Lack of relationship between below-ground competition and allocation to roots in 10 grassland species

JAMES F. CAHILL JR
Department of Biological Sciences, University of Alberta, Edmonton, AB T6G 2E9, Canada

Summary

1 A field experiment in a native grassland in Central Alberta, Canada, tested whether plants alter relative allocation to roots vs. shoots in response to below-ground competition, and whether the mass of a species’ root system accounts for interspecific differences in below-ground competitive response.
2 Seedlings of each of 10 native species were transplanted into the naturally occurring vegetation in the field at the start of the growing season. Root interactions between the target plants and their neighbours were manipulated through the use of PVC root exclusion tubes, with target plants grown with or without potential root interactions with their neighbours. Neighbour shoots were also tied back, forcing any target–neighbour interactions to be below ground.
3 Below-ground competition generally reduced plant growth, with its relative magnitude varying among species.
4 An allometric analysis indicated that competition below ground did not result in an increase in the relative biomass allocated to roots for any of the 10 target species. This is counter to the growth-balance hypothesis (and optimal foraging theory). Below-ground competition did increase root : shoot ratios, but this was due to reduced plant size (small plants have larger root : shoot ratios), rather than adaptive plasticity.
5 A species’ below-ground competitive ability was not related to its root system size. Although this finding is counter to commonly made assumptions, it is supported by other work demonstrating below-ground competition to be generally size-symmetric.
6 Despite the majority of plant–plant interactions in grasslands being below ground, our understanding of plant competition above ground is significantly more robust. Several wide-spread assumptions regarding below-ground competition are suspect, and more multispecies studies such as this are required to provide a fuller picture of how plants respond to, and compete for, soil resources.

Key-words: balanced-growth hypothesis, below-ground competition, community ecology, growth allometry, size-symmetric competition

Introduction

Competition for soil resources is often as strong or stronger than competition for light (Casper & Jackson 1997). Although competition reduces individual plant growth regardless of whether it is for light or soil resources, the mechanisms by which plants compete, how plants respond to competition, and how the strength of competition varies in natural communities, is different for above- and below-ground resources (Casper & Jackson 1997). Although we can make sweeping statements about below-ground competition in general, the detail of our understanding of the ecological consequences of and morphological responses to below-ground competition in natural communities is limited.

For example, little is known about how plants change biomass allocation patterns in response to below-ground competition. Many plants respond to shading by other plants by changing shoot architecture and biomass allocation (Schmitt & Wulff 1993; Aphalo et al. 1999), and can alter root : shoot ratios (Reynolds & Antonio 1996), root architecture (Fitter & Stickland 1991) or uptake capacity (Jackson & Caldwell 1991) in response to low soil resource availability. Plants can also alter fine root growth in response to the presence of neighbouring plants (Gersani et al. 2001), and competition...
in general can alter plant rooting depths (Wardle & Peltzer 2003). Studies describing changes in root allocation specifically in response to below-ground competition are rare. Wilson & Tilman (1995) found root : shoot ratios increased with below-ground competition, inferring it to be an adaptive response. However, increased root : shoot ratios can be due ontogenetic shifts, rather than adaptive plasticity (Gedroc et al. 1996; McConnaughay & Coleman 1999; Muller et al. 2000; but see Shipley & Meziane 2002), and increased root : shoot plasticity is not consistently related to competitive ability (Reynolds & Antonio 1996). To date, no study has separated these aspects, and such information is critically important to our understanding of below-ground competition in natural communities.

The effects of below-ground competition on individual plant growth are easily measured, and generally vary among species (Wilson & Tilman 1995), yet little is known about which plant traits make different species effective competitors below ground. Much as it has been assumed that plants will increase root allocation in response to root competition, it has also been assumed that root system size is positively associated with below-ground competitive ability (e.g. Tilman 1988; Wilson & Tilman 1995; Rajaniemi 2002). However, empirical support for this idea is limited (e.g. Aerts et al. 1991). Casper & Jackson (1997) suggest a variety of reasons why root abundance alone may not be a good indicator of below-ground competitive ability, including: (i) higher root densities can result in increased competition within a single plant’s root system; (ii) root location may matter more than amount; (iii) mycorrhizas may be very important to resource capture; and (iv) uptake kinetics could be crucial to determining the outcome of below-ground competition. Evidence is also accumulating that, in contrast to competition for light, below-ground competition is size-symmetric (Weiner et al. 1997; Cahill & Casper 2000; Blair 2001; von Wettberg & Weiner in press). As a result, the growth consequence of below-ground competition should be directly, but not disproportionately, related to root system size.

