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# Larger *Triticum aestivum* plants do not preempt nutrient-rich patches in a glasshouse experiment

Eric J. von Wettberg[1,2,*] and Jacob Weiner[1]
*[1]Botany Section, Department of Ecology, Royal Veterinary and Agricultural University, Rolighedsvej 21, Frederiksberg, DK-1958, Denmark; [2]Current address: Ecology and Evolution, Department of Biology, Brown University, Providence, RI, USA; *Author for correspondence (e-mail: Eric_von_Wettberg@Brown.edu)*

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## Abstract

Plant competition belowground generally appears to be size-symmetric, i.e. larger plants only obtain a share of belowground resources proportional to their size, and therefore do not suppress smaller individuals. The experimental evidence for size-symmetric belowground competition comes primarily from experiments with homogenous soil conditions. It has been hypothesized that the presence of high nutrient patches that can be pre-empted by larger plants can make competition belowground size-asymmetric. We tested this hypothesis by growing *Triticum aestivum* individuals singly and in pairs in containers with aboveground dividers so that competition occurred only belowground. Plants grew in either a homogenous soil mixture, or in the same mixture with a band of enriched soil between them. Initial size differences were generated by a seven day difference in sowing date. There was no evidence of size-asymmetric competition with or without soil heterogeneity. Large plants did not have a disproportionate effect on smaller plants, nor did they perform disproportionately better when paired with a small neighbor. Our results suggest that in heterogeneous soil conditions, roots of larger plants that reach nutrient patches first are not able to prevent roots of smaller plants that arrive later from obtaining resources from the patch.

## Introduction

Size is fundamental in competitive interactions among plants. Plant competition is usually size asymmetric, in that larger plants are able to obtain a disproportionate share of resources (for their relative size) and suppress smaller plants (Weiner 1990). When this occurs, even a small initial size advantage becomes larger over time. Size asymmetric competition occurs when there is competition for resources that can be pre-empted by larger plants (Schwinning and Weiner 1998). One resource that can be preempted is light, because higher leaves shade lower leaves but not vice versa. There is substantial evidence that light can be preempted and that this results in asymmetry of aboveground competition (Hikosaka et al. 1999; Berntson and Wayne 2000).

Evidence to date, summarized below, generally supports the hypothesis that belowground competition is size symmetric (Casper and Jackson 1997). Plants with larger root systems are able to obtain more resources when competing with plants with smaller roots, but we know of no evidence to date for the ″over-proportional″ size advantage usually observed in competition above ground. Most of the evidence for the size-symmetry of belowground competition comes from experiments under homogenous soil conditions. It has been hypothesized that the presence of high nutrient patches could make belowground competition size-asymmetric. If larger plants reach high nutrient patches first due to their larger root systems and then deplete the resources in the patch before smaller plants' roots can obtain a share, the result would be size-asymmetric competition below ground (Casper and Cahill 1996; Schwinning and Weiner 1998).

### *Evidence that belowground competition is size-symmetric*

There are several methods that have been used to determine if competition is size-symmetric or -asymmetric. One approach is to ask if increases in plant density result in increased size inequality (Weiner and Thomas 1986). Although highly unequal size distributions can occur due to other factors such as intrinsic differences in resource uptake rates due to size, large increases in size inequality in populations grown at higher densities are generally considered evidence for size-asymmetric competition. Another way of determining if competition is size asymmetric is to measure the success of plants of varying initial sizes competing against each other (Thomas and Weiner 1989; Schwinning and Fox 1995).

