

Interactions between root and shoot competition vary among species

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Understanding how the competition varies with productivity is essential for differentiating among alternative models of plant community organization. Prior attempts to explain shifts in root and shoot competition along gradients have generally assumed an additive interaction between the two competitive forms, using an experimental design which does not fully separate both above- and belowground processes. At the most basic level, few field studies have separated root and shoot competition, and we have limited knowledge about both the relative importance of these processes, and how they interact to affect plant growth in the field. Presented here are findings from a field study in which root and shoot competition were experimentally separated by using root exclusion tubes and neighbor tiebacks in an early successional community. Individuals of four species (*Abrutylon theophrasti*, *Amaranthus retroflexus*, *Rumex crispus*, and *Plantago lanceolata*) were grown at two levels of fertilization with full competition, aboveground competition only, belowground competition only, or neither above- nor belowground competition. Competition was measured as competitive response, which is the natural log of the relative biomass of a target plant grown with competition compared to growth without competition. In contrast to predictions from current models of productivity-competition relationships, but in agreement with other experimental studies, there was no change in the strengths or root, shoot, or total competition with a modest increase in productivity. Despite no effect of fertilization on the strength of competition, the form of interaction between root and shoot competition varied both as a function of species identity and fertilization. For both of the rosette forming species, the combined effects of root and shoot competition were less than predicted assuming no interaction (a “negative interaction”), with one species switching from a negative to an additive interaction with fertilization. The fact that fertilization caused a shift in the root-shoot interaction, but not in the total strength of root and shoot competition, suggests that the root-shoot interaction is itself a highly labile variable. If root-shoot interactions are common in natural systems, then simply measuring the strength of one form of competition in no way provides any information about the overall importance of that competitive form to plant growth.

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There exist contrasting predictions about how the relative strengths of root and shoot competition vary with habitat productivity. Some researchers argue that under low levels of resource supply, interactions between neighboring plants are rare, and competition is unimportant to plant growth (Grime 1973, 1979, Grime and Hodgson 1987, Keddy 1989). As resource supply in-

creases, plant growth is greater, and there will be an increase in the total strength of competition (Huston 1979), as well as increases in the strength of both root and shoot competition (Grime 1973, 1979, Keddy 1989). Others argue there exists a trade-off in the ability of plants to compete for soil resources and light (Tilman 1988, Wilson and Tilman 1991, 1993, 1995),

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with the total strength of competition being invariant along a productivity gradient (Newman 1973, Chapin and Shaver 1985, Grubb 1985, Tilman 1988) due to a shift from root to shoot competition with increased resource availability and plant productivity (Newman 1973, Grubb 1985, Tilman 1988).

Testing these predictions requires independent measures of root and shoot competition at different levels of productivity. Prior experimental results vary, with evidence for no correlation between the intensity of full competition and productivity (Wilson and Tilman 1991, Wilson 1993a, Wilson and Tilman 1993, Reader et al. 1994, Belcher et al. 1995, Peltzer et al. 1998, Cahill 1999), a positive correlation (Reader and Best 1989, Reader 1990, Kadmon 1995, Twolan-Strutt and Keddy 1996, Sammul et al. 2000), and a negative correlation (Davis et al. 1998, meta-analysis Goldberg et al. 1999). Root competition can decrease (Putz and Canham 1992, Wilson 1993b, Wilson and Tilman 1993, 1995, Cahill 1999), or remain constant with increased productivity (Belcher et al. 1995, Twolan-Strutt and Keddy 1996, Peltzer et al. 1998). Shoot competition may increase (Putz and Canham 1992), or remain constant with increased productivity (Cahill 1999). Quite simply, no clear pattern emerges from these prior studies, and our understanding of any competition-productivity relationship is poor.

One possible explanation for the lack of consensus among the various studies could be that root and shoot competition interact to affect plant growth, and therefore a linear relationship between root and shoot competition is unlikely. Although many recent studies have purported to measure the strength of root, shoot, and full competition, most did not measure shoot competition directly. Instead, it is commonly assumed that the combined effects of root and shoot competition are the sum of each effect by itself, with the intensity of shoot competition estimated as the difference between the intensities of full and root competition (Wilson and Tilman 1991, 1993, Belcher et al. 1995, Twolan-Strutt and Keddy 1996, Peltzer et al. 1998). By making this statistical assumption, prior researchers have made the biological assumption that root competition does not affect shoot competition (and vice versa). However, there is greenhouse (see review Wilson 1988), and field evidence (Dillenburg et al. 1993, Cahill 1999) demonstrating that this assumption is not always valid.

The combined effects of root and shoot competition can be (1) greater than the sum of the parts (a positive interaction), (2) less than the sum of parts (negative interaction), or (3) equal to the sum of their parts (additive). There are several reasons to believe that root and shoot competition likely do interact to affect plant growth in the field. For example, biomass allocation within a plant can vary as a function of the competitive environment (Casper et al. 1998), resource conditions (Reynolds and Pacala 1993, Hoddinott and Scott 1996),

and plant size (Gedroc et al. 1996). The amount and/or morphology of competing organs can influence competitive ability (Aerts et al. 1991, Schmitt et al. 1995, Schwinning and Weiner 1998), and thus changes in allocation patterns that increase the ability of plants to compete above ground may come at the cost of below ground competitive ability (or vice versa). Alternatively, if there is a single morphological/physiological response to competition, regardless of whether it is occurring above- or below ground, then one may expect competition above ground to enhance below ground competitive ability (or vice versa), resulting in a negative interaction between competitive forms. Interactions between individual plants and their local neighborhood can also result in interactions between root and shoot competition. Cahill (1999) demonstrated that early season root competition decreases initial plant growth, reducing their ability to compete in the size-asymmetric competition for light (Harper 1977, Weiner and Thomas 1986, Schwinning and Weiner 1998). Positive and negative interactions between root and shoot competition have long been demonstrated in greenhouse studies (Donald 1958, reviewed by Wilson 1988), though negative interactions have yet to be explicitly demonstrated in the field. The limited field evidence for non-additive interactions is likely the result of prior experimental designs which prevented their detection, rather than a rarity of the process. As ecologists have yet to fully describe these phenomena we know little about the conditions under which certain forms of interactions between root and shoot competition would be more or less likely to occur.