In this study, I address two questions essential for a mechanistic understanding of plant competition. (i) Do plants alter relative allocation to roots vs. shoots in response to below-ground competition? (ii) Does the mass of a species’ root system account for interspecific differences in below-ground competitive response? These questions were investigated through measures of root and shoot biomass of target plants in a field experiment in a rough fescue grassland in central Alberta, Canada. Target plants consisted of individuals of 10 native species, grown either with or without interactions with neighbouring roots.

Materials and methods

STUDY SITE AND TARGET SPECIES

The experiment was conducted from May to August 2001 within the 3200 ha Kinsella Beef Cattle Research Ranch, in Alberta, Canada (53° N, 111° W). The field site has never been seeded or tilled, and is grazed annually in the fall by cattle. Vegetation is primarily graminoid, dominated by Festuca hallii, Stipa curtiseta and Koeleria macrantha. Common forbs include Achillea millefolium, Comandra umbellata and Solidago missouriensis. Species nomenclature follows that of Moss & Packer (1994), except for Festuca hallii and Helianthus petiolaris, which follow that of the USDA PLANTS Database (USDA, NRCS 2001). Woody plants are present (e.g. Rosa arkansana), but contribute little to standing biomass. Over 60% of the phytomass in this system is below ground, mostly in the upper 20 cm of soil (Cahill, personal observation). Annual precipitation during the study year was 57% below the 27-year average (average = 322 mm), and precipitation the winter preceding this study was 90% below average.

Individuals of 10 native species were used as target plants (Table 1), with seed obtained from field collections and local native seed suppliers. Seed was sown into glasshouse flats (72 cells per flat) on 1 April (Festuca, Geum, Potentilla) and 19 April (Achillea, Galium, Agoseris, Coreopsis, Linum, Kohleria, Helianthus), and placed in a growth chamber (16L:8D; 20 °C). Seedlings

<table>
<thead>
<tr>
<th>Species code</th>
<th>Family</th>
<th>Life history</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ac</td>
<td>Asteraceae</td>
<td>Perennial</td>
</tr>
<tr>
<td>Ag</td>
<td>Asteraceae</td>
<td>Perennial</td>
</tr>
<tr>
<td>C</td>
<td>Asteraceae</td>
<td>Annual</td>
</tr>
<tr>
<td>H</td>
<td>Asteraceae</td>
<td>Annual</td>
</tr>
<tr>
<td>F</td>
<td>Gramineae</td>
<td>Perennial</td>
</tr>
<tr>
<td>K</td>
<td>Gramineae</td>
<td>Perennial</td>
</tr>
<tr>
<td>L</td>
<td>Linaceae</td>
<td>Perennial</td>
</tr>
<tr>
<td>Ge</td>
<td>Rosaceae</td>
<td>Perennial</td>
</tr>
<tr>
<td>P</td>
<td>Rosaceae</td>
<td>Perennial</td>
</tr>
<tr>
<td>Ga</td>
<td>Rubiaceae</td>
<td>Perennial</td>
</tr>
</tbody>
</table>
were thinned to one individual per cell, and all flats were placed outside at the field site 1 week prior to transplantation.

**EXPERIMENTAL DESIGN**

Ten 9 × 16 m blocks were established throughout a 20-ha area of native grassland at the ranch. Each block was divided into a 2 × 5 array of 10 plots (2 × 3 m each), with 1 m separating plots and six individuals of one randomly selected species transplanted into each plot. Within each plot, seedlings were arranged in a 3 × 2 array, with each seedling separated by 1 m from the nearest other transplanted seedling. The original design of this experiment involved each of these individuals receiving one of six treatments (manipulating below-ground competition, shoot competition, and potential hyphal growth). However, the drought resulted in the shoot competition and fungal growth treatments being abandoned during the growing season, and they will not be discussed further. This paper deals specifically with two of the six individuals of each of 10 species in each of 10 blocks, comparing plants grown with root interactions with those grown without root interactions.