Several experiments have looked for size-asymmetric belowground competition in glasshouse conditions where aboveground competition was removed by opaque dividers or physical separation of aboveground parts (Newbery and Newman 1978; Weiner 1986; Wilson 1988a; Weiner et al. 1997). None of these experiments found evidence for size-asymmetric competition belowground. Homogenous soil mixtures were used in all of these experiments. Field experiments evaluating the size-symmetry of belowground competition by removing or reducing aboveground competition have also been performed. When plants of six species of varying initial sizes were transplanted into field conditions with (a) no neighbors, (b) only the shoots of neighbors, (c) only the roots of neighbors, or (d) both the roots and shoots of neighbors, no significant interaction between initial transplant size and the competitive treatment were observed (Gerry and Wilson 1995). It was concluded that greater initial size does not give plants a size-asymmetric advantage in competition below ground. Experiments on *Amaranthus retroflexus* with root exclusion tubes have provided evidence that belowground competitive intensity is directly related to root biomass (Cahill and Casper 2000), suggesting that competition below ground is size-symmetric. There was some evidence that larger individuals took up more nitrogen per unit size than smaller individuals in competing *Xanthium canadense* populations, but nitrogen loss rates per unit size were also larger for larger individuals (Hikosaka and Hirose 2001). The size-asymmetry of competition in these populations was primarily due to competition for light (Hikosaka et al. 1999). Estimates of nitrogen uptake per unit root length in competing *Betula alleghaniensis* seedlings support the hypothesis that competition for nitrogen is size-symmetric (Berntson and Wayne 2000).

Several glasshouse experiments have investigated the effects of soil heterogeneity on plant size inequality, and, by inference, the size-asymmetry of competition. *Abutilon theophrasti* populations growing on soils with a patchy distribution of nutrients did not show a greater size inequality than populations on homogeneous soils (Casper and Cahill 1996, 1998). In these studies, the overall size distributions appear to be largely the result of aboveground competition, whereas soil heterogeneity determined which plants were the larger and the smaller individuals. Soil heterogeneity did not increase size inequality in glasshouse populations of *Ipomoea tricolor* (Blair 2001). While some researchers have found increased size inequalities under heterogeneous soil conditions (Fransen et al. 2001), this occurred when aboveground competition was not eliminated, so it is not clear if the size-asymmetry observed was due to an interaction between increased initial size of plants that get nutrient patches first and later competition for light, or to belowground competition itself.

In the present study we redesigned the experimental approach of Weiner et al. (1997) to create conditions that theory suggests could result in size-asymmetric competition belowground. By comparing plants competing belowground in homogenous soil to plants competing with a band of high nutrient soil between them, we investigate one proposed way in which nutrient heterogeneity can affect the size-symmetry of competition.

## Materials and methods

Ten liter, 22 cm diameter and 28 cm deep pots were filled with one of two soil mixtures (Figure 1). Homogenous mixture treatments were filled with a mixture of 52% sand, 35% sphagnum, 7% sphagnum based potting mixture (Færdigblanding, Pindstrup Mosegaard, Ryomgaard Denmark), 5% perlite, and less than one percent vermiculite. In the heterogeneous soil mixture, a high fertility band of soil was placed in the center of the pots, and surrounded by the soil used in the homogenous soil treatment. The band of enriched soil mixture contained 51% com-

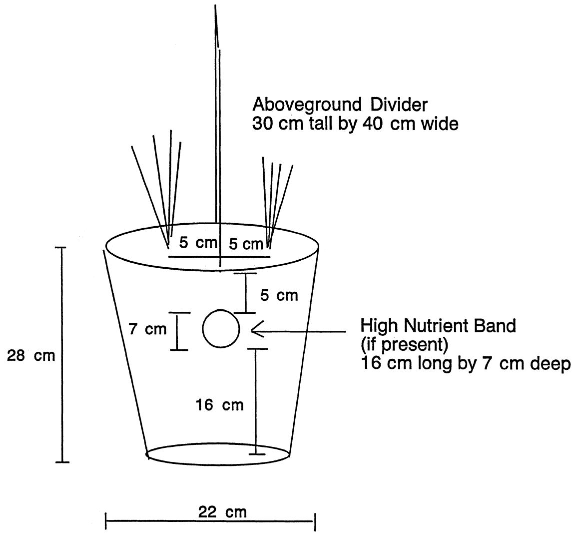

*Figure 1.* Schematic diagram of the experimental units. The band of high nutrient soil, when present, is 5 cm below the surface in the 10 liter pots. Above ground dividers were 40 cm wide by 30 cm tall, and were expanded upward when plants overtopped them.

