piece of PVC pipe covered on the bottom

with Nitex© fabric (42 µm pore size) to allow water flow while preventing root growth. The tubes were installed flush with the soil prior to transplanting. The *L. lewisii* plants in the NN and SN treatments were planted inside an exclusion tube in each mesocosm. Shoot competition was reduced by tying back the shoots surrounding the focal plants in the NN and RN treatments using a 15-cm<sup>2</sup> piece of netting centred over the focal plant, flush with the soil immediately adjacent to the focal plant and with the corners raised 10 cm. The netting was adjusted weekly.

**HARVEST**

Plants were harvested between 7 and 11 August 2002, 9 weeks after planting. The presence of exclusion tubes and netting could alter the growth of the surrounding plants, and thus only the plants from the two most easterly planting units (Fig. 1) were used for calculation of root and shoot biomass and diversity (18 plants per mesocosm). Each plant was clipped at the soil surface, dried and weighed. Below-ground biomass was estimated at the mesocosm level by taking and pooling two randomly located soil cores (2 cm diameter × 12 cm depth) from each mesocosm. Roots were washed over a 1-mm sieve, dried and weighed. Cores were not taken directly over the taproot of any individual, and thus these measures are relative measures of fine root biomass. Roots of the focal *L. lewisii* plants were not extracted because the roots were intermeshed, and accurate root extraction of individuals was not feasible (Cahill 2002b). Community structure was measured as evenness, as all mesocosms had the same species richness. Evenness was calculated as Simpson’s Diversity (1/D) divided by the number of species (Smith & Wilson 1996).

**COMPETITION INTENSITY**

The intensities of root, shoot and total competition were measured as competitive response (Cahill 1999). Below-ground competitive response (BCR) was measured as  $\ln(\text{RN}/\text{NN})$ , above-ground competitive response (ACR) as  $\ln(\text{SN}/\text{NN})$  and total competitive response (TCR) as  $\ln(\text{AN}/\text{NN})$ , where NN represents focal plant biomass when grown with no neighbours (tube and netting), RN is focal plant biomass when grown with the roots, but not shoots of neighbours, SN is focal plant biomass when grown with the shoots, but not roots, of neighbours and AN is focal plant biomass when grown with all neighbours (roots and shoots). Positive values of the  $\ln\text{RR}$  indicate facilitation while increasingly negative values indicate increasing intensity of competition. We chose the  $\ln\text{RR}$  because it is a commonly used index with two very useful features: (i) it is symmetrical for both competition and facilitation, and (ii) the logarithm functions to both linearize the metric and normalize the sampling distribution (Weigelt & Jolliffe 2003). Indices of competition can be problematic because they require the assumption that competitive ability does not vary with plant size (Lamb *et al.* 2006), however, structural equation modelling (SEM) requires separate measures of competition from each mesocosm, so statistically more rigorous alternatives for assessing competition such as ANCOVA could not be used.

**COMPETITION IMPORTANCE**

The  $C_{\text{imp}}$  index (Brooker *et al.* 2005) was used to measure the importance of competition, or the impact of competition on plant performance relative to the impact of soil nutrient levels on plant performance. Root competition importance was measured as  $(\text{RN} - \text{NN})/$

Species	Family	Life-history	Seed source
<i>Abutilon theophrasti</i>	Malvaceae	Annual	Valley Seed Service
<i>Achillea millefolium</i>	Asteraceae	Perennial	Bedrock Seeds
<i>Agropyron trachycaulum</i>	Poaceae	Perennial	UA Bio. Sci.
<i>Coreopsis tinctoria</i>	Asteraceae	Annual	Bedrock Seeds
<i>Elymus canadensis</i>	Poaceae	Perennial	Bedrock Seeds
<i>Koeleria macrantha</i>	Poaceae	Perennial	UA Ren. Res.
<i>Linum lewisii</i>	Linaceae	Perennial	UA Bio. Sci.
<i>Phalaris canariensis</i>	Poaceae	Annual	Bedrock Seeds
<i>Polygonum lapathifolium</i>	Polygonaceae	Annual	UA Bio. Sci.