Root interactions between the target plants and their neighbours were manipulated through the use of 15-cm diameter × 20-cm lengths of PVC pipe (‘root exclusion tubes’). On 7–9 May 2001, the exclusion tubes were installed by digging two holes in each plot and placing a tube into one hole (– roots treatment), but not the other (+ roots treatment). Large roots were removed from the excavated soil, the holes were refilled, and the naturally occurring vegetation surrounding the holes was left intact. On 15 May 2001, seedlings of the appropriate species were transplanted into each plot. Transplanting consisted of making a small depression in the soil, either in the centre of the tube or in the hole without a tube, and inserting one seedling. The seedlings were watered daily for 7 days, at which time any dead individuals were replaced.

Root and shoot competition can have non-additive effects on plant growth (Cahill 1999, 2002a). As this study was specifically focused on below-ground competition, the potentially confounding effects of shoot competition were eliminated as advocated in Cahill (2002b). Shoot competition between neighbours and target plants was prevented by using thin tree netting (2 × 2 cm squares, 1 mm thick netting) to tie back the shoots of the neighbouring vegetation. A 50 × 50 cm square of netting was centred over each target plant, anchored such that its centre was flush with the ground. The four corners were then staked 15 cm above the soil surface and the neighbouring vegetation pulled away from the target plant and towards the netting edges. The netting is similar in diameter to fishing line, casting little shade (93% light penetration). Similar netting has been used in other studies without adverse effects on neighbouring vegetation (Wilson & Tilman 1991; Twolan-Strutt & Keddy 1996; Cahill 1999, 2002a).

Repeated measures of morphological traits (e.g. height) can alter the intensity of herbivory (Cahill et al. 2001), above-ground biomass production (Hik et al. 2003), and relative biomass allocation within a plant (Cahill et al. 2002). As a result, non-destructive measures were not taken during this experiment and, on 20 August 2001, all target plants were harvested. Harvest consisted of cutting each plant at the soil surface and extracting the root systems from the soil. Roots were then washed free of soil, and the roots and shoots were dried separately at 70 °C and weighed. It is not possible to fully extract root systems from the field, particularly when target plant roots are entangled with those of the neighbouring vegetation (Cahill 2002b). At a minimum, the tap root (when present) and larger roots of all target plants were recovered here. Though the excavations failed to recover some unknown proportion of the fine roots that are likely to contribute most to root length, they were successful in recovering the majority of the larger roots that contribute most to root biomass (Smit et al. 2002).

**ANALYSES**

The effects of root interactions and species identity on target plant mortality were analysed using a generalized linear mixed model (GLMM). Specifically, plant status (living or dead) served as a binomially distributed response variable, with species identity and root exclusion treatment as fixed effects, and block, block × species, block × treatment, and block × species × treatment, as random effects in the model. All analyses were conducted using SAS v8.0 (SAS 1999), with the %GLIMMIX macro in PROC MIXED allowing use of binomially distributed data (Littel et al. 1996). The effects of root exclusion and species identity on target plant biomass were analysed using a similar statistical model, with the exception being that the response variable (Ln(total biomass)) was normally distributed and %GLIMMIX was not used.

There is no consensus on the best way to analyse questions of plant allometry (Muller et al. 2000), and thus I used a linear modelling approach similar to that used in related studies (Muller et al. 2000; Shipley & Meziane 2002). The effects of species identity and root exclusion on the relative allocation to roots were determined using a GLMM, with Ln(root biomass) as the response variable and Ln(shoot biomass) as a covariate. A significant root exclusion effect would indicate a difference in relative biomass allocation to roots as a function of below-ground competition, independent of any allometric shift in root : shoot ratios (i.e. evidence of adaptive plasticity). An additional analysis was conducted to determine whether there were any covariate × fixed effect (e.g. root exclusion) interactions, which would indicate that the root exclusion treatment alters relative allocation to roots in a size-dependent manner.