mercial blended potting mixture, 45% sand, 3% perlite, less than one percent vermiculite, and five grams of field 21-3-10 NPK field fertilizer per ten liters of soil volume. The high fertility band was seven cm wide and 16 cm long (615 $cm^2$). The band was placed under the surface of the pot so that five cm of the background soil could be placed above it. The bands were intended to mimic the fertilizer and manure banding practices of conventional farmers in Denmark. Danish farmers frequently place bands of fertilizer or manure five cm deep and five cm from crop rows (Jens Petersen, personal communication).

There are two alternative approaches to this design, and each has advantages and disadvantages. One approach (1) is to keep the total amount of resources the same by using the same proportion of high and low nutrient soil mix in the heterogeneous and homogeneous soil treatments (e.g. Casper and Cahill (1996) and Blair (2001)), while an alternative approach (2) is to have the same ″background″ resource level in both treatments, while adding one or more high-nutrient patches in the heterogeneous treatment. It can be argued that in design 2 heterogeneity is confounded with total resource supply. But a disadvantage of design 1 is that seedlings face different conditions in the homogeneous and heterogeneous treatments immediately after they germinate. If initial growth rates have a major effect on final size, i.e. if growth is more influenced by initial resource condition than total resource availability, design 1 may confound heterogeneity and initial growth conditions. The experiment presented here was initially planned and executed with design 1 but the effects of initial growth as influenced by soil nutrient immediately after germination dominated plant growth and final size, so we repeated the experiment with design 2.

To prevent shoot competition, 40 cm wide and 30 cm tall metal dividers covered on both sides with white plastic were set up across the pots, and arranged in such a way that they stood over the strip of enriched soil. White plastic dividers were placed over the metal dividers on all pots when plants began to overtop the metal dividers. Pots with only one plant also received dividers and divider extensions. Although the divided pot method used in this experiment is limited in the extent to which it can replicate realistic field conditions (McPhee and Aarssen 2001), it is appropriate for testing the type of general hypothesis we pose.

To generate initial size differences, *Triticum aestivum* cv Cortez (winter wheat) seeds were planted on two separate days. ″Large″ plants were planted on 6 September 2000. ″Small″ plants were planted seven days later. There were five planting combinations: 1) ″large″ plants alone, 2) ″large plants″ with ″large″ neighbors, 3) ″large″ plants with ″small″ neighbors, 4) ″small″ plants with ″small″ neighbors, and 5) ″small″ plants alone. Three seeds were placed near the center of the area between the divider and the pot edge and seedlings were thinned to one plant after 10 days. Seeds were planted so that the distance to the band of high nutrient soil (if present) would be 5 cm for both plants in the pot. Plants planted without a neighbor were planted in the same position. An automatic watering system kept the soil moist. Overhead lighting (400 W high pressure sodium light bulbs from KB, Sweden) was used to supplement daylight, and extended day length to 16 hours.

Pots were arranged approximately 10 cm apart on the floor in the greenhouses of the Royal Veterinary and Agricultural University in Taastrup, Denmark. There were three replicate blocks, each containing all five combinations of ″large″ and ″small″ plants in both soil conditions. As plants grew, pots were set approximately 25 cm apart. Dividers were oriented north to south to equalize sunlight reaching both sides of the pot. Pots were rotated three times weekly, and positions between and within the blocks were randomized once a week.

