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FERTILIZATION EFFECTS ON INTERACTIONS BETWEEN ABOVE- AND BELOWGROUND COMPETITION IN AN OLD FIELD

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Abstract. Recent theoretical and experimental studies have addressed whether the relative importance of aboveground and belowground competition changes along gradients of biomass productivity. Results have been contradictory, with some researchers finding a decrease in the importance of belowground competition and an increase in aboveground competition with increased productivity, and others finding either no relationship, or a positive correlation between the various factors. Belowground competitive intensity (BCI), resulting from root interactions, and total competitive intensity (TCI), resulting from both root and shoot interactions, have usually been measured as the proportional growth reduction due to competition (relative to growth without competition). Instead of direct measurement, aboveground competitive intensity (ACI) has been estimated by assuming that aboveground competition and belowground competition do not interact to affect plant growth, and therefore ACI + BCI = TCI. In this study, *Abutilon theophrasti* was used as a focal species to determine whether an interaction between the two competitive forms could exist. Target plants were grown with varying degrees of interaction with the roots of neighboring plants, through the use of modified root exclusion tubes, and by tying back the aboveground neighboring vegetation. In total, 16 combinations of varying intensities of aboveground and belowground interactions with neighbors were created at each of two fertilization levels. The strength of belowground competition decreased with fertilization, while neither aboveground competition nor total competition (occurring both above- and belowground simultaneously) varied among fertilization treatments. Not only was there evidence for an interaction between above- and belowground competition, the form of interaction varied with productivity, switching from no interaction in the unfertilized block to a positive interaction in the fertilized block. With fertilization, belowground competition decreased a plant's ability to compete in asymmetric competition for light. These results contrast with existing models of the role of competition in plant communities, and a new model is presented. In order to understand the role of aboveground and belowground competition in plant communities, the potential for interactions between the two competitive forms must be considered in future studies.

Key words: Abutilon theophrasti; *asymmetric competition; community organization; nonadditive effects; old field; positive interaction; productivity gradient; root competition; root exclusion tubes; shoot competition.*

INTRODUCTION

Competition is an important factor affecting the composition of many plant communities (Gleason 1926, Grime 1979, Tilman 1982, 1988, Connell 1983, Schoener 1983). Measuring the effects of competition on plant growth in natural communities is critical to testing current ideas about how the role of competition changes along productivity gradients. Some researchers have argued that the negative effects of competition should be greater with increased productivity (Grime 1973, 1979, Keddy 1989). Others predict that it will not change with increased soil resources (Newman 1973, Tilman 1982, 1988, Wilson and Tilman 1991, 1993, 1995), but should instead shift from occurring primarily belowground to primarily aboveground (Tilman 1988, Wilson and Tilman 1991, 1993, 1995). Resolution of this issue requires the experimental separation of the effects of aboveground competition from those of belowground competition. While many field studies have measured growth reductions caused by competitive interactions (for reviews see Fowler 1986, Goldberg and Barton 1992, Gurevitch et al. 1992), relatively few have completely separated those interactions into aboveground and belowground components.

Inherent in recent considerations of how competition changes with productivity has been the explicit assumptions that (1) belowground and aboveground competition are independent in their effects on plant growth, and (2) their combined effects are additive at all levels of community productivity. It has been as-

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sumed that aboveground competition does not influence a plant's ability to compete belowground, and vice versa (Wilson and Tilman 1993, 1995, Belcher et al. 1995, Twolan-Strutt and Keddy 1996, Peltzer et al. 1998). This assumption is reflected in the methods used to measure competition. Belowground competitive intensity (BCI) has been measured as the relative decrease in target plant growth when interacting with neighbors belowground, but not aboveground, as compared to growth with no competitors. Similarly, total competitive intensity (TCI) is the relative growth decrease when plants interact simultaneously above- and belowground with neighbors. In contrast, aboveground competitive intensity (ACI) is rarely measured directly, but is estimated as the difference between TCI and BCI, i.e., ACI = TCI − BCI (Wilson and Tilman 1993, 1995, Belcher et al. 1995, Twolan-Strutt and Keddy 1996, Peltzer et al. 1998). Obviously, these estimates of ACI are valid only if above- and belowground competition do not interact and are indeed additive in their effects on plant growth.

The possibility of an interaction between above- and belowground competition has been considered for a long time (Clements et al. 1929, Donald 1958, Caldwell 1987, Wilson 1988*a*) with limited experimental evidence. In a review of interspecific-competition studies conducted in greenhouses, Wilson (1988*a*) concluded that 15 of 48 experiments might provide evidence of nonadditive interactions between aboveground and belowground competition. Since two-thirds of the cited experiments showed no interaction, this review has been used as support for the assumption that above- and belowground competition are independent. However, since pot size itself, independent of nutrient levels, can influence plant growth (McConnaughay and Bazzaz 1991), results from greenhouse experiments may have limited applicability to natural systems.