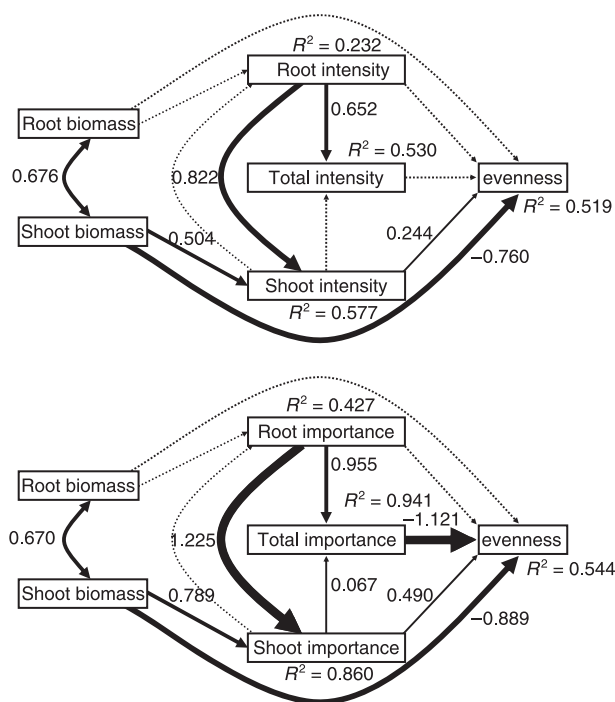
**Table 1.** Species descriptions and sources of seed used in the study. UA Bio. Sci. refers to seed produced in the University of Alberta Department of Biological Sciences greenhouse; UA Ren. Res. refers to seed donated by the University of Alberta Department of Renewable Resources, Bedrock Seeds is a local seed producer in Edmonton, AB, and Valley Seed Service is a weed seed provider in Fresno, CA

(MaxNN – Min(NN,RN)), shoot competition importance was measured as  $(SN - NN)/(MaxNN - Min(NN,SN))$ , and total competition importance as  $(AN - NN)/(MaxNN - Min(NN,AN))$ . NN is focal plant biomass when grown with no neighbours (tube and netting), and MaxNN is the biomass of the largest single NN plant in the entire experiment. RN is focal plant biomass when grown with the roots, but not shoots, of neighbours, SN is focal plant biomass when grown with the shoots, but not roots, of neighbours and AN is focal plant biomass when grown with all neighbours (roots and shoots). Positive values of the  $C_{imp}$  indicate facilitation while increasingly negative values indicate increasing importance of competition.

#### STATISTICAL ANALYSIS

We used SEM using observed variables (Path modelling) to separate the direct and indirect effects of root, shoot, and total competition intensity and importance on the diversity of the experimental mesocosms. SEM allows the direct and indirect theoretical causal relationships between a series of intercorrelated variables to be tested (Shipley 2000; Grace 2006). In a SEM, each single-headed arrow represents a causal relationship such that the variable at the tail of the arrow is a direct cause of the variable at the head. A double-headed arrow indicates an unresolved correlation between two variables. An initial SEM is specified based on prior theoretical knowledge, and is then tested to determine whether the covariance structures implied by the model adequately fit the actual covariance structures of the data. An initial theory-based model that adequately fits the data is a powerful confirmation of the validity of the theory used to construct the initial model. If the initial model does not adequately fit the data then model modification indices provide a strong tool for data exploration and hypothesis generation (Grace 2006).

The initial SEM was developed to separate the direct and indirect effects of root, shoot, and total competition intensity and importance on the diversity of the experimental mesocosms (Fig. 2). An undirected correlation was included between root and shoot biomass because the variables were measured on the same plants and hence should be correlated for allometric reasons. Root biomass directly influenced root competition, while shoot biomass directly influenced shoot competition. There is abundant evidence that increasing shoot biomass increases the shading of subordinate plants and hence increases the strength of shoot competition (e.g. Grime 2001; Keddy 2001). Similarly, increasing fine root biomass should lead to increased depletion of available soil nutrients and hence increased root competition. Both root and shoot competition are components of the total competition a plant experiences (Cahill 1999). Direct paths from shoot competition to root competition and *vice versa* were included to account for root–shoot competition interactions (Cahill 1999; 2002a). Finally, all three components of competition may