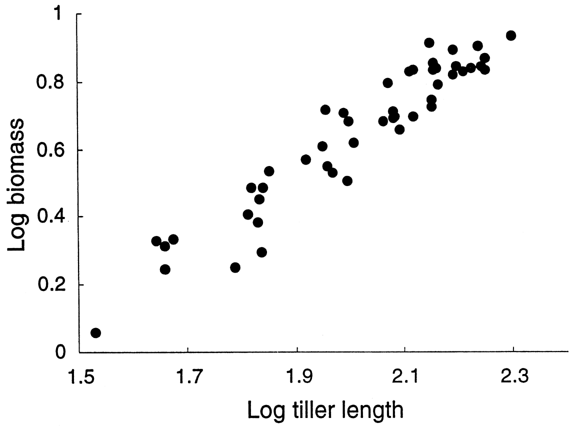

*Figure 2.* Relationship between log total tiller length and log final biomass of all plants at harvest; $r^2 = 0.91$.

In this variety of winter wheat, the log total height of all the tillers is highly correlated with the log final biomass ((Figure 2), $r^2 = 0.91$). We used the total tiller length as a non-destructive measure of biomass over time. Each week total tiller length was determined by measuring each tiller of each plant from the soil surface to the base of the blade of the top leaf. Plants did not flower, but senescence of some leaf tissue had begun by the end of the experiment. On 1 November all plants were clipped at the soil surface, separated into living and dead tissue, dried at 80 °C for two days, and weighed.

Our analysis followed that used by Weiner et al. (1997). Since plants can only compete after they are large enough to interact, and the intensity of competition increases as plants grow, asymmetry is most likely to appear later in growth. Our analysis consequently emphasizes the last week of growth as well as final biomass. Both absolute and relative growth rate have advantages and disadvantages as dependent variables, and both are size-dependent. We analysed the absolute growth rate (AGR), square root transformed, because this gave homoscedasticity and normally distributed residuals. Plant growth over the final seven days of the experiment was closer to linear than to exponential (see Results), suggesting that analysis of absolute growth rate may be more appropriate.

To measure the strength of competition, we calculated a Competition Index (CI = [biomass alone − biomass in competitive treatment]/[biomass alone]; Miller (1996)), and we evaluated the effects of plant age, neighbor age, and soil treatment on this index with ANOVA.

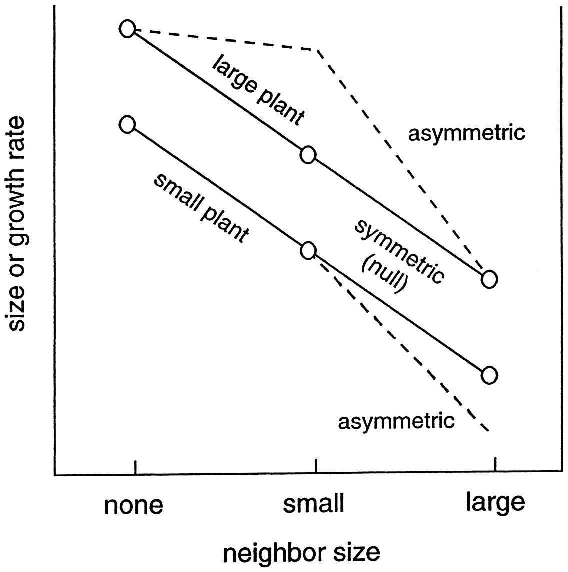

*Figure 3.* Prediction of results of competition under the null hypothesis of size-symmetric competition (solid lines) and the hypothesis of asymmetric competition (dotted lines). The null hypothesis is represented as a straight line for convenience, although it could be non-linear. All that is required is that the decrease in size with increasing neighbor size is monotonic. Modified from Weiner et al. (1997).