To determine whether a species’ below-ground competitive ability was related to its root system size, a
Root allocation and below ground competition

GLM was conducted. Mean Ln(shoot biomass) for each species served as the dependent variable \( (n = 10 \) species), the root exclusion treatment was a fixed effect, and root system biomass served as a covariate. Root system biomass for each species was measured as the mean root biomass of all individuals of that species when grown without below-ground competition. This approach provides a measure of potential root biomass during this experiment, rather than a theoretical maximum that would be provided from glasshouse studies or herbarium specimens. The strength of below-ground competition is indicated as the difference in shoot biomass between the +/− roots treatments. If this difference changes as a function of root system size it would indicate that below-ground competitive ability is influenced by root system size. This would be indicated as a significant covariate × root exclusion interaction in the GLM. Total biomass could not be used as the response variable in this analysis as there would have been shared data in both axes, a factor that can cause spurious correlations (Jackson & Sonners 1991).

Results

The root exclusion tubes were effective in preventing neighbour root growth around the target plants and reducing root competition, as evidenced by lower neighbour root densities (Cahill, personal observation) and higher soil moisture (HydroSense Soil Water Measurement; Campbell Scientific, Edmonton, Canada; mean ± SD: exclusion tube 11.00 ± 2.64, no tube 7.65 ± 1.63, \( F_{1,9} = 22.43; P = 0.001 \)) inside the exclusion tubes than outside the tubes. There was no visual evidence that the tubes restricted target plant root growth, and the largest root system of any target plant was 0.74 g by dry weight (41 g m\(^{-2}\) within the exclusion tube) while standing root biomass outside of the tubes was 20× higher (mean ± SD: 905 ± 350 g m\(^{-2}\)).

Mortality, plant growth and biomass allocation

Mortality varied among species, but was not affected by root exclusion or the species × root exclusion interaction (Fig. 1a; species \( F_{9,81} = 2.43, P = 0.017 \); root exclusion \( F_{1,9} = 0.16, P = 0.695 \); species × root \( F_{9,81} = 0.61, P = 0.786 \)). Although the species × root exclusion treatment was not significant, visual inspection suggests that mortality of some species (e.g. Festuca) was more strongly influenced by root exclusion than others. Separate chi-square for each species failed to detect any significant differences in mortality as a function of root exclusion for any of the 10 species (all \( P > 0.20 \)).

The effects of root exclusion on target plant biomass varied among species (Table 2; Fig. 1b). Neighbour roots reduced biomass for most species, though only four of the 10 species showed a significant effect in posthoc tests (Fig. 1b). For only one species (Festuca) was there a trend towards higher biomass in the + roots than the – roots treatment (\( P = 0.22 \)).

Relative allocation to root biomass varied among species but was not affected by root exclusion (Table 2, Fig. 2a) nor were there any significant covariate × factor (e.g. root exclusion treatment, species) interactions (all

---

**Table 2** GLMM results for the analyses of total plant biomass and relative biomass allocation to roots. In both models, block was treated as a random factor, and species identity and root exclusion treatment served as fixed effects. As quantifying variation among blocks was not a goal of this study, the significance of block effects is not presented. In the latter analysis, Ln(root biomass) served as the response variable, with Ln(shoot biomass) as the covariate. No factor × covariate interactions were significant (\( P > 0.25 \)), meeting that assumption of ANCOVA. d.f. in both analyses were calculated using Satterthwaite’s method (Littel et al. 1996).

<table>
<thead>
<tr>
<th>Factor</th>
<th>Ln(total biomass)</th>
<th>Ln(root biomass)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>( F_{\text{DF}} )</td>
<td>( P )-value</td>
</tr>
<tr>
<td>Ln(shoot biomass)</td>
<td>–</td>
<td>63.22(_{,18,4} )</td>
</tr>
<tr>
<td>Species</td>
<td>8.57(_{,67,1} )</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Treatment</td>
<td>16.34(_{,81,7} )</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Species × treatment</td>
<td>2.98(_{,56,3} )</td>
<td>0.006</td>
</tr>
</tbody>
</table>

---

When using average values for each of the 10 species, root and shoot biomass were correlated across species ($F_{1,17} = 15.36; P < 0.01$), and root interactions reduced target shoot biomass ($F_{1,17} = 5.68; P = 0.029$; Fig. 2b), both supporting results of prior analyses (Figs 1b and 2a). However, the size of a species’ root system had no impact on the strength of below-ground competition, as evidenced by homogeneity of slopes in the GLM (root biomass × root exclusion treatment $F_{1,16} = 0.36; P = 0.557$; Fig. 2b).