**Fig. 2.** The final structural equation models. Non-significant 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.

influence community structure. There is abundant evidence that shoot competition can influence community structure, both directly and as a component of total competition (e.g. Grime 2001; Keddy 2001). Current evidence suggests that symmetric root competition has little influence on community structure (Lamb & Cahill 2008), however relationships between root competition intensity and community structure have been observed (Rajaniemi 2002; Rajaniemi *et al.* 2003). Finally, root and shoot biomass was included as direct causes of diversity because those variables may influence community structure through a variety of mechanisms other than competition.

Each bivariate relationship represented by an arrow in the initial path models 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 to the fit of a model with a quadratic relationship using the *glm* function in the R Package (R Development Core Team 2006). Three significant nonlinear bivariate relationships were identified. The nonlinear relationship

between evenness and ln-transformed shoot biomass ( $F_{1,36} = 9.88$ ,  $P = 0.003$ ) was reduced, but not eliminated by ln-transformation of evenness ( $F_{1,36} = 5.57$ ,  $P = 0.023$ ). Nonlinear relationships between shoot competition importance and both root competition ( $F_{1,35} = 17.63$ ,  $P < 0.001$ ) and total competition ( $F_{1,35} = 4.17$ ,  $P = 0.049$ ) importance were also found. Inspection of the relationship between ln-evenness and ln-shoot biomass showed that this relationship was predominantly a decline in evenness with increasing biomass. Similarly, the nonlinear relationships involving shoot competition importance were both predominantly for an increase in root and total competition importance with increasing shoot importance. Since none of the nonlinear relationships were unimodal, we chose to treat them as linear in the SEM.

The SEMs were fit using M-plus 4.1 (Muthén & Muthén 2006). The  $\chi^2$  test of model fit was used to determine whether the fit between model and data was adequate ( $P > 0.05$ ). The  $\chi^2$  test of model fit is recommended since a non-significant result is a strong indication of an adequate fit between model and data (Grace 2006). The fit between the initial and data was adequate for the intensity model ( $\chi^2_3 = 0.770$ ,  $P = 0.857$ ) so no modifications were made to the model structure. The initial importance model could not be solved. Inspection of the data identified an outlying value for shoot competition importance  $c. 3\times$  higher than any other value. Removal of this data point resulted in an importance model with adequate fit ( $\chi^2_3 = 0.470$ ,  $P = 0.925$ ). 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 small sample size in this study, coefficients with  $P < 0.100$  were considered significant. Non-significant paths were retained in the final model. The SEM was non-recursive (i.e. containing a loop between root and shoot competition), so the variance explained for the endogenous variables was estimated using the blocked error method (Hayduk 2006).

**Results**

The final SEMs for both intensity ( $\chi^2_3 = 0.770$ ,  $P = 0.857$ ; Fig. 2; Table 2) and relative importance ( $\chi^2_3 = 0.470$ ,

$P = 0.925$ ; Fig. 2; Table 3) adequately fit our data. Both models were very similar, as there was a high degree of correlation between the intensity and relative importance of root (0.791,  $P < 0.001$ ), shoot (0.679,  $P < 0.001$ ) and total (0.721,  $P < 0.001$ ) competition. Focal plants experienced intense and important root and total competition, but facilitation by neighbouring shoots occurred in 20 of the 39 experimental mesocosms. Increasing shoot biomass led to a decline in both shoot competition intensity and importance, and a shift to facilitation at higher levels of productivity. Increasing intensity and importance of shoot competition led to reduced evenness, but neither root competition intensity nor importance had any direct effects on evenness (Fig. 3). Increasing root competition intensity and importance increased both shoot and total competition intensity and importance. Shoot competition intensity did not influence total competition intensity, however, increasing shoot competition importance caused a small increase in the total importance of competition. Increasing root competition intensity and importance indirectly reduced evenness through the effects of increased root competition on shoot competition. Increasing root competition importance also had a positive effect on evenness through the effects of root competition on total competition importance.