The null hypothesis is that competition is size-symmetric, meaning that large and small plants are equally affected by large and small neighbors (Figure 3). Under asymmetric competition, larger plants would have a larger effect on small plants than on larger plants, and smaller plants would have less effect on large plants than on small plants. In an analysis of variance on a measure of growth, evidence of asymmetry should appear in the significance of the age × neighbor interaction term. If size-asymmetric competition can be caused by soil heterogeneity, we would expect to find a significant age × neighbor age interaction only in the heterogeneous soil treatment. Since plant growth is size dependent, a measure of size at the beginning of the period is included as a covariate. Absolute growth rate was square root transformed to fit the assumptions of analysis of variance. As in most local competition studies, we analyzed both plants in a treatment. We do not consider this to be a serious violation of the assumption of independence, although it could increase the probability of a Type I error. ANOVA has been shown to be largely robust against violations of independence (Legendre and Legendre 1998). All ANOVAs are Type III sum of squares calculated with PROC GLM in SAS.

Another form of evidence for asymmetry is the effect of neighbors as a function of their size. If competition is size-symmetric, we expect the effect of neighbors on a plant to be a function of their size (Schwinning and Weiner 1998). If competition is size asymmetric, on the other hand, we expect effects of neighbors per unit size to be different when the neighbors are of different sizes. The effect of a neighbor of a given size should be different when the target plant is larger than when the target plant is smaller than the neighbor. Therefore we looked at growth over a period as a function of the size of the neighbor and tested for homogeneity of slopes for subject plants of different sizes to determine whether or not competition was asymmetric.

A third form of evidence for size-asymmetric competition is the amount of size variation under different competitive regimes. Since size-asymmetric competition exacerbates size differences, we calculated the coefficient of variation (CV) for pairs of plants growing together, and performed an ANOVA to see if the CV varied with soil treatment.

## Results

Competition was significant. Plants with neighbors were 81.5% of the size of plants without neighbors. Competitive intensity, measured as our modified competitive index, increased with plant size (SS = 0.54957, DF = 1, P < .0001). There was also a significant interaction between plant size and neighbor size on CI (SS = 0.1579, DF = 1, P = 0.0136), indicating that small plants suffered greater competitive interference from large neighbors than they did from small neighbors. The presence of a high nutrient patch did not have a significant effect on CI (SS = 0.01597, DF = 1, P = 0.3936), indicating that our soil treatment did not affect competitive intensity.

Date of planting (SS = 124.23; DF = 1, P < 0.0001), size of neighbor (SS = 12.69; DF = 2; P = 0.0002), and the presence of the soil treatment (SS = 11.427; DF = 1; P < 0.0001) had significant effects on plant biomass. There was a significant age × neighbor interaction (SS = 7.83; DF = 2; P = 0.0029), but the interaction was not in the direction predicted for size-asymmetric competition (Figure 4). Small plants with small neighbors were larger than small plants with large neighbors, while large plants with small neighbors were not larger than large plants with large neighbors. The shape of the curve in (Figure 4) is opposite that predicted for asymmetric competition (Figure 3). Plants in pots with the high nutrient patch were larger than plants in pots without the high nutrient patch when tested in a full model with plant size, neighbor size, and the interaction between the two (SS 11.427, DF 1, P < 0.001). There was no significant interaction between the presence of the high nutrient patch and any other experimental treatment affecting plant size.

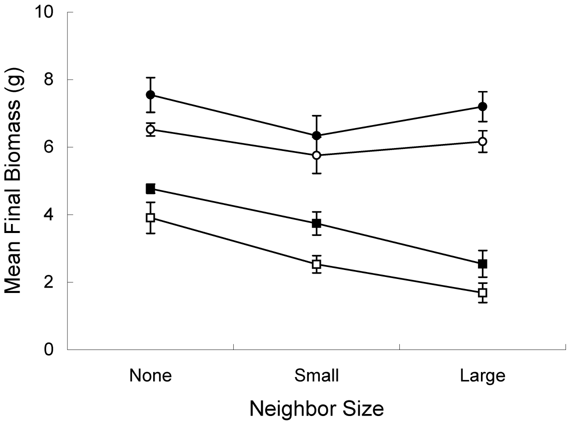

*Figure 4.* Mean dry mass of large (●: with nutrient patch; ○: without patch) and small (■: with patch, □: without patch) plants with no, small, or large neighbors. Error bars represent one standard error.