**Discussion**

When neighbouring roots altered target plant growth, their effects were generally negative (Fig. 1b). Four of the 10 target species showed a significant effect of below-ground competition on plant growth, and 9 of the 10 species had a trend in that direction (Fig. 1b). These results are consistent with prior studies, with Gerry & Wilson (1995) and Cahill (2002a) finding no evidence of facilitation through root interactions for any of their 10 species, and Wilson & Tilman (1995), who found only trends towards facilitative effects and even then for only two of the eight species in their undisturbed plots. There appear to be no widespread net facilitative effects of root interactions in these terrestrial herbaceous plant communities, although facilitation could still occur via interactions with plant shoots. *Festuca hallii*, however, had trends towards both reduced mortality and increased growth in the presence of neighbour roots. The consistency of these results warrants further investigation on the nature of biotic interactions involving this species, as it is a dominant member of this community.

**DO PLANTS ALTER RELATIVE ALLOCATION TO ROOTS IN RESPONSE TO BELOW-GROUND COMPETITION?**

Root : shoot ratios increased with below-ground competition, though this was due to changes in plant size, rather than an adaptive response to below-ground competition (Table 2, Fig. 2a). Demonstrating increased root : shoot ratios with below-ground competition is not new (Wilson & Tilman 1995), though prior studies have not differentiated between adaptive plasticity and ontogenetic responses (Gedroc *et al.* 1996; McConnaughay & Coleman 1999; Muller *et al.* 2000).

Variation in root allocation as a function of plant size rather than in response to limiting resources, is counter to the balanced-growth hypothesis, which is built into many models of competition and community
Root allocation and below-ground competition

The balanced-growth hypothesis states that plants preferentially allocate resources to the organs responsible for acquiring the most limited resource (Shipley & Meziane 2002). In this study soil resources were limiting (Fig. 1b), and yet there was no increase in root allocation in response to below-ground competition. Although Muller et al. (2000) also rejected the balanced-growth hypothesis, Shipley & Meziane (2002) found support for it in their study of 22 plant species, and suggest four reasons to explain the differing results: (i) greater statistical power; (ii) Muller et al. (2000) ran their study for 4 months vs. 35 days for Shipley & Meziane (2002); (iii) Shipley & Meziane (2002) used a more frequent, and thus temporally homogeneous, supply of resources; and (iv) there may have been competition in the study by Muller et al. (2000). Here, competition did not alter root allocation (Fig. 1c), rejecting argument (iv). The fact that both this study and that of Muller et al. reached similar answers suggests this is not due to statistical power alone. This study was also longer than Shipley & Meziane’s (2002), and field conditions certainly result in temporally heterogeneous resource supply. In a greenhouse study using a fertilization regime similar to Muller et al. (2000), Gedroc et al. (1996) found plasticity in root-shoot allocation was greatest for very young plants, and root:shoot ratios in low and high resource conditions converged as the plants aged. This suggests that the age of harvest used by Shipley & Meziane (2002) is more likely to support the balanced-growth hypothesis than that used by Muller et al. (2000) and here. It is clear that under certain circumstances, plants can alter root-shoot allocation in response to environmental conditions. The more important question that remains is whether any such shifts in allocation, no matter how short term, confer any advantage. This is a decidedly more difficult question to answer, and one for which we have little information.