**Discussion**

Root competition was very strong relative to shoot competition, yet root competition had no direct influence on plant community structure. Root competition only indirectly influenced community structure, reducing evenness through root–shoot competition interactions. Root–shoot competition interactions have been shown to influence individual plants (Cahill 1999, 2002a), but this is the first study to demonstrate that root–shoot competition interactions can also have consequences at the community level.

**Table 2.** Unstandardized and standardized path coefficients, the standard error of the unstandardized coefficients and  $t$ -test results from the structural equation model of competition intensity. The paths described in each section of the table were from the variables in lower case to the variable at the top in bold

	Unstandardized path coefficients	Standard error	$t$ -value	$P$ -value	Standardized coefficients
<b>Root intensity</b>					
Root biomass	-0.335	0.309	-1.084	0.285	-0.237
Shoot intensity	-0.545	0.743	-0.733	0.468	-0.558
<b>Shoot intensity</b>					
Shoot biomass	0.571	0.224	2.549	0.015	0.504
Root intensity	0.842	0.440	1.912	0.063	0.822
Total intensity					
Root intensity	0.675	0.121	5.561	< 0.001	0.652
Shoot intensity	0.168	0.119	1.420	0.164	0.166
<b>Evenness</b>					
Root intensity	0.062	0.060	1.046	0.302	0.177
Shoot intensity	0.084	0.046	1.847	0.072	0.244
Total intensity	-0.020	0.055	-0.359	0.722	-0.058
Shoot biomass	-0.297	0.064	-4.660	< 0.001	-0.760
Root biomass	0.074	0.076	0.965	0.34	0.148
<b>Root–shoot biomass covariance</b>	0.260	0.074	3.496	0.001	0.676

**Table 3.** Unstandardized and standardized path coefficients, the standard error of the unstandardized coefficients and *t*-test results from the structural equation model of competition importance. The paths described in each section of the table were from the variables in lower case to the variable at the top in bold

	Unstandardized path coefficients	Standard error	<i>t</i> -value	<i>P</i> -value	Standardized coefficients
<b>Root importance</b>					
Root biomass	-0.167	0.184	-0.905	0.371	-0.299
Shoot importance	-0.751	0.793	-0.947	0.349	-1.341
<b>Shoot importance</b>					
Shoot biomass	0.587	0.169	3.472	0.001	0.789
Root importance	2.187	0.646	3.386	0.002	1.225
<b>Total importance</b>					
Root importance	0.934	0.03	31.093	< 0.001	0.955
Shoot importance	0.037	0.017	2.190	0.035	0.067
<b>Evenness</b>					
Root importance	0.793	0.588	1.349	0.185	0.834
Shoot importance	0.261	0.077	3.381	0.002	0.490
Total importance	-1.090	0.610	-1.787	0.082	-1.121
Shoot biomass	-0.352	0.068	-5.171	< 0.001	-0.889
Root biomass	0.034	0.077	0.445	0.659	0.065
<b>Root–shoot biomass covariance</b>	0.247	0.072	3.432	0.001	0.670