The resolution of this last issue may help in resolving aspects of the long-standing debate regarding the role of competition in structuring plant communities. If plant responses to one form of competition alters their ability to compete in another form of competition, the combined effects will not be simple sum of the parts. For example, if plant responses to root competition reduce the severity of shoot competition, then it would be possible for both root and shoot competition to be individually strongest at high productivity and still find the combined effects of the two competitive forms to be invariant along a productivity gradient. As the ability to make morphological shifts in response to changes in the environment is species specific, it is also likely that interactions between root and shoot competition vary among species. This would suggest that the intensity of competition experienced by individual plants is not a characteristic of the community (as is implied by the use of the term "competitive intensity"), but instead an interaction between the neighborhood surrounding an individual plant and that plant's ability to respond.

Based upon the idea that plants are dynamic organisms and can respond to their competitive environment, an alternative model of competition-productivity relationships has been proposed in which the relationship

between root and shoot competition varies from positive, negative, and additive as a function of productivity (Cahill 1999). Species identity and habitat productivity are predicted to alter the strengths of the three competitive forms, as well as the form of interaction between root and shoot competition. Specifically, it was predicted that positive interactions would be found in species which have the potential to reach the plant canopy, and not in plants adapted to more stressful conditions (e.g. low-growing species in dense vegetation). Negative interactions between root and shoot competition were predicted to occur if at a particular level of productivity the individual effects of both root and shoot competition severely limited plant growth. Empirical tests of these predictions are lacking, and the original model was based upon the growth response of a single species conducted in a single year (Cahill 1999). Here I present findings of a study conducted to explore the relationship between competition, productivity, and the interaction between competitive forms, using four early successional species of two contrasting growth forms. Root and shoot interactions were isolated in a factorial design at two levels of fertilization, allowing for independent measures of the strengths of root and shoot competition.

Methods

Field site and target species

Fieldwork was conducted in the Laurels Conservation Preserve in Chester County, Pennsylvania. The field site was last cut for hay in 1994, four years prior to this study. Vegetation is primarily herbaceous, dominated by grasses (e.g. *Festuca* spp., *Dactylis glomerata*), Canada thistle (*Cirsium arvense*), and poison ivy (*Rhus radicans*). Rooting depth is shallow, with most roots located in the upper 15 cm of soil (Cahill 1999). Plant growth is nutrient limited, with growth responses occurring with either fertilization or elimination of root competition (Cahill 1999). Further details of the study site are found in Cahill (1997).

Four target species were chosen for use in this study, exhibiting two different life histories and growth forms. *Abutilon theophrasti* Medic. and *Amaranthus retroflexus* L. are erect annual species, common to the old-fields of northeastern United States. *Rumex crispus* L. and *Plantago lanceolata* L. are short-lived perennials (biennial) also common to the fields of the northeast. These species were chosen because (1) they co-occur at the Laurels, (2) their seeds germinate rapidly in the field, and (3) the contrasting growth forms will allow me to test prior predictions about the factors which influence interactions between root and shoot competition.

Competition treatments

Isolating root and shoot competition was done using four treatments: (1) target plants interacting with no neighbors either above- or belowground (NN), (2) target plants interacting with the roots, but not shoots of neighbors (RN), (3) target plants interacting with the shoots, but not roots of neighbors (SN), and (4) target plants interacting simultaneously with the roots and shoots of neighbors (AN). Differences in target plant biomass at harvest in each of the four treatments were compared. If plants were smaller when interacting with neighbors than when grown with no neighbors, competition is assumed to have occurred. Increased plant size with neighbors compared to growth with no neighbors would be evidence for facilitation.

Root interactions between targets and neighbors were manipulated using 10 cm diameter \times 20 cm length PVC root exclusion tubes. Tubes were inserted vertically into the ground, until flush with the soil surface. All individuals inside the tube were removed, and seeds of one of the four target species were sown in the tube center. Vegetation surrounding the tube was left intact, with its roots unable to penetrate the PVC. In the control plots I simulated inserting a tube by cutting the soil and removing all rooted individuals within a 10 cm diameter. Seeds of one of the four target species were sown, and since no tube was in the ground, there was the potential for root interactions between the target plant and the neighboring vegetation.

Aboveground interactions between neighbors and target plants were modified by using thin tree netting (2 \times 2 cm squares, 1 mm thick netting) to tie back the shoots of the neighboring vegetation. A 50 \times 50 cm square of netting was centered over the plot with the center anchored flush with the ground and the four corners anchored approximately 15 cm above the soil surface. Neighboring vegetation underneath the netting was pulled towards the netting edges, eliminating shading of the target plant by the neighbors. The integrity of the aboveground treatments was maintained by regularly pulling the growing neighbors beneath the netting and away from the target plants. The second aboveground treatment consisted of no netting, allowing for shoot interactions between neighbors and target plants. The netting is similar in diameter to fishing line, and its shading effects are negligible (approximately 93% light penetration). Similar netting has been used in other studies without adverse effects on neighboring vegetation (Wilson and Tilman 1991, Twolan-Strutt and Keddy 1996, Cahill 1999).