Plants possess a variety of mechanisms by which they can perceive the presence of neighbouring roots, and neighbouring roots can influence root distributions (Mahall & Callaway 1992; Brisson & Reynolds 1994; Gersani et al. 2001). Results from this study suggest that such information does not alter the total amount of carbon going to the root system, although it could allow for fine-scale adjustments as to where the roots are placed. Such a response parallels that of shoot competition, where natural shading does not necessarily change the proportion of plant biomass that is in the shoots, but can alter relative allocation between stems and leaves (Casper et al. 1998). Together, these findings suggest that whole plant allocation patterns, though variable among species and as a function of plant size, are not nearly as plastic as is often argued. As roots serve functions other than resource capture (e.g., structural support and storage) it is likely that adjustments made in response to below-ground competition are more subtle than patterns of whole plant biomass allocation. This argument is supported by the findings that young plants do seem to have more biomass plasticity than do older plants (Gedroc et al. 1996), as it is sensible that the roots of seedlings are primarily responsible for anchorage and uptake, and not nutrient storage. As plants mature, root weight becomes concentrated in the larger storage roots, and thus root biomass is likely to be a reasonable indicator of below-ground foraging effort for juvenile, but not older, plants.

Does the Mass of a Species’ Root System Account for Interspecific Differences in Below-Ground Competitive Response?

A species’ root system size was not a predictor of its below-ground competitive response (Fig. 2b), and one cannot assume that increased allocation to roots will increase below-ground competitive ability (e.g. Wilson & Tilman 1995; Rajanieni 2002). What factors actually confer competitive advantage below ground are unknown, although there is reason to believe it should not be biomass. There is growing evidence that below-ground competition is size-symmetric, with the effects of neighbour roots on target plant growth being proportional to their abundance (Gerry & Wilson 1995; Weiner et al. 1997; Cahill & Casper 2000; Blair 2001; von Wettberg & Weiner in press). Under size-symmetric competition, a plant’s relative competitive ability below ground should be independent of its root biomass, as found here (Fig. 2b). Comparative studies of competition in general have found contradictory results regarding the effects of plant mass on competitive ability (Gaudet & Keddy 1988; Wardle et al. 1998). As there is no clear consensus on whether certain traits make a good competitor in general, it is not too surprising that this study provides no support for the idea that root biomass confers greater below-ground competitive ability.

We are left with a rather interesting puzzle. We know that species vary in their below-ground competitive ability (Gerry & Wilson 1995; Wilson & Tilman 1995; Twolan-Strutt & Keddy 1996; Cahill 2002a), and this is apparently not due to differences in root allocation (Fig. 2b). Though we can refute one potential explanation, an understanding of what factors lead to interspecific variation in below-ground competition is lacking. I propose there are three main sets of plant traits that influence a plant’s below-ground competitive ability:

- **Root traits.** Some traits that influence below-ground competitive ability will be a function of the root system itself. For example, recent work with *Arabidopsis thaliana* indicates that root hairs enhance competitive ability under low, but not high P conditions (Bates & Lynch 2001). Importantly, root hairs do not increase anchorage (Bailey et al. 2002), indicating that a functional analysis of plant roots will require experimental separation of the different roles of root systems (anchorage, support, uptake). Numerous other root traits have...
been suggested or demonstrated to influence below-ground competitive ability, including (but not limited to) root proliferation (Robinson *et al.* 1999), root architecture (Rubio *et al.* 2001), and uptake kinetics (Caldwell *et al.* 1991). For the most part, studies linking specific root traits with below-ground competitive ability are lacking, and we know much less about the functional ecology of roots than of leaves (Pregitzer *et al.* 2002).

**Shoot and whole plant traits.** Above- and below-ground competition interact to affect plant growth (Cahill 1999, 2002a), and thus traits that influence above-ground competitive ability may also alter below-ground competitive ability. For example, if below-ground competitive ability is somehow related to C supply to the roots, then a plant’s ability to compete for light (and acquire C) will influence its below-ground competitive ability. Similarly, overall rates of water extraction are related to competitive ability among desert grasses (Eissenstat & Caldwell 1988). Water extraction is not a specific trait itself, but instead is influenced by a variety of factors including phenology, root length and transpiration rates. Studies designed to specifically contrast traits associated with above- and below-ground competition are lacking, and would be a significant step forward in our understanding of not only the similarities and differences between these two key ecological processes, but also the general mechanisms of plant–plant interactions.