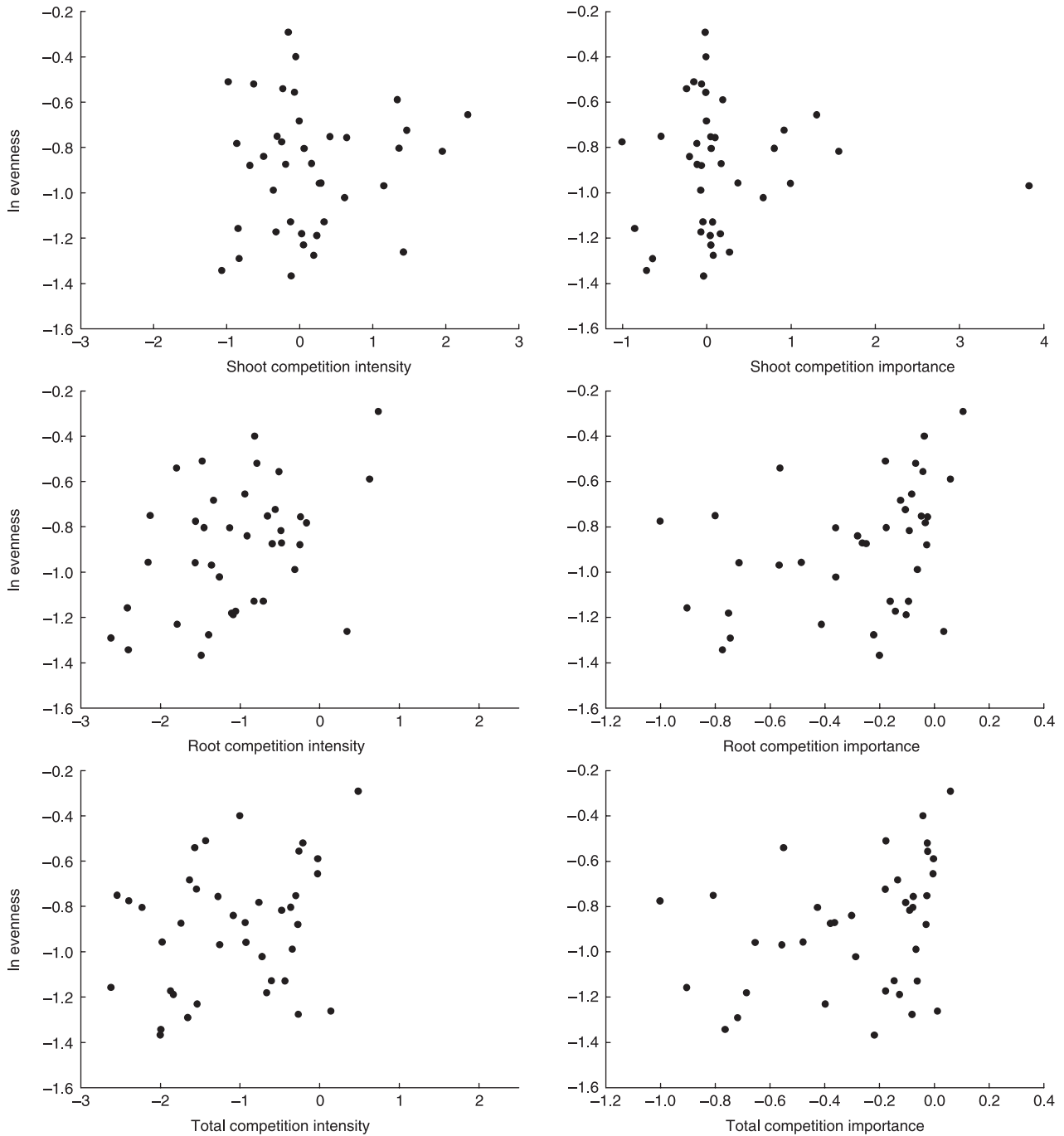
There is a growing body of evidence supporting the theory that size-symmetric root competition has little direct impact on plant community structure. We found that neither the intensity of root competition nor the importance of root competition relative to a fertility gradient influenced evenness in an experimental plant community. Lamb & Cahill (2008) similarly found that variation in competition intensity in a native fescue grassland was unrelated to plant community species richness, evenness or composition. Indirect supporting evidence includes the lack of consistent relationships between plant root biomass and root competition intensity (e.g. Belcher *et al.* 1995; Peltzer *et al.* 1998; Cahill 1999; Cahill & Casper 2000; Lamb *et al.* 2007), and the lack of links between root biomass or competition intensity and diversity (Cahill 2003; Lamb 2008). Together these studies and others clearly demonstrate that even though root competition is intense in many plant communities (Casper & Jackson 1997; Keddy 2001), root competition is not necessarily important in structuring those communities (Welden & Slauson 1986; Grace 1991; Brooker *et al.* 2005; Brooker & Kikvidze 2008; Lamb & Cahill 2008).