Experimental layout

Within an approximately 0.25 ha portion of the Laurel's preserve, forty 5 \times 5 m blocks were arranged into

four rows of ten blocks, with 2 m separating adjacent blocks in each direction. Within each row, five blocks were randomly chosen to receive fertilization and five blocks were chosen as unfertilized controls. In late April 1998, each of the 20 fertilized blocks received 60 gm² Osmocote slow-release fertilizer (14-14-14 NPK), for an addition of 8.4 gm⁻² NPK. This fertilization treatment was similar to that used in prior work at this site (Cahill 1999).

Within each block, 16.075 × 0.75 m plots were established, with 0.5 m separating plots on all sides. The two root and two shoot competition treatments were crossed, resulting in four competition treatments imposed on individuals of each of the four species. In total, there was one replicate of each species × root competition × shoot competition treatment in each of 40 blocks for a total of 640 plots. With blocks nested in fertilization treatment, there were 20 replicates of each fertilization × root × shoot × species combination.

Root treatments were installed May 20–27, 1998. Seeds of each species were soaked in water for 24 hours, sown into each plot on June 12, and watered daily for 5 days. Within seven days, seedlings were thinned to one individual per plot, and the shoot treatments were installed. All volunteer seedlings of all species growing within the exclusion tubes (or similar area) were weeded out for the duration of the experiment. To reduce insect herbivory, each plot was sprayed twice with 6.7 ml/l of the generalist insecticide ISOTOX. The insecticide treatment should have eliminated any differential rates of herbivory that could have occurred simply through the regular visitation of the plots associated with maintaining the integrity of the above ground treatments (Cahill et al. 2001).

After approximately 10 weeks of growth, target plants were cut at the soil surface, dried at 70°C for 48 hours, and weighed. To estimate the effects of fertilization on neighbor biomass, 20 blocks were chosen to have all vegetation within a 0.1 × 1.0 m plot located in the block center cut, dried and weighed. Living and dead vegetation were not separated, and thus block biomass measures are relative, rather than absolute, estimates of productivity.

Measures of plant responses to competition

Target plant biomass in the presence of competition, relative to target plant biomass without competition was measured as competitive response (CR). CR measures were calculated independently for total, root, and shoot competition (eqn. 1–3).

$$\text{Total competitive response: } \text{TCR} = \ln\left(\frac{\text{AN}}{\text{NN}}\right) \quad (1)$$

Aboveground competitive response:

$$\text{ACR} = \ln\left(\frac{\text{SN}}{\text{NN}}\right) \quad (2)$$

Belowground competitive response:

$$\text{BCR} = \ln\left(\frac{\text{RN}}{\text{NN}}\right) \quad (3)$$

where NN is mean target biomass when grown with no neighbors above and below ground. SN is target biomass when grown with the shoots, but not roots of neighbors (exclusion tubes only), and RN is target biomass when grown with the roots, but not shoots of neighbors (netting only). Values of TCR, ACR, and BCR were calculated for all plants that could potentially interact with their neighbors (i.e. all plants except those in the NN treatment). The biomass of each competing plant was compared against the mean NN target plant biomass of the same species and fertilization treatment.

The competitive response metric is similar to both the response ratio described in Goldberg et al. (1999), and competition intensity (CI) used in several studies (Wilson and Tilman 1991, 1993, Twolan-Strutt and Keddy 1996), where $\text{TCR} = \ln(1 - \text{CI})$. Competitive response measures are appropriate for studies designed to test the interaction between root and shoot competition. For example, suppose plant biomass with root competition is 20% that of NN controls, and biomass with shoot competition is 60% that of NN controls. In an arithmetic scale, I assume that if root and shoot competition do not interact to affect plant growth, there will be a multiplicative effect between the two competitive forms. Thus, plant biomass with full competition should be the product of the individual competitive effects = (0.6)(0.2) = 12% that of controls. When these values are converted to logarithmic scale, as is done in the measures of competitive response (eqn. 1–3), the total strength of competition assuming no interaction between root and shoot competition is simply additive where $\text{TCR} = \text{ACR} + \text{BCR}$. Further justifications for using competitive response are described in Cahill (1999).

To test whether root and shoot competition interact to affect plant biomass, TCR was calculated in two ways for each plant that was simultaneously experiencing both root and shoot competition (AN): (1) direct determination from experimentation ($\text{TCR}_{\text{TRUE}} = \text{eqn. 1}$), and (2) estimated assuming no interaction between root and shoot competition ($\text{TCR}_{\text{PREDICTED}} = \text{eqn. 2} + \text{eqn. 3}$). If $\text{TCR}_{\text{TRUE}} = \text{TCR}_{\text{PREDICTED}}$, root and shoot competition do not interact to affect plant growth (additive); $\text{TCR}_{\text{TRUE}} < \text{TCR}_{\text{PREDICTED}}$ would indicate a positive interaction between competitive forms, and $\text{TCR}_{\text{TRUE}} > \text{TCR}_{\text{PREDICTED}}$ would indicate a negative interaction.

In prior work (Cahill 1999), $\text{TCR}_{\text{PREDICTED}}$ was calculated by adding the values of ACR and BCR

within each block. In the current study mortality was severe, with only 113 of 640 plants surviving for the duration of the experiment. Mortality was likely caused by slugs soon after germination, the rate of which did not vary with fertilization, species identity, or competition treatment. As there were generally less than four measures of root or shoot competition remaining for each species \times fertilization combination, calculations within blocks were impossible. Therefore, a bootstrapping procedure was used to determine $TCR_{PREDICTED}$. An array of all possible ACR + BCR combinations was constructed for each fertilization \times species combination. A second array was then created consisting of the same number of cells as the original data, with cell values chosen through resampling with replacement. Resampling was repeated 10 000 times for each species \times fertilization combination, from which mean and 95% confidence limits for $TCR_{PREDICTED}$ were generated.

Statistical analyses

Due to high mortality, blocks could not be incorporated into any analysis, and sample sizes are unequal among cells in ANOVA. To estimate independent sums of squares for the treatment effects and interactions in ANOVA with unequal cell sizes, PROC GLM in SAS v7.0 (SAS Institute 1998) was used with type III SS used to determine the appropriate F ratios (Littell 1991).

Although the elimination of blocks in the statistical models could arguably result in pseudoreplication, there are several reasons to believe that blocks were not biologically relevant in this study, and thus their elimination is justified. (1) The entire experiment was conducted within a small portion (0.25 ha) of a larger old-field, with little variation in biomass among blocks (coefficient of variation = 13.6%). (2) There was no obvious species composition gradient within the experimental area. In fact, to reduce variation among blocks, this study site was chosen explicitly because it appeared homogeneous in terms of species composition. (3) When the data are pooled by species and competition treatments (16 plots per block), the number of surviving plants (chi-square) did not vary among blocks in either of the fertilization treatments (chi-square $p > 0.30$ for each fertilization treatment).

The effects of species identity, fertilization, root treatment, and shoot treatment on plant biomass were determined in a four-way ANOVA. A significant root \times shoot treatment interaction would indicate that above- and belowground competition interact to affect target biomass. A significant root \times shoot \times fertilization interaction would indicate that the interaction between root and shoot competition is itself dependent upon fertilization. Biomass was ln transformed to satisfy the assumption of normally distributed data in ANOVA.

To determine whether competition varied among species or with fertilization, separate ANOVA were conducted using BCR, ACR, and TCR_{TRUE} as separate dependent variables. In each ANOVA, fertilization treatment and species identity served as two fixed effects.

A randomization procedure was used to determine whether the combined effects of root and shoot competition differed from that predicted assuming an additive interaction between the two competitive forms, with a separate analysis conducted for each of the eight species \times fertilization combinations. Following the methods of Manly (1997), the actual difference between mean TCR_{TRUE} and $TCR_{PREDICTED}$ was first calculated. The values of TCR_{TRUE} and $TCR_{PREDICTED}$ were then randomly assigned among the true and predicted classifications, with the resulting mean difference recorded. Randomization was repeated 10 000 times. If the proportion of randomized mean differences greater than or equal to the actual mean difference is less than 0.025, then there would be a significant difference between TCR_{TRUE} and $TCR_{PREDICTED}$ in a two-tailed test. The $TCR_{PREDICTED}$ values used in the randomization procedure consisted of all possible combinations of ACR + BCR for a particular species \times fertilization combination. Clearly this array of values is greater than the number of TCR_{TRUE} samples that were used. Restricting the randomized sample size of $TCR_{PREDICTED}$ to be equivalent to that actual sample size of TCR_{TRUE} for a particular species \times fertilization combination had no effect on which species \times fertilization combinations were found to be significant. Determining the presence of non-additive interactions between root and shoot competition was the central goal of this experiment, and thus these pair-wise test are a priori contrasts, for which no adjustment of alpha is justified. ANOVA were conducted on SAS for Windows 7.0 (SAS Institute 1998), and the randomization procedures were conducted on MS Excel 2000, using the Resampling Add-in (Resampling Stats 1999).

Results

Plant growth

Target plant biomass was significantly affected by species identity and fertilization as main effects, and by shoot competition in interaction with root competition (Table 1, Fig. 1). In the absence of competition, three of the four species were larger with fertilization than without (Fig. 1). Plants were smaller when grown with neighbor roots and/or neighbor shoots than when grown alone. The lack of significant species \times root (or shoot) interactions indicates that root and shoot competition had similar effects on the growth of all species. The significant root \times shoot treatment interaction indi-

Table 1. ANOVA results for ln-transformed target plant biomass at the end of the experiment. Species identity, fertilization, shoot treatment, and root treatment served as four fixed effects. Due to severe herbivory, blocks could not be included in the model, and sample sizes are unequal among treatments. A significant root competition \times shoot competition interaction in ANOVA indicates that root and shoot competition interact to affect plant biomass.

| Source | DF | Type III SS | F | P |
|--|-----|-------------|-------|--------|
| Species | 3 | 138.83 | 27.00 | <0.001 |
| Fertilization | 1 | 12.09 | 7.05 | <0.001 |
| Shoot Trt. | 1 | 42.78 | 24.96 | <0.001 |
| Root Trt. | 1 | 75.21 | 43.88 | <0.001 |
| Spp. \times Fert. | 3 | 11.92 | 2.32 | 0.082 |
| Spp. \times Shoot | 3 | 8.81 | 1.71 | 0.171 |
| Spp. \times Root | 3 | 3.60 | 0.70 | 0.554 |
| Fert. \times Shoot | 1 | 0.49 | 0.29 | 0.594 |
| Fert. \times Root | 1 | 0.07 | 0.04 | 0.836 |
| Shoot \times Root | 1 | 25.97 | 15.15 | <0.001 |
| Spp. \times Fert. \times Shoot | 3 | 9.02 | 1.75 | 0.163 |
| Spp. \times Fert. \times Root | 3 | 3.38 | 0.66 | 0.581 |
| Spp. \times Shoot \times Root | 3 | 1.94 | 0.38 | 0.769 |
| Fert. \times Shoot \times Root | 1 | 0.56 | 0.33 | 0.569 |
| Spp. \times Fert. \times Shoot \times Root | 3 | 1.55 | 0.30 | 0.825 |
| Error | 112 | 138.85 | — | — |

icates that the two competitive forms had a non-additive effect on target plant biomass (Table 1). On average, plant size did not differ as a function of whether plants grew with neighbor roots only, with neighbor shoots only, or with both neighbor roots and shoots (Fig. 1). In a planned comparison contrasting erect versus rosette forming species, the two erect species (*Abutilon* and *Amaranthus*) were larger than the two rosette forming species (*Rumex* and *Plantago*; $F_{1,81} = 73.47$,

$p < 0.0001$; Fig. 1). The root \times shoot interaction did not vary as a function of growth form ($F_{1,81} = 0.328$, $p = 0.568$).

Although fertilization caused a significant increase in the size of the target plants, there was only a marginal increase in the combined biomass of the living and dead neighboring vegetation (ANOVA $F_{1,18} = 3.24$, $P = 0.089$; means [SD]: unfertilized: 1089[251]; fertilized: 1304[256]).

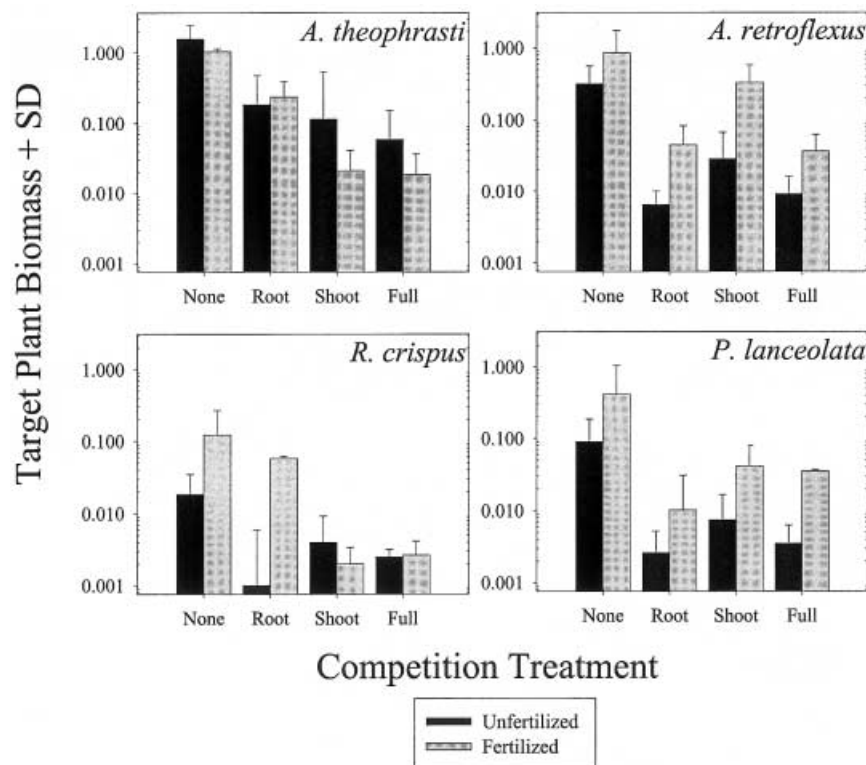


Fig. 1. Mean aboveground biomass (ln) measured after 10 weeks of growth as a function of species identity and fertilization treatment. Error bars represent one standard deviation. In ANOVA, there was a significant shoot \times root treatment interaction indicating that the two forms of competition interact to affect plant growth.

Table 2. ANOVA results for aboveground competitive response (ACR), belowground competitive response (BCR), and total competitive response (TCR) as measured by differences in target plant biomass when plants grew with competition relative to growth without competition. To calculate measures of competitive response, plants that could interact with neighbors above- and/or belowground were paired with the mean value of the no neighbor treatment of the same species \times fertilization treatment combination. Fertilization had no effect on the strength of root, shoot, or full competition.

| Source | DF | BCR | | ACR | | TCR | |
|------------------------|----|-------|-------|-------|-------|-------|-------|
| | | SS | P | SS | P | SS | P |
| Species | 3 | 21.92 | 0.011 | 1.73 | 0.887 | 7.01 | 0.277 |
| Fertilization | 1 | 0.05 | 0.864 | 0.26 | 0.762 | 2.50 | 0.238 |
| Species \times Fert. | 3 | 9.11 | 0.153 | 12.52 | 0.264 | 6.32 | 0.319 |
| Error | 24 | 37.92 | — | 30.18 | — | 26.58 | — |

Competitive response

Root, shoot, and full competition severely reduced the growth of all species (Table 2, Fig. 2). The strength of root competition varied among species (Table 2, Fig. 2), with the negative effects of root competition stronger for *Plantago* than for *Abutilon* (Fisher's PLSD $p < 0.01$), but not varying significantly among any other species combinations (Fisher's PLSD $p > 0.05$). The strengths of shoot and full competition did not vary among species, nor did fertilization alter the strength of either of the three competitive forms (Table 2, Fig. 2). Similarly, the strengths of the three competitive forms did not vary as a function of plant growth form (planned comparisons, $p > 0.10$).

Interactions between root and shoot competition

Despite there being no effect of fertilization, and only limited effects of species identity on the strength of the various competitive forms, the interaction between root and shoot competition varied as a function of both species identity and fertilization (Table 3, Fig. 2). For *Abutilon* and *Amaranthus*, the true strength of full competition did not significantly differ from that predicted assuming an additive interaction between root and shoot competition at either level of fertilization (Table 3, Fig. 2). For both *Rumex* and *Plantago* the combined effects of root and shoot competition were less than that predicted assuming no interaction between competitive forms (Table 3, Fig. 2), evidence of

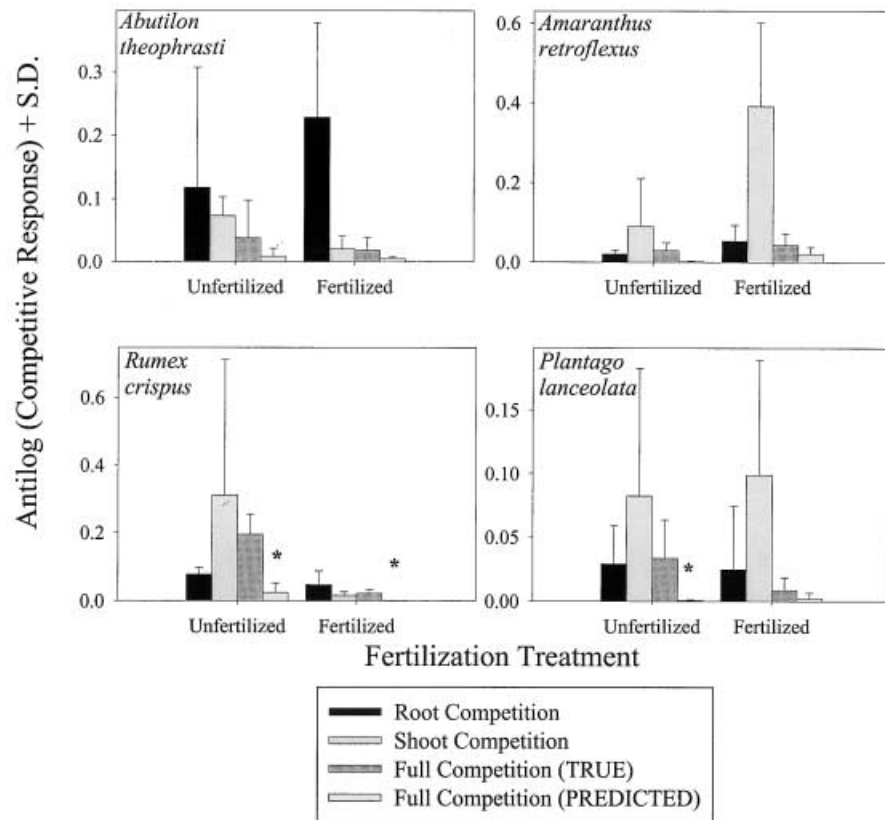


Fig. 2. Mean competitive response (antilog) as a function of species identity, fertilization treatment, competitive form (aboveground, belowground, or both above- and belowground), and method of calculation (actual TCR versus predicted TCR). Error bars represent one SD. Competitive response is the natural log of the proportional growth of target plants when grown with neighbors, compared against growth without neighbors (Eqn. 1–3). Asterisks represent significant contrasts between TCR_{TRUE} and $TCR_{PREDICTED}$.

negative interactions between root and shoot competition. *Plantago* switched from a negative interaction to no interaction with fertilization (Fig. 2), while *Rumex* exhibited a negative interaction at both levels of fertilization. In short, both erect species exhibited an additive interaction at both levels of fertilization, and both rosette forming species exhibited a negative interaction at least one level of fertilization.

Discussion

There is little empirical evidence to support the assumption that as a rule, root and shoot competition are independent (Table 1, 3, Fig. 1, 2). Results presented here, and in prior work, support the hypothesis made by Cahill (1999) that the combined effects of root and shoot competition could, at various times, be greater than predicted assuming additivity (Cahill 1999), additive (Cahill 1999, Fig. 2), or less than predicted assuming additivity (Fig. 2). The idea that “any such interaction would presumably occur at all levels of standing crop” (Twolan-Strutt and Keddy 1996) is also not supported, as the form of interaction between root and shoot competition can shift with even modest fertilization (Cahill 1999, Fig. 2).

This study provides the first direct evidence that negative interactions between root and shoot competition occur in the field. In a review of greenhouse studies, Wilson (1988) found one-half of all interactions between root and shoot competition to be negative, suggesting they could occur from a “law of limiting factors”. Exact mechanisms that could cause such an interaction are unclear. One possible explanation would be that shading could reduce soil nutrient uptake by a target plant (Chapin 1980), and thus uptake by neighbors should have reduced effects on plant growth.

Alternatively, reduced uptake due to strong root competition could cause decreased leaf N (Chapin 1980), which may reduce the photosynthetic capacity of a plant, reducing the negative effects of shading. The physiological mechanisms by which one form of competition may influence another are virtually unexplored.

Competition-productivity relationships

The strengths of root, shoot, and the total competition did not change with a modest increase in productivity (Table 2, Fig. 2). The rate of fertilization used may have been too low to cause a large shift in neighbor biomass and thus competition, however it was large enough to cause a significant increase in target plant size and a shift in root-shoot interactions (Fig. 1, 2).

Although there is yet to emerge a clear understanding of how competition varies with productivity, a few general results have been found: (1) root competition may or may not get weaker with increased productivity (Wilson and Tilman 1991, Putz and Canham 1992, Wilson 1993a, b, Wilson and Tilman 1993, Belcher et al. 1995, Wilson and Tilman 1995, Cahill 1997, Peltzer et al. 1998), but it has not been shown to get stronger with increased resource supply and/or productivity, and (2) shoot competition may or may not get stronger at higher productivity (Fig. 2, Cahill 1999, Putz and Canham 1992), but there is no evidence it gets weaker. In other words, root and shoot competition has never been shown to be strongest when the respective resource (light or soil nutrient) is in the greatest supply. This contradicts at least part of Grime’s (1973) assertion that the strength of root competition should be strongest at the highest levels of resource availability and productivity. The fact that root competition does not always decrease with productivity, and that the

Table 3. Results of randomization procedures to determine whether the combined effects of root and shoot competition are additive in their effects on plant growth. The reported values of the mean differences and resulting significance were calculated in the back-transformed arithmetic scale. To determine the significance value for each test, the true difference between TCR_{TRUE} and $TCR_{PREDICTED}$ was calculated as: true minus predicted. The individual values of TCR_{TRUE} and $TCR_{PREDICTED}$ were then randomly assigned to true and predicted classification, with the resulting mean difference recorded. Values were randomized 10 000 times, with significance being determined as the proportion of mean differences from the randomized values greater than or equal to the actual difference between TCR_{TRUE} and $TCR_{PREDICTED}$. Values presented in boldface represent significant differences between actual and predicted values ($p < 0.025$ in two-tailed test). Since the $TCR_{PREDICTED}$ values were generated by forming all combinations of $ACR \times BCR$, there were more data points for $TCR_{PREDICTED}$ than TCR_{TRUE} . There was no change in which species \times fertilization combinations were significant at the $p = 0.025$ level when I allowed for the greater n or when I restricted the predicted n to be the same as that for the TCR_{TRUE} .

| Species | Fertilization Treatment | Difference between means (Actual TCR – Predicted TCR) | Percent of randomized differences greater than or equal to true difference between means |
|-------------------|-------------------------|---|--|
| <i>Abutilon</i> | Unfertilized | 0.029 | 0.066 |
| | Fertilized | 0.013 | 0.102 |
| <i>Amaranthus</i> | Unfertilized | 0.028 | 0.028 |
| | Fertilized | 0.022 | 0.224 |
| <i>Rumex</i> | Unfertilized | 0.171 | 0.014 |
| | Fertilized | 0.021 | 0.024 |
| <i>Plantago</i> | Unfertilized | 0.031 | 0.008 |
| | Fertilized | 0.006 | 0.136 |

total strength of competition does not always remain invariant along a productivity gradient (Reader and Best 1989, Reader 1990, Wilson and Tilman 1991, Putz and Canham 1992, Wilson 1993a, b, Wilson and Tilman 1993, Reader et al. 1994, Belcher et al. 1995, Kadmon 1995, Wilson and Tilman 1995, Cahill 1997, Peltzer et al. 1998, Goldberg et al. 1999) contradicts Tilman's model (Tilman 1988). Although both models have accurately predicted some aspects of the relationship between competition and productivity, neither can account for the variety of results that have been obtained. The lack of experimental support for these models is evidence that it is time to move away from additional tests of this aspect of the "Grime-Tilman" debate (Thompson 1987, Tilman 1987, Thompson and Grime 1988), and instead focus efforts on the development and testing of alternative models to explain the contradictory patterns that actually occur.

One alternative is based upon the hypothesis that plants do not directly respond to neighbor biomass, and instead respond to changes in net resource supply (Davis et al. 1998). Under the net resource supply theory (S-D), competition will be strongest when the net supply of limiting resources is lowest (Davis et al. 1998), independent of neighbor biomass. Only when net supply of the limiting resource is lowest at highest productivity should there be a relationship between productivity and competition. Although plants may be responding directly to resource supply and not neighbor biomass, per-gram competitive effects of neighbors are well documented (Goldberg 1987, 1990), suggesting that even if net resource supply is the variable to which plants respond, it is often tightly correlated with neighbor biomass, and thus correlations between neighbor biomass and the components of competition should still be found. A more serious concern with the S-D theory is raised when interactions between root and shoot competition are considered. If the effects of root competition on total plant growth are in fact dependent upon a plant's performance in size-asymmetric competition for light, then it is likely that size, not just net resource supply, matters.

A second, non-exclusive explanation for the lack of generalization from competition-productivity studies is the reliance on the assumption that one can ever separate the effects of root competition from those of shoot competition. From this current, and the prior study (Cahill 1999), it is clear that the strength of one competitive form may be a poor indicator of its overall importance in limiting plant growth. For example, even if the absolute strength of root competition is small, that may be enough to reduce a plant's ability to compete aboveground, and thus even a little root competition would contribute a great deal to the full strength of competition (Cahill 1999). Alternatively, if root competition is intense, it would appear to be quite important to plant growth (Table 3, Fig. 2). However,

with the occurrence of negative interactions between root and shoot competition, simply demonstrating that one form of competition can greatly reduce plant growth in no way indicates that the absence of that particular competitive form will result in increased plant growth (Fig. 1, 2). When root and shoot competition interact, the strength of an individual effect does not necessarily equal its overall importance.

Relationship to Cahill's 1999 competition-productivity model

In prior work I presented a graphical model allowing for interactions between root and shoot competition to vary as a function of productivity (Cahill 1999). Specific predictions were made as to when one should expect positive or negative interactions to occur. In general, results from this current study support the model, with specific examples presented below.

1. *Positive interactions.* I hypothesized that "as long as the target plant has the potential to reach the canopy, the interaction between above- and below-ground competition should become increasingly positive as productivity increases" (Cahill 1999). In the current study, target plants were transplanted after the neighboring vegetation had already experienced several weeks of growth, and thus already had established a size hierarchy. As a result, the transplanted target plants were always shorter than their neighbors (Cahill, pers. obs.), and morphological adjustments to reduced R:FR ratios (Schmitt and Wulff 1993) were not great enough to compensate for this initial growth difference. Therefore, root competition could not reduce above-ground competitive ability as these plants already had lost in competition for light.