**Traits related to other ecological processes.** An individual plant’s ability to compete below ground is likely to be determined not only by traits internal to that individual, but will also include traits related to how a plant uses, and is used by, other species. For example, grazing by ungulates can stimulate root growth (Frank *et al.* 2002), and root characteristics vary widely as a function of root order (Pregitzer *et al.* 2002). As a result, grazing may alter below-ground competitive ability through changes in root architecture and other related root properties. As different plant species respond differently to grazing (Diaz *et al.* 2001), grazing could cause increased interspecific variation in below-ground competitive ability of the species within a community. Such indirect effects on below-ground competition may also involve plant–fungal interactions. Interspecific variation in mycorrhizal associations, along with the potential for resource sharing of interconnected individuals, can alter diversity (Hartnett & Wilson 1999), potentially through altered competitive hierarchies. Additionally, recent work indicates that mycorrhizas can enhance the competitive ability of an invasive species (Marler *et al.* 1999). There are numerous other ecological processes that are likely to influence a plant’s ability to compete for soil resources. Although a better understanding of plant competition is dependent upon a more active exploration of the functional ecology of roots, it is equally important that this work be brought to the field to allow for the determination of the potential strengths of these indirect effects on competition below-ground.

**Comments on experimental methods**

There are two components to plant competition: response and effect (Goldberg 1990). Target plant studies, such as this one, measure the growth of individuals that are interacting with many neighbouring plants (competitive response). Other experimental designs determine how one species alters resource supply and the growth of other species (competitive effect). As different traits may be associated with competitive response and effect (Goldberg & Landa 1991), the results here are limited to competitive response.

If the ability to extract roots from the soil differs as a function of the root exclusion treatment, one will recover proportionally fewer target roots in the + roots treatment than in the – roots treatment (Cahill 2002b). Although I found no evidence of a shift in root allocation as a function of the root treatment, it is possible that there may have actually been increased allocation in response to below-ground competition, with reduced root extraction in the + roots treatment obscuring the detection of the pattern. It is therefore important to explore the potential impact of systematic bias in extraction efficiencies. As the magnitude of root loss during extraction is unknown, I went back to the raw data and artificially increased the root biomass of the + roots target plants in 5% increments. After each increase, I reran the GLMM looking to see at what point the root exclusion treatment was significant in its effects of root allocation. The root biomass of the + roots plants would have to increase between 25 and 30% before the root treatment term becomes significant at the $P = 0.05$ level. It is unlikely that over 25% of the target root biomass went uncollected, as it is in fact the larger, stronger and heavier roots that are most reliably recovered (Smit *et al.* 2000). This suggests the lack of support for the growth-balance hypothesis found here is real, rather than an experimental artefact. This finding also supports my contention that if one is interested in a proxy measure of fitness in a study of below-ground competition, measuring solely shoot biomass may be sufficient (Cahill 2002b). This also appears to satisfy Zobel & Zobel’s (2002) criteria that ‘Shoot biomass of perennial plants could easily be used as a sufficient proxy for root and total biomass responses only if root/shoot allocation is predictable’.

As above- and below-ground competition interact to affect plant growth, it was necessary to experimentally isolate the factor of interest – below-ground competition – through the removal of shading by the neighbouring plants. Although this is the appropriate approach for the questions addressed here, it does leave other questions unanswered. For example, if plants detect the presence of neighbouring roots by piggybacking on their phytochrome system to detect shoot competition, then this study would have prevented them from perceiving such competition. Thus this study clearly shows that below-ground competition itself does not cause a shift in root allocation, though
the combined effects of root and shoot competition may (Wardle & Peltzer 2003). Understanding both the individual effects of above- and below-ground competition, as well as the mechanisms of root–shoot interactions would seem to be a potentially fruitful way of understanding the causes and consequences of plant–plant interactions in natural systems.

Acknowledgements

I thank Malcolm Coupe, Josh Haag, Alexandra Rutherford and Bryon Shore for assistance in the field, Barry Irving for facilitating ecological research at the Kinsella ranch, and Brenda Casper and Duane Peltzer for comments that improved the quality of this manuscript. Financial support for this research was provided by a research grant from the Natural Sciences and Engineering Research Council of Canada.

References


Cahill, J.F. (2002b) What evidence is necessary in studies of above- and below-ground interactions would seem to be a potentially fruitful way of understanding the causes and consequences of plant–plant interactions in natural systems.


Received 10 September 2002
revision accepted 7 April 2003