Root competition may not have a direct role in structuring plant communities; however, these results demonstrate that interactions between root competition and shoot competition are an indirect mechanism through which root competition can structure communities. In this study interactions influencing evenness occurred through both the influence of root competition intensity and importance on shoot competition, and the direct influence of root competition importance on the total importance of competition. Incorporating root–shoot competition interactions into a comprehensive theory of the importance of competition is challenging because root–shoot competition interactions are widespread but poorly understood (Wilson 1988; Cahill 1999, 2002a). In general, root–shoot competition interactions occur when one

component of competition affects a plant's ability to compete for the other component. For example, root competition may reduce shoot growth and thus affect a plant's ability to reach the canopy and compete for light. The potential for root–shoot competition interactions is predicted to be highest when root and shoot competition are of similar intensity, but this has not been empirically tested (Cahill 1999).

We propose that the effects of root and shoot competition and root–shoot competition interactions on community structure can be integrated with the direct effects of shoot competition through a new state variable: the total size-asymmetry of competition (Fig. 4). We suggest that the overall size-asymmetry of competition is the mechanism directly driving the influence of competition for plant community structure. Increasing either the intensity or relative importance of shoot competition should increase the overall size-asymmetry of the competition a plant experiences, and hence the effect of that competition on plant community structure. There should be no direct relationship between size-symmetric root competition and size-asymmetry, but root competition is likely to indirectly influence the overall size asymmetry of competition through root–shoot competition interactions.

Integrating root and shoot competition into a single axis of competitive size-asymmetry can explain why root competition can be strong, but inconsequential, while relatively weaker shoot competition and root–shoot competition interactions can have strong effects on community structure. Cahill (2003) and Lamb & Cahill (2008) have shown that there are few relationships between competition and community structure in low-statured communities with intense root competition but little or no shoot competition. Similarly, Rajaniemi *et al.* (2003) showed that root competition had no effect on diversity in unfertilized artificial communities but a negative effect in fertilized treatments. Shoot biomass, light interception and presumably shoot competition intensity

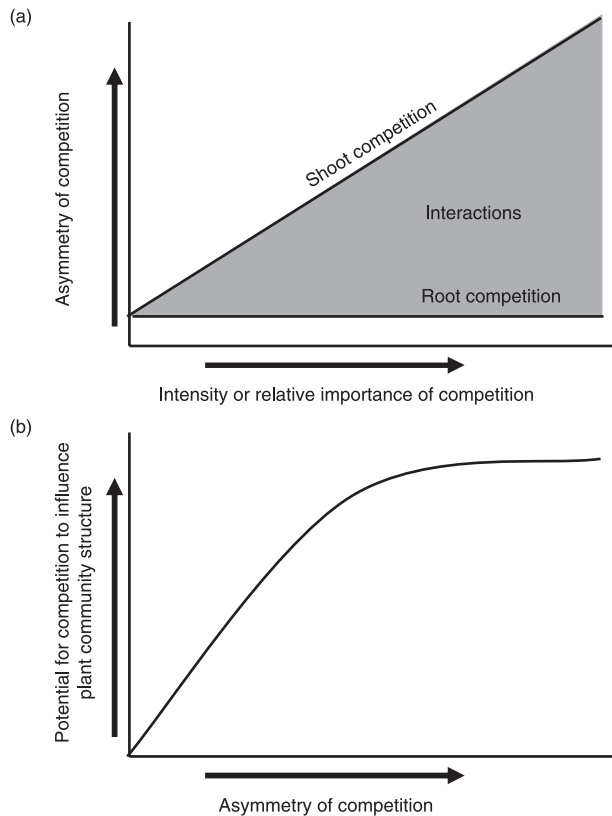


**Fig. 3.** Relationships between shoot, root, and total competition intensity and relative importance and plant community evenness. More negative values of competition intensity and importance indicate stronger competition, while positive values indicate facilitation.

increased with fertilization in that study, consistent with our prediction that root competition will only influence plant community structure when there is the potential for root–shoot competition interactions.