The total tiller length of plants was highly correlated with biomass (Figure 2). Plants with neighbors had significantly less total tiller length than those without neighbors. Planting date (SS = 52016; DF = 1; P < 0.0001), neighbor size (SS = 12379; DF = 2; P < 0.0001), and soil treatment (SS = 4684; DF = 1; P = .0011) all had significant effects on total tiller length. There was no significant age × neighbor age interaction (SS = 1399; DF = 2; P = 0.1691). Both plant size (SS = 53.68, D = 1, P < 0.001) and neighbor size (SS = 23.19, DF = 1, P < 0.0046) had highly significant effects on growth over the subsequent week, but the presence of a nutrient patch did not (SS = 4.15, DF = 1, P = 0.1450; Figure 6). No interaction terms were significant.

There was a negative relationship between growth of a plant over a week and the size of its neighbor at the beginning of the week (Figure 7). The slope of the relationship was not significantly different between plants of different age classes or fertility treatments. The coefficient of variation of the biomass of plants with neighbors did not vary significantly with soil treatment (SS = 575.67; DF = 1; P = 0.2215).

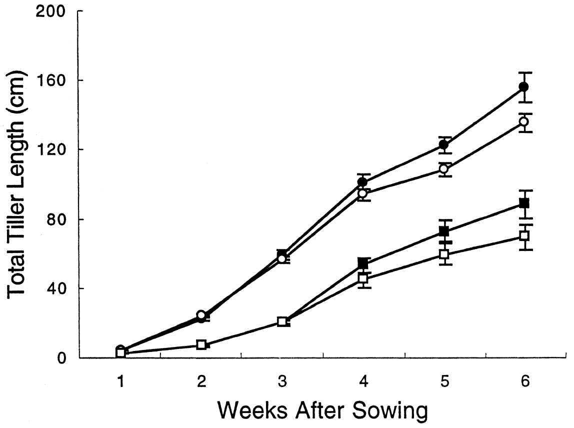

*Figure 5.* Mean total tiller length for large and small plants with high nutrient patches (● and ■, respectively) and without nutrient patches (○ and □, respectively). Error bars represent one standard error.

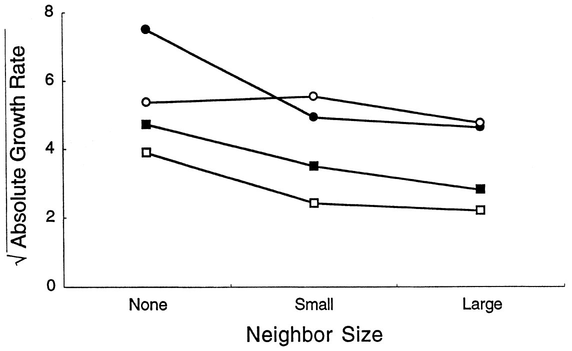

*Figure 6.* Square root of absolute growth rate (change in total tiller length) during the final week of the experiment for large (above) and small (below) plants with no, small, and large neighbors. ●: large plants with a nutrient patch; ○: large plants without a patch, ■: small plants with a patch, and □: small plants without a patch. Plant size (P < .0045) and neighbor size (P < .0001) had highly significant effects, while the presence of nutrient patches did not (P = .1453). There were no significant interaction terms.

## Discussion

Competition occurred and was more intense when one or both plants were large. The presence of a high nutrient patch increased plant size, but did not alter the competitive effect of a neighboring plant. The increase in soil fertility and nutrient heterogeneity did not affect the size-symmetry of competition. Thus, the type of soil heterogeneity we created did not generate size-asymmetric competition. Our results support the generalization that belowground competition is not size asymmetric.