2. *Negative interactions.* I hypothesized that negative interactions between root and shoot competition would most likely be found when both root and shoot competition strongly limited plant growth (Cahill 1999). Clearly such a situation occurred in this current study (Fig. 2), and negative interactions were found for two of the four species. However, root and shoot competition were strong for all four species, and yet negative interactions were not found for two of the species. It is unclear whether the failure to find these interactions is due to the fact they are not actually there (a failure of the model), due to limited power of the analyses, or a result of variation in growth form.

3. *Life history and/or growth form effects.* The species chosen in this study fall into two classes: (1) annual plants with tall, erect stems, and (2) perennials (biennial) with low growing rosettes in the first year. Both of the erect species exhibited additive interactions at both levels of fertilization, while the two perennial, rosette forming species exhibited negative interactions at least one level of fertilization (Table 3, Fig. 2). I had

previously hypothesized that plants adapted to low resource environments, such as prostrate species in old-fields, would be unlikely to demonstrate positive interactions between root and shoot competition (Cahill 1999). Although prostrate species are different from the overall growth of biennial species, the resource environment experienced with a low-stature growth-form of prostrate species is similar to that experienced by the rosette stage of *Rumex* and *Plantago* in this study. These findings suggest that species adapted to low resource environments may be more able to compensate in response to competition, thereby reducing the combined effects of above and below ground interactions.

Intensity vs importance

Additional issues arise in discussion of the relative importance, rather than intensity, of competition in plant communities (Sammul et al. 2000). Sammul et al. (2000) found the intensity and importance to be positively correlated, both increasing with productivity, with *Anthoxanthum odoratum* populations increasingly suppressed at higher levels of productivity. The overall importance of competition within a community could be influenced by the ability of NPP to sustain herbivore populations (Oksanen and Oksanen 2000). Without many herbivores, competition can be extremely intense, even with low levels of productivity (Olofsson et al. 1999). As interactions between trophic levels can result in different patterns of interactions within a trophic level (Holt 1977), a more explicit incorporation of how herbivory intensity may also change with productivity could result in a more accurate view of how the relative importance of competition varies along productivity gradients. Such efforts have been initiated, with the important first step of understanding how these processes interact in natural communities (Reader and Bonser 1998). However, severely lacking in natural systems is an understanding of the intensity of below ground herbivory (Brown and Gange 1989). As root feeding likely influences root competition, understanding the intensity of grazing by all vertebrate and invertebrate herbivores is likely key to the development of a more accurate model of how the importance of competition varies with productivity.

Comments on methods

Isolating root competition using exclusion tubes requires that no neighboring plants (or their roots) grow inside the tube along with the target plants. As it is impossible to completely remove a neighbor's root system without significant soil disturbance, neighbor shoots were cut at the soil surface, leaving neighbor roots to decompose and potentially increase nutrient

levels. Such weeding would be unlikely to bias the results as (1) neighbors were pulled from all treatments, and thus all plots should be equally affected, and (2) in this time scale root decomposition is unlikely to alter target plant growth (McLellan et al. 1995). Since the intensity of plant competition is often related to neighbor distances (Bonan 1993), removing the nearest neighbors may have underestimated the true strength of competition. Nonetheless, competition reduced target growth by greater than 90% for all four species (Fig. 1).

The degree to which neighboring root systems overlapped with target plant roots systems varied among plots with tubes (no root overlap), and plots without tubes (complete intermeshing of neighbor and target roots). As this was a productive, grass-dominated field, it is impossible to fully extract the target root systems without losing some unknown proportion of the target roots. The accuracy of root recovery is greatly diminished when neighbor and target roots are intermeshed, and thus, the accuracy of belowground biomass measures varied systematically among belowground treatments. Root biomass measures that vary in accuracy as a direct consequence of the treatment of interest are useless for making biological meaningful conclusions, and thus only aboveground biomasses were recorded and are presented. This is not the first time concern on the accuracy of root extraction resulted in the collection and presentation of only aboveground biomass in studies of plant competition, even when belowground processes were specifically of interest (Belcher et al. 1995, Levine et al. 1998). Further discussion of this issue can be found in Cahill (2002). The inability to reliably extract the target root systems means that the interpretation of the effects of competition on plant growth presented in this study is limited to current year effects of the various treatments. Although this is not an issue for the two annual species, it does limit the interpretation of the two biennial species.

Conclusions

Results from this study provide further evidence that root and shoot competition are not independent, but instead interact to affect plant growth. The form of interaction between root and shoot competition is highly labile, as even small changes in productivity can cause it to vary between additivity and a negative interaction. This strongly suggests that simply measuring the strength of one component of competition along a productivity gradient will tell us very little about the overall importance of that competitive form on plant growth.

An important result from this study is the contrasting results for *Abutilon* compared to prior work with this species (Cahill 1999). These studies suggest that interactions between root and shoot competition may not be

species specific traits, but are instead determined by a plant's relative position within a size hierarchy. A plant's size ranking is a complex interaction between resource availability, the timing of growth, and species-specific traits. It isn't just how productive or how abundant resources are at a particular site, but also whether a plant has the potential to access them. I suggest the best approach to understanding the importance of competition in structuring natural communities will use a holistic view, focusing not only on target plants and resource availability, but also on population size structure development and phenotypic plasticity. This blending of neighborhood and population level phenomena with larger scale community problems provides a unique perspective which hopefully will contribute to the resolution of the competition-productivity debate.

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