The potential for root–shoot competition interactions to structure plant communities depends on the ability of such interactions to modify the size-asymmetry of shoot competition. Little is known about how root–shoot competition interactions are likely to influence size-asymmetry. Cahill

(1999) predicted that there should be a peak in the strength of root–shoot competition interactions when root and shoot competition is similar in intensity, but this has not been directly tested. In the absence of any actual data, here we assume Cahill’s prediction to be correct, and also that shoot competition and root–shoot competition interactions contribute additively to overall size-asymmetry. We predict that when root competition is more intense than shoot competition, root–shoot competition interactions should increase the overall



**Fig. 4.** Conceptual model relating competition intensity, size-asymmetry and the impact of competition on plant community structure. (a) Relationships between the intensity and size-asymmetry of root and shoot competition. Total competition size-asymmetry will often fall in the shaded region due to interactions between root and shoot competition. (b) Relationship between the overall size-asymmetry and the potential for competition to impact plant community structure. The relationship may saturate if the impact of root–shoot competition interactions on community structure declines at high levels of shoot competition.

size-asymmetry of competition. When shoot competition is more intense than root competition, however, the influence of interactions should decline, counterbalancing the increasing size-asymmetry of shoot competition (Fig. 4).

Despite the high level of productivity, shoot competition was very weak in this study, with facilitation (measured as intensity) occurring in 51% of the mesocosms. One explanation for the high intensity of facilitation is a bias introduced into the lnRR by the lack of initial biomass data (Kikvidze *et al.* 2006). When the experimental control is a plant grown without neighbours, the directional bias causes measures of competition intensity to be more conservative than measures of facilitation intensity. This bias can explain why the intensity of facilitation was much greater than the importance of facilitation, since the importance index is unaffected by the bias (Fig. 3). It remains unclear, however, why facilitation was so common at higher levels of productivity. Fifty percent light penetration occurred in the most heavily fertilized mesocosms in July (PFD *c.* 600  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ), suggesting that shading may not have been deep enough to cause significant

light competition. Facilitative effects from neighbouring shoots, such as increased humidity and reduced evaporation, may have mitigated the negative effects of shading (Bertness & Hacker 1994). Alternatively, *L. lewisii* may simply be a good response competitor for light (*sensu* Goldberg 1990), leading to an underestimate of community-wide shoot competition. Finally, with only one phytometer, we cannot discount the possibility our results may have arisen from a shift in the competitive hierarchy among the species along the fertilization gradient.

The increase in both intensity and importance of facilitation with increasing plant community biomass and nutrient availability is counter to the Stress-Gradient-Hypothesis (SGH) (Brooker *et al.* 2008). The SGH proposes that the strength of facilitation should increase with the severity of environment stresses. Our results could be explained if *L. lewisii* was responding to a stress associated with increased fertilization that the other species in the experiment were much less sensitive to. Alternatively, several studies have found patterns of facilitation and environmental stress that do not conform to the SGH (e.g. Tielbörger & Kadmon 2000; Pennings *et al.* 2003; Maestre & Cortina 2004), suggesting that the relationship between facilitation and stress may be more complex than the SGH.

Facilitative effects present no challenges to our model of size-asymmetry, however. Competition and facilitation are simply points on a continuum of negative through positive ‘neighbour effects’. Interactions between competition and facilitation often occur in natural communities (Callaway 1995; Callaway & Walker 1997; Brooker *et al.* 2008); such interactions are as easily integrated by the total size-asymmetry state variable as root–shoot competition interactions.

In summary, this study demonstrates that while root competition does not directly influence plant community diversity, root competition may indirectly structure diversity through root–shoot competition interactions. It may seem surprising that an ecological process such as root competition that has such a severe impact on individual plants should have so little direct effect on community structure, but these observations are predictable from the symmetrical nature of root competition. While root competition may not directly influence plant community structure, we show that root competition indirectly structured this plant community through root–shoot competition interactions. We propose that this indirect effect of root competition occurred because root–shoot competition interactions altered the overall size-asymmetry of competition. We propose that the total size-asymmetry of competition should be used as a new state variable integrating the separate influences of shoot competition and root–shoot competition interactions on community structure.

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