Although no field study has explicitly tested whether an interaction between above- and belowground competition does occur, several have included the four treatments necessary to address this question: target plants experiencing no competition, belowground competition only, aboveground competition only, and both above- and belowground competition (Aerts et al. 1991, Gill and Marks 1991, Putz and Canham 1992, Dillenburg et al. 1993, Gerry and Wilson 1995, Riegel et al. 1995, Grubb et al. 1997). Data from some of these studies are suggestive of interactions between above- and belowground competition in natural systems, although the appropriate statistical tests were not conducted. The most direct evidence comes from Dillenburg et al. (1993) who found that solely belowground (but not solely aboveground) interactions between *Liquidamber styraciflua* and the vine *Lonicera japonica* reduced *L. styraciflua* growth. The combined effects of above- and belowground interactions were significantly greater than the effects of belowground interactions by themselves, suggesting belowground competition increased the intensity of aboveground competition.

There is no a priori reason to expect the effects of aboveground and belowground competition to be additive. In fact, in many situations this assumption is numerically impossible. For example, if aboveground competition reduces growth by 40% and belowground competition reduces growth by 80%, it is impossible for the combined (additive) effect to reduce growth by >100%. This fact by itself necessitates research into the issue of competitive additivity in natural communities. More importantly, there is reason to believe that the form of interaction between above- and belowground competition may itself vary with productivity and the relative intensities of aboveground and belowground competition. There are three possible ways the combined effects of aboveground and belowground competition could affect plant growth:

1. *Positive interaction.*—One form of competition amplifies the effects of the alternative form. Competition for light is generally one sided or ''size asymmetric'' (Harper 1977, Weiner 1985, Weiner and Thomas 1986, but see Schwinning 1996), with larger plants having a disproportionate advantage in competition for light by shading smaller ones, resulting in initial size differences being compounded over time. Any factor that reduces the initial growth rate of a plant initiates a positive feedback loop that decreases the likelihood of the plant obtaining a dominant position in the developing size hierarchy. If belowground competition occurs early in the development of size hierarchies, it could reduce a plant's aboveground competitive ability (positive interaction). This form of interaction could also occur if shading reduces a plant's ability to take up nutrients (e.g., Jackson and Caldwell 1992). Reduced nutrient uptake should result in reduced aboveground growth, thereby compounding the effects of asymmetric competition for light. Based on these potential mechanisms, I hypothesize that a positive interaction is most likely to occur in systems in which growth is nutrient-limited and competition for light is associated with the annual development of distinct size hierarchies and asymmetric competition (e.g., grassland systems).

2. *No interaction (i.e., additive).*—The effects of one form of competition in no way alter the ability of a plant to compete in the other from of competition. For this to occur, there can not be the potential for positive feedback and compounded effects of competition. This lack of interaction may occur in communities that: (1) do not have a pronounced size hierarchy, so ''losing'' aboveground competition is of relatively low cost, (2) have a perennial size hierarchy (e.g., forests) in which subordinate species are likely to be adapted to low light, and therefore size differences are not compounded, or (3) competition is symmetric. In contrast to aboveground competition, there is growing evidence that competition belowground is symmetric (Wilson

1988*b*, Gerry and Wilson 1995, Cahill 1997, Weiner et al. 1997), with individuals competing proportional to their size. In communities in which competitive interactions are primarily belowground, some shading (but not severe enough for asymmetric competition for light) should not result in compounded effects on plant growth, and, therefore, one form of competition should not affect the other.

3. *Negative interaction.*—One form of competition reduces the severity of the other form. Plant growth is often simultaneously limited by a variety of factors (Chapin et al. 1987), and an increase in the availability of one resource may not result in increased plant growth. Wilson (1988*a*) has suggested that this form of interaction could be due to a law of limiting factors in which the growth of a light-limited plant should be less affected by low nutrient availability than when growth is not light limited (and vice versa). As a result, the combined effect of aboveground and belowground competition is not likely to be much greater than the stronger effect by itself.

In summary, I hypothesize that any factor that alters the overall symmetry of competition within a community should then influence the type of interaction between the two competitive forms. If the asymmetry of competition increases with productivity, then there should be a shift from no interaction or negative interactions to positive interactions as productivity increases.

I tested this hypothesis in a field study in which target plants were grown under different combinations of belowground and aboveground competition at two levels of fertilization. Competition treatments were created using novel experimental methods that allowed me to independently vary the potential intensities of above- and belowground competition. The form of interaction between above- and belowground competition was then examined statistically at a broad range of competitive intensities.

METHODS

Field site and target species

The experiment was conducted in an early successional grassland community in Chester County, Pennsylvania, USA (a 2.5 ha plot that is part of the Laurels Conservation Preserve, owned by the Brandywine Conservancy), last cut for hay in August, 1994, two years prior to this study. Dominated by grasses (e.g., *Festuca* spp., *Dactylis glomerata*) and Canada thistle (*Cirsium arvense*), the field site contains >45 species of herbaceous flowering plants.

Abutilon theophrasti Medic. (Malvaceae), an old-field annual native to Asia (Spencer 1994), was chosen as the focal species in this study for several reasons. *A. theophrasti* is a common weed throughout the northeastern United States, with seeds germinating readily in the field. Although never a dominant member of the community, *A. theophrasti* is common within the Laurels, with some individuals >1 m in height. *A. theophrasti* has a high photosynthetic rate, similar to that of other early successional species (Bazzaz 1979), and in response to aboveground crowding, populations form pronounced size hierarchies. Those individuals failing to obtain a dominant position early in the growing season are destined to remain small (Casper and Cahill 1996, 1998). Belowground competition does reduce the growth of *A. theophrasti* in this field, with significant effects occurring within 4 wk of germination (Cahill 1997). For these reasons, this species is likely to exhibit a positive interaction between above- and belowground competition. Previous work also indicates that *A. theophrasti* responds to fertilization at levels similar to those used in this study. It is unknown what effect fertilization will have on the competitive ability of this species.

Experimental layout

Four aboveground, four belowground, and two fertilization treatments were crossed in all orthogonal combinations and arranged in a randomized block design with one replicate of each of the 16 competition treatments per 5 × 5 m block. Forty-six blocks were established and arranged into six rows of seven blocks and one row of four blocks, with ~2 m between the blocks. Half of the blocks (23) were randomly selected to receive fertilizer supplementation; the remaining 23 blocks were not fertilized. Within each block, the individual experimental plots (0.75 × 0.75 m) were organized into rows and columns of four plots, with 0.5-m walkways between plots. Each plot consisted of naturally occurring vegetation surrounding a target plant that was growing within a 15 cm diameter root exclusion tube located in the plot center. The aboveground vegetation within each plot was modified according to a randomly assigned aboveground treatment.

Construction of aboveground and belowground treatments

Previous work has demonstrated that the intensity of belowground competition experienced by a focal plant can be altered by drilling varying numbers of holes in root exclusion tubes, thereby altering the accessibility of the soil surrounding a target plant to neighboring roots (Cahill 1997). This basic approach was modified in this study to create gradients in the intensity of both belowground and aboveground competition between neighbors and target plants.

The root exclusion tubes used here consisted of a cylinder (15-cm diameter × 20-cm length) of thin plastic sheeting (3 mm thick), with five 10-cm^2 holes to permit lateral water movement. To alter the accessibility of the soil within the tubes to neighboring roots, different numbers of holes were covered with a nylon fabric (NITEX 30-μm pore size) that allows passage of fungal hyphae and water while excluding roots

(George et al. 1992, Mader et al. 1993). Three belowground treatments were created in which all five (I_{BG}), three of five (II_{BG}), or zero of five (III_{BG}) of the holes were covered with fabric. Thus water and fungal hyphae should have been equally accessible to target plants in treatments employing tubes. Belowground Treatment IV_{BG} used no plastic.

To insert the tubes into the ground, 736 holes (15-cm diameter × 25-cm depth) were drilled using a gas-powered auger. The soil was excavated from each plot, and the hole was lined with the plastic tube. In Treatment IV_{BG}, holes were still drilled, but no plastic was inserted. The excavated soil was pooled among all 16 plots in each block to reduce soil resource heterogeneity. It was then used to refill the holes. Since not all of the excavated soil could be recovered, additional soil obtained from the perimeter of the field site was added to each block.

A gradient in the potential intensity of aboveground competition was also created, using four aboveground treatments: (I_{AG}) No aboveground neighbors, (II_{AG}) shading by one-third of neighbors, (III_{AG}) shading by two-thirds of neighbors, and (IV_{AG}) shading by all neighbors. These treatments were created by holding back the requisite amount of vegetation with tree netting. Where all of the neighboring vegetation was tied back (Treatment I_{AG}), a 50 × 50 cm square of netting was centered over the plot and anchored to the ground in its center using steel pins. Each of the corners of the netting was then pulled taught and anchored approximately 15 cm above the soil surface. In Treatments II_{AG} and III_{AG}, 240° and 120° wedges of netting were used to tie back neighboring vegetation. The integrity of the aboveground treatments was maintained throughout the experiment by regularly pushing the growing neighboring vegetation beneath the netting. Similar netting has been used in other studies to remove aboveground interactions without killing neighboring plants (e.g., Wilson and Tilman 1991). Due to the small diameter of the thread in the netting (similar to fishing line), effects of shading are negligible.

Soil moisture and light availability

To determine if there was variation in soil moisture among the belowground treatments, gypsum resistance blocks were placed within each of the four belowground treatments and in the center of each of 14 blocks. Soil moisture readings were taken using a Model KS-D1 soil moisture tester (Delmhorst Instrument Company) immediately following heavy rainfall and, again, four days after a rain. Since the first set of readings was taken within 1 wk of installation of the belowground treatments, it was assumed that any differences in soil moisture would be due to differences in drainage, not to differences in uptake by roots growing inside the tubes. Soil moisture did not vary among the belowground treatments (ANOVA, main effect of belowground treatment, $F_{4,48} = 0.71$, $P = 0.59$), nor was there a significant time × belowground treatment interaction ($F_{4,48} = 1.85$, $P = 0.14$).

To verify that a gradient in light levels at the soil surface was created, I measured light availability in each plot within 14 blocks, 62 d following sowing. Measures were taken using a Li-Cor 1000 Datalogger with a LI-190SA Quantum Sensor and are reported as a proportion of the light available above all vegetation.

Fertilization, sowing, and protection from herbivory

Approximately 20 seeds, which had been soaked in water overnight, were placed in the center of each experimental plot on 24 May 1996. To aid in seedling establishment, the neighboring vegetation was allowed to shade each plot for 14 d following sowing. After that time, the aboveground treatments were installed and seedlings were thinned to one per plot.

The 23 blocks selected for fertilization received 60 g/m^2 Osmocote slow-release fertilizer (14-14-14, NPK), for an addition of 8.4 g/m^2 NPK. Fertilizer was broadcast by hand seven days after sowing. This rate of fertilization is low, and falls within the range of soil resource levels that naturally occur in this field. Osmocote fertilizers release nutrients over the course of the growing season (3–4 mo), decreasing the likelihood of fertilizer burn.

To maintain a reasonable sample size, I attempted to reduce herbivory in this experiment by installing a 0.8 m tall hardware cloth exclosure (0.64 × 0.64 cm cell size) around the perimeter of the experiment, buried to a depth of 15 cm. Small mammals inside the exclosure were trapped; they were released outside the exclosure. Trapping continued sporadically during the growing season, ensuring the removal of most of the small mammals. To reduce insect herbivory, each target plant was sprayed three times (at 4-wk intervals) with 6.7 mL/L of the insecticide Isotox, as has been used in other ecological studies (e.g., Louda and Potvin 1995). A greenhouse experiment provided some evidence that Isotox has a small fertilization effect on *A. theophrasti* ($<10\%$ increased growth; Cahill, *unpublished data*), but, since all plants of all treatments were sprayed, there should have been no bias due to its application.

Estimates of neighbor biomass and plant harvest

Four weeks after sowing, plant height was measured for each target plant in 14 of the 46 blocks. After 70 d of growth, all target plants were cut at the soil surface, dried, and weighed.

To determine the effects of fertilization on the aboveground biomass of the naturally occurring vegetation within each block, a 0.25-m^2 sample was taken from the block center 75 d following sowing. The vegetation was cut at the soil surface, dried, and weighed. To measure the effects of fertilization on neighbor root biomass within each block, soil cores (5-cm diameter × 15-cm depth) were taken from all 46 blocks at the end of the experiment. To determine the vertical root distributions of neighboring roots, a second set of soil cores 15–30 cm deep were taken from seven blocks of each fertilization treatment. Roots were removed from the cores by passing the soil through a 2-mm sieve, dried at 70°C, and weighed.

Measures of plant response to competition

Relative measures of plant response to competition (sensu Goldberg 1990, 1996) were calculated from the biomass data in order to determine whether: (1) plant growth in the presence of aboveground, belowground, or total competition varied with fertilization, (2) above- and belowground competition interacted to affect plant growth, and (3) whether the form of any interaction between above- and belowground competition was dependent upon soil fertility.

Competitive response (CR) is defined in this study as the proportion of control-plant biomass that remains following competition. Plant biomass is standardized to plant size when plants are grown with no neighbors. The purpose is to compare the strength of competition, independent of any effects of fertilization on plant size. The following equations were used to quantify plant response to total, belowground, and aboveground competition:

Total Competitive Response (TCR)

$$= \ln\left(\frac{T_{\mathrm{AN}}}{T_{\mathrm{NN}}}\right) \tag{1}$$

Aboveground Competitive Response (ACR)

$$= \ln\left(\frac{T_{\mathrm{SN}}}{T_{\mathrm{NN}}}\right) \tag{2}$$

Belowground Competitive Response (BCR)

$$= \ln\left(\frac{T_{\mathrm{RN}}}{T_{\mathrm{NN}}}\right) \tag{3}$$

where T_{NN} is the target plant aboveground biomass in each plot in which the target plant was interacting with no neighbors above- or belowground; T_{AN} is the target plant biomass when plants were interacting simultaneously with neighbors above- and belowground; T_{SN} is the target plant biomass in each plot when interacting with neighboring shoots but not roots; and T_{RN} is the target plant biomass when interacting with the roots but not shoots of neighbors. To account for the natural heterogeneity occurring in the field site, measures of ACR, BCR, and TCR were calculated separately within each block. Due to loss of nearly one-third of the plants from herbivory, not all measures of competitive response could be determined for each block. Because aboveground biomass and reproductive output are highly correlated for this species (Casper and Cahill 1996), only aboveground biomass is used to calculate CR.

These measures of competitive response are very similar to those of competitive intensity (CI) used in prior studies (e.g., Wilson and Tilman 1995, Twolan-Strutt and Keddy 1996). Total competitive intensity (TCI) is the proportion of target plant biomass lost due to competition, whereas total competitive response (as measured in this study) is the proportion of plant biomass remaining following competition. Thus, TCR = ln(1 − TCI), as calculated in prior studies. The metric used here facilitates testing for interactions, assuming the multiplication of proportional plant growth from each form of competition.

To determine whether belowground competition affected plant response to aboveground competition (or vice versa), their null relationship (i.e., no interaction) was assumed to be multiplicative, not additive. This reasoning is drawn from a study by Turner (1988), in which she tested for nonadditive effects of various forms of disturbance on the growth of *Spartina alterniflora*. She argued that since summation of separate effects could yield unrealistic values of the combined effects, a proportional approach was necessary. For example, in this study, if belowground competition results in 30% of control-plant growth (70% reduction), and aboveground competition alone results in 60% growth (40% reduction), the null, combined effect should be (0.30)(0.60) = 0.18. In other words, with no interaction between above- and belowground competition, plants should grow only 18% of what they would have in the absence of any competition. If additivity, instead of multiplicity, were assumed, a meaningless null value would be created. In the above example, an additive assumption would predict a 110% reduction in growth, i.e., a biologically meaningless value. Therefore, the assumption of an additive relationship between above- and belowground competition can be rejected a priori.

To test for an interaction between the two forms of competition, the combined effects of aboveground and belowground competition on plant growth were calculated in two ways: (1) total competitive response ($\mathrm{TCR}_{\mathrm{True}}$), as directly determined through experimentation (Eq. 1); and (2) total competitive response ($\mathrm{TCR}_{\mathrm{Predicted}}$), as predicted assuming a noninteractive (multiplicative) relationship between above- and belowground competition (Eq. 4). The predicted (null) TCR was calculated by adding the experimentally derived values of above- and belowground competition. Since these values were calculated in a logarithmic scale, this is identical to multiplying the proportional plant growth of each form of competition in an arithmetic scale:

$$\mathrm{TCR}_{\mathrm{Predicted}} = \mathrm{ACR} + \mathrm{BCR}. \tag{4}$$

For example, to determine whether the one-third of aboveground neighbors (Treatment $\mathrm{II}_{\mathrm{AG}}$) and the no plastic belowground treatment (Treatment $\mathrm{IV}_{\mathrm{BG}}$) interact to affect plant growth, $\mathrm{TCR}_{\mathrm{True}} = \ln(T_{\mathrm{II}_{\mathrm{AG}},\,\mathrm{IV}_{\mathrm{BG}}}/T_{\mathrm{I}_{\mathrm{AG}},\,\mathrm{I}_{\mathrm{BG}}})$, where $T_{\mathrm{II}_{\mathrm{AG}},\,\mathrm{IV}_{\mathrm{BG}}}$ is the aboveground biomass of the target plant grown with aboveground Treatment $\mathrm{II}_{\mathrm{AG}}$

and belowground Treatment IV_{BG}, and $T_{I_{AG}, I_{BG}}$ is the aboveground biomass of the target plant grown with aboveground and belowground Treatments I_{AG} and I_{BG} (no neighbors, i.e., NN in Eqs. 1–3). $TCR_{Predicted} = \ln(T_{II_{AG}, I_{BG}}/T_{I_{AG}, I_{BG}}) + \ln(T_{I_{AG}, IV_{BG}}/T_{I_{AG}, I_{BG}})$. Since these values are calculated separately in each experimental block, both TCR measures are replicated, allowing for statistical analysis. In ANOVA, a significant effect of the method of calculation (True vs. Predicted) would be evidence that above- and belowground competition interact to affect plant growth. If $TCR_{True} < TCR_{Predicted}$, then plant growth is less than that predicted assuming no interaction (a positive interaction), and $TCR_{True} > TCR_{Predicted}$ indicates a negative interaction. Both measures of TCR were calculated separately for all nine treatments in which plants were interacting simultaneously above- and belowground at each level of fertilization. This allowed for analysis of whether the relative strengths of above- and belowground competition affected the form of interaction, or whether the relative strengths of above- and belowground productivity affected the form of interacation.

Experimental technique

Although root exclusion tubes are commonly used in ecological studies, they may introduce a variety of artifacts (see Casper and Jackson 1997 for review). The modifications I made to this standard technique (covering varying numbers of holes with fabric) appear to have been successful in removing many of the potential problems:

1) Ninety-five percent of all neighboring roots located in the top 30 cm of soil were found within the top 15 cm (Means + SD, [g/core]: 0–15 cm = 0.630 ± 0.634 [$N = 46$], 15–30 cm = 0.036 ± 0.028 [$N = 14$]). Therefore, the use of 20 cm deep tubes likely eliminated most of the potential belowground competitive effects of neighbors.

2) There was no evidence that tying back the aboveground vegetation of the neighboring plants reduced the growth of neighboring roots and, thus, their ability to compete belowground with target plants. If, due to tying, there were fewer neighboring roots to compete with target plants, measures of belowground competition made in this study should be overestimated. However, in unfertilized plots, target plant growth with belowground competition was only 12% that of the control plants, as shown in Figs. 1 and 2. Clearly, tying back the neighbors could not have greatly inflated the measured belowground competitive response. Rather than decreasing total neighbor growth by tying back the vegetation, I simply changed which neighbors were destined to grow large; those plants immediately under the netting grew around the netting and were large, while those plants pressed against the soil surface were deeply shaded and grew little.

3) Additionally, by installing the tubes in early spring, I maximized the likelihood that neighbors would be able to grow into and exploit the artificial microsites created by drilling the holes. If neighbors were not able to fully exploit the belowground microsites during the experiment, then the measured effects of belowground competition would be underestimates.

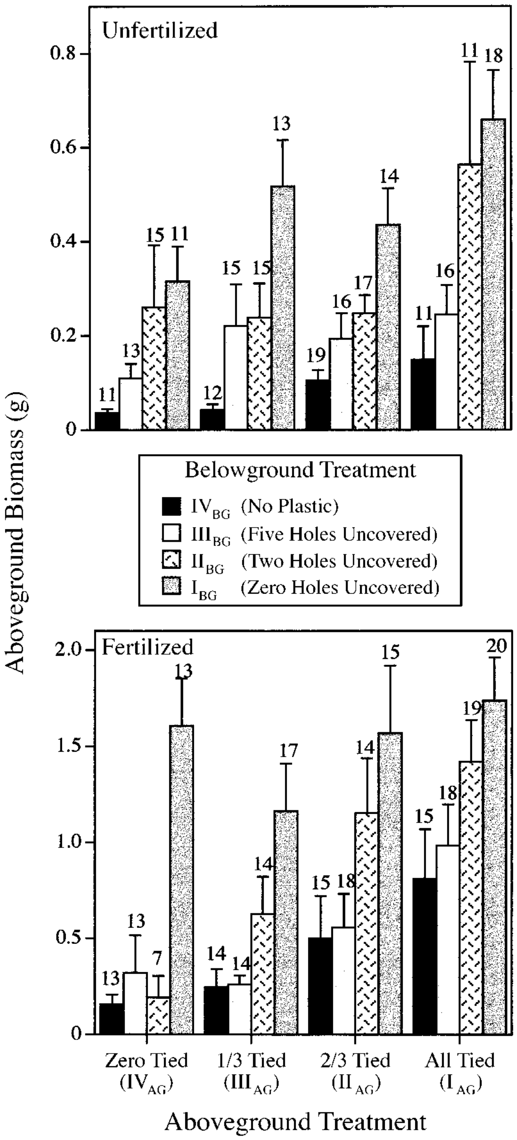

FIG. 1. Mean dry aboveground (AG) biomass, as measured after 10 wk of growth. Error bars represent 1 SE. Values above the columns are sample sizes at the end of the experiment. The main effects of fertilization, aboveground treatment, belowground treatment, and the AG × BG interaction had $P < 0.05$ in ANOVA. All of the other interactions had significance levels ≤ 0.10. Note that the y-axes have different scales; plant growth was much greater with fertilization than without it.

Statistical analyses

Despite precautions taken to prevent herbivory, nearly one-third of the plants were killed during the course of the experiment, most likely by the common wood-

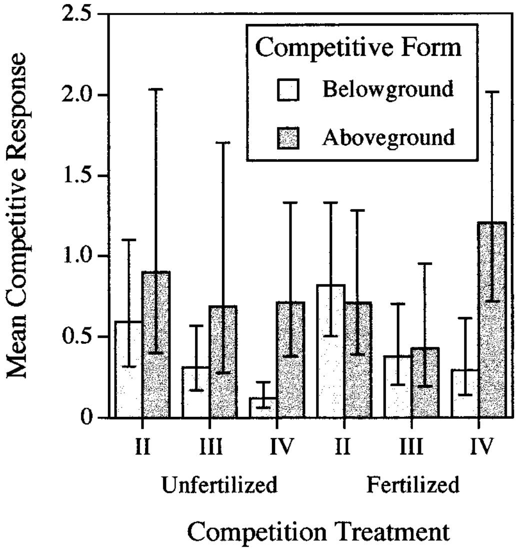

FIG. 2. Mean competitive response (CR) as a function of fertilization treatment, competitive form (aboveground [AG] vs. belowground [BG]), and the competition treatment (II_{AG}, III_{AG}, IV_{AG}, II_{BG}, III_{BG}, or IV_{BG}) for plants experiencing only one of the two competitive forms. Moving from II_{AG} to IV_{AG} or from II_{BG} to IV_{BG} corresponds to an increase in the potential intensity of the above- and belowground treatments, respectively. Measures of belowground competition were made only when plants experienced no aboveground interaction with neighbors (Treatment I_{AG}). Similarly, aboveground competition was measured only when plants experienced no belowground interactions with neighbors (Treatment I_{BG}). Table 4 presents mean CR values for plants experiencing both forms of competition simultaneously. Means are back-transformed from the logarithmic scale used to calculate and analyze the data. The asymmetrical error bars represent CL (95%).

chuck, *Marmota monax.* Since herbivory was not concentrated in specific blocks, blocks could not be used as a factor in ANOVA. Therefore, ANOVA were run as unbalanced designs, with sample sizes reported in the figures and tables. All analyses were conducted using the statistical program, Statistica, for the Macintosh (Statsoft 1994).

To determine the effects of competition and fertilization on plant growth, an ANOVA was conducted in which the aboveground, belowground, and fertilization treatments served as independent variables and dry aboveground biomass (ln-transformed to satisfy assumptions of ANOVA) served as the dependent variable. A significant belowground × aboveground interaction would indicate that the two forms of competition exhibit an interactive effect on plant growth. A significant three-way interaction would suggest the interaction between above- and belowground competition is itself dependent upon soil fertility. A similar ANOVA was conducted using plant height (after 4 wk) as the dependent variable.

A third ANOVA was conducted using only those plants that were experiencing *either* aboveground *or* belowground competition to determine whether above- and belowground competition varied among competition treatments or with fertilization. Competition treatment (II, III, or IV), competitive form (above- or belowground), and fertilization treatment served as the three fixed effects. Competitive response (due to either above- or belowground competition) served as the dependent variable. A significant form × fertilization interaction would indicate that above- and belowground competition respond differently to fertilization.

To directly test the assumption of no interaction between above- and belowground competition, an ANOVA was conducted using only the plots in which target plants were interacting simultaneously with neighbors above- and belowground. Fertilization, aboveground treatment, belowground treatment, and the method of calculating the total competitive response (True vs. Predicted) served as the independent variables, with total competitive response as the dependent variable. A significant main effect of the method of calculation would indicate that above- and belowground competition interact to affect plant growth. A significant fertilization × method of calculation interaction would indicate that the direction of the interaction between above- and belowground competition is dependent upon soil fertility. Significant belowground × method, aboveground × method, or higher order interactions would indicate that the relative intensities of above- or belowground competition also influenced the direction of the interaction. Technically, these methods of testing for an interaction are assessing the assumption of additivity, since aboveground competitive response and belowground competitive response are summed to calculate the predicted value. However, since these CR measures are on a logarithmic scale, this is identical to testing whether there is a multiplicative relationship between above- and belowground competition, when measured in an arithmetic scale.

To determine whether the aboveground treatments altered light availability at the soil surface within the experimental plots, fertilization treatment, belowground treatment, aboveground treatment, and block (random, nested in fertilization treatment) were the independent variables in an ANOVA, with the proportion of the available light reaching the soil surface in the center of the plots serving as the dependent variable.

RESULTS

Plant growth

Fertilization increased the aboveground biomass of the neighboring vegetation (ANOVA $F_{1,44} = 6.31$, $P < 0.05$; means [SE; gm^{-2}]: unfertilized, 267.4 [36.5]; fertilized, 328.5 [19.1]), but not belowground biomass (ANOVA $F_{1,44} = 0.42$, $P = 0.53$). Light availability was affected by both the fertilization and the aboveground treatments, but not by the belowground treatment or any interaction term (ANOVA, main effect of fertilization, $F_{1,12} = 0.787$, $P = 0.02$; main effect of

TABLE 1. ANOVA results for dry aboveground biomass (ln-transformed) at the end of the experiment and plant height 28 d after sowing. Fertilization (FERT), belowground treatments (BG), and aboveground treatments (AG) served as the three independent variables (fixed effects).

Source of variation	Aboveground biomass				Plant height			
	MS	df	F	P	MS	df	F	P
FERT	94.26	1	75.89	<0.0001	27.06	1	3.23	0.07
BG	81.29	3	65.46	<0.0001	70.85	3	8.46	<0.0001
AG	34.61	3	27.87	<0.0001	27.99	3	3.34	0.02
FERT × BG	2.66	3	2.14	0.09	4.61	3	0.55	0.65
FERT × AG	2.91	3	2.34	0.07	2.10	3	0.25	0.86
BG × AG	2.51	9	2.02	0.04	4.69	9	0.56	0.83
FERT × BG	2.03	9	1.63	0.10	14.63	9	1.75	0.08
Error	1.24	434	···	···	8.37	180	···	···

Note: Since herbivory was severe, blocks were not incorporated into either analysis, and the models were unbalanced.

aboveground treatment, $F_{3,36} = 94.52$, $P < 0.0001$). As expected, a greater proportion of the light at the top of the canopy reached the soil surface when all neighbors were tied back than when no neighbors were tied back (means [SD]: unfertilized—all tied, 0.839 [0.193]; none tied, 0.259 (0.276); fertilized—all tied, 0.860 [0.200]; none tied, 0.086 [0.108]). Intermediate aboveground treatments had intermediate light measures.

Target plant aboveground biomass was significantly affected by fertilization, aboveground neighbor treatments, belowground neighbor treatments, and the belowground × aboveground interaction (Table 1, Fig. 1). These results provide evidence that above- and belowground competition do interact to affect plant growth. Plants were largest when fertilized and grown in the absence of both aboveground and belowground neighbors (Fig. 1).

After only 4 wk of growth, both the aboveground and belowground treatments significantly affected plant height (Table 1). In the absence of aboveground interactions, plants were significantly taller without any belowground interactions with neighbors (Treatment I_{BG}) than when grown with full belowground interactions (Treatment $\mathrm{IV}_{\mathrm{BG}}$) (Fisher's PLSD, $P < 0.05$, mean [SD] in centimeters: unfertilized—full root exclusion [Treatment I_{BG}], 8.86 [3.26]; no plastic [Treatment $\mathrm{IV}_{\mathrm{BG}}$], 5.64 [2.53]; fertilized—Treatment I_{BG}, 6.28 [4.71]; Treatment $\mathrm{IV}_{\mathrm{BG}}$, 6.07 [2.30]). In the absence of belowground competition, plants were taller when shaded by neighbors than when all neighbors were tied back (Fisher's PLSD, $P < 0.05$, mean [SD] in centimeters: unfertilized—all tied [Treatment I_{AG}], 8.86 [3.26]; none tied [Treatment $\mathrm{IV}_{\mathrm{AG}}$], 11.50 [3.04]; fertilized—Treatment I_{AG}, 6.29 [4.70]; Treatment $\mathrm{IV}_{\mathrm{AG}}$, 12.70 [3.27]).

Independent effects of above- and belowground competition

When plants experienced only one form of competition, plants were larger with aboveground competition than they were with belowground competition (Table 2, Fig. 2). A nonsignificant fertilization × competitive form interaction, suggests that the relative intensities of above- and belowground competition did not shift with fertilization (Table 2, Fig. 2). However, several studies (e.g., Grime 1973, 1979, Tilman 1982, 1988) have made specific predictions about changes in above- and belowground competition along productivity gradients. To relate results from this study to these others, it is necessary to know how the full strength of above-, below-, and total competition varied with fertilization in the present study. Plant growth in response to full belowground interactions (Treatment $\mathrm{IV}_{\mathrm{BG}}$) in the unfertilized blocks was significantly less than in the fer-

TABLE 2. Results from ANOVA comparing effects of fertilization (FERT), competitive form (aboveground [AG] or belowground [BG]), and competition treatment (II, III, or IV) on competitive response when plants experienced only one of the two potential competitive forms.

Source of variation	MS	df	F	P
FERT	0.95	1	0.80	0.373
Competitive form	16.97	1	14.21	<0.001
Competition treatment	6.53	2	5.47	0.005
FERT × Form	1.84	1	1.54	0.217
FERT × Treatment	2.45	2	2.05	0.133
Form × Treatment	7.47	2	6.25	0.003
FERT × Form × Treatment	0.11	2	0.09	0.910
Error	1.19	137	···	···

Notes: Measures of BG competition (Treatments $\mathrm{II}_{\mathrm{BG}}$, $\mathrm{III}_{\mathrm{BG}}$, $\mathrm{IV}_{\mathrm{BG}}$) were made only when plants experienced no aboveground interactions with neighbors (Treatment I_{AG}); similarly, measures of AG competition (Treatments $\mathrm{II}_{\mathrm{AG}}$, $\mathrm{III}_{\mathrm{AG}}$, $\mathrm{IV}_{\mathrm{AG}}$) were made only when plants experienced no belowground interactions with neighbors (Treatment I_{BG}). Tables 3 and 4 present results when plants experience competition from both forms simultaneously.

TABLE 3. ANOVA results for competitive response (CR) when plants interacted simultaneously with neighbors aboveground (AG) and belowground (BG). Fertilization (FERT), belowground treatment ($\mathrm{II}_{\mathrm{BG}}$, $\mathrm{III}_{\mathrm{BG}}$, or $\mathrm{IV}_{\mathrm{BG}}$), aboveground treatment ($\mathrm{II}_{\mathrm{AG}}$, $\mathrm{III}_{\mathrm{AG}}$, or $\mathrm{IV}_{\mathrm{AG}}$), and the method of determination of CR (true vs. assuming additivity) served as the independent factors.

Source of variation	MS	df	*F*	*P*
FERT	0.17	1	0.07	0.788
BG	22.40	2	9.39	<0.001
AG	12.53	2	5.25	0.006
Method	45.13	1	18.92	<0.001
FERT × BG	7.21	2	3.02	0.050
FERT × AG	0.84	2	3.92	0.704
BG × AG	1.69	4	0.71	0.587
FERT × Method	13.22	1	5.54	0.019
BG × Method	2.67	2	1.12	0.328
AG × Method	9.36	2	3.92	0.021
FERT × BG × AG	0.66	4	0.28	0.894
FERT × BG × Method	0.20	2	0.08	0.920
FERT × AG × Method	10.60	2	4.44	0.013
BG × AG × Method	0.55	4	0.23	0.921
FERT × BG × AG × Method	1.49	4	0.63	0.644
Error	2.39	31	⋯	⋯

tilized blocks (Fisher's PLSD, $P = 0.048$). Relative plant growth with full aboveground interactions (Treatment $\mathrm{IV}_{\mathrm{AG}}$) did not differ with fertilization (Fisher's PLSD, $P = 0.315$).

In the absence of belowground competition, aboveground competitive response did not vary among aboveground treatments in either the unfertilized or fertilized blocks. In the absence of aboveground competition, belowground competitive response did vary among belowground treatments. A greater proportion of plant biomass remained when only two of five holes were uncovered in the plastic tubes than when no plastic was inserted (Fisher's PLSD, $P < 0.05$). These results are reflected in a significant competitive form × competition treatment interaction (Table 2, Fig. 2).

Effects of above- and belowground competition in combination

Total competitive response (TCR) did not vary with fertilization when plants were interacting simultaneously with neighbors above- and belowground (Tables 3 and 4). More specifically, TCR for both full above- and full belowground interactions (Treatment $\mathrm{IV}_{\mathrm{AG}}$, $\mathrm{IV}_{\mathrm{BG}}$) did not differ between fertilization treatments (Fisher's PLSD, $P > 0.05$, Table 4).

A significant fertilization × method interaction (Tables 3 and 4), provides evidence that the form of interaction between above- and belowground competition does change with fertilization. $\mathrm{TCR}_{\mathrm{True}}$ and $\mathrm{TCR}_{\mathrm{Predicted}}$ significantly differed in the fertilized blocks, but not in the unfertilized blocks (Fig. 3).

When plants were interacting simultaneously above- and belowground