These results suggest that high nutrient patches cannot easily be pre-empted by larger plants. In our experiment smaller plants arriving in high nutrient patches later than their larger neighbors still had access to these patches in proportion to their size. Of course, it is possible that another type of soil heterogeneity, or more intense belowground competition, or interspecific competition could generate size-asymmetry, but it has not been observed to date.

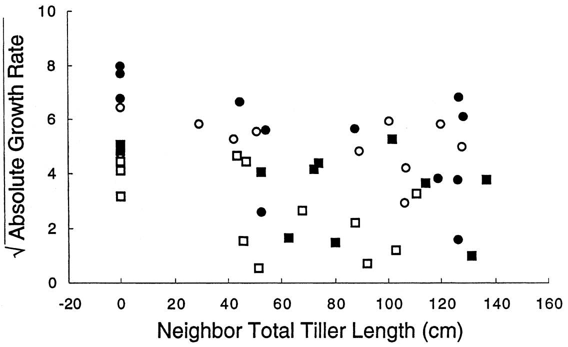

*Figure 7.* Relationship between plant growth rate and neighbor size (total tiller length in cm) during the final week of the experiment. ●: large plants with a nutrient patch; ○: large plants without a patch, ■: small plants with a patch, and □: small plants without a patch. The slope of the relationship does not vary with date of planting or soil treatment, indicating that the impact of neighbors on plant growth is size-symmetric.

Our data suggest that something approaching ″completely symmetric″ competition (Schwinning and Weiner 1998), where all plants have an equal access to contested resources, independent of their size, could sometimes occur belowground. Biomass, shoot length and growth rate of larger (but not smaller) plants are approximately equally negatively impacted by neighbors, regardless of the size of neighbors (Figures 4 and 5). If belowground competition occurs by overlapping depletion zones, there may be a point at which additional neighbor root biomass has little effect on target plant growth (Casper and Jackson 1997; Cahill and Casper 2000). Competition below ground may favor smaller individuals in some situations, thus reducing the disadvantages of being smaller.

As in many studies, we were not able to measure belowground biomass. There was a high density of roots occupying the entire soil volume by the end of the experiment, but not to the extent that would suggest that space itself was a limiting belowground resource (McConnaughay and Bazzaz 1991). We attempted to separate root tissue, but found that we could not reliably recover most of the fine root tissue from the soil and that we could not reliably attribute roots to a particular plant. It is possible that belowground competition affects plants' root:shoot ratio (Gersani et al. 2001), and that accounting for this biomass could alter the results. Although shoot biomass may be all that can be obtained in many ecological experiments (Cahill 2002), methods to accurately measure the belowground biomass of individuals growing with neighbors are needed (Zobel and Zobel 2002).

The size-symmetry of belowground competition has many implications for competitive interactions in plant communities. The interaction of competition for several major resources, such as soil nutrients and light, is poorly understood. Wilson (1988b) found non-additive interactions between above and belowground competition to be rare, but there is evidence that non-additive interactions occur in many species (Casper and Jackson 1997). If competition below ground is size symmetric, it could minimize the effects of size-asymmetric aboveground competition, reducing the abilities of larger plants to suppress smaller neighbors. Conversely, if access to nutrients at an earlier stage in growth can give a young plant a slight size advantage over a neighbor, this will lead to that plant being able to pre-empt more incoming light later. The size-asymmetries observed in some studies (Fransen et al. 2001) may have been due to interactions of competition for different resources. In cases where it is desirable to maximize the competitive abilities of some plants, such as in agricultural situations, such interactions could be useful. Practices such as fertilizer banding may be helpful in weed control, in that they can maximize the size advantage of crop plants over weeds early in the growing season (Rasmussen et al. 1996), which can result in a large advantage in size-asymmetric competition for light later in the growing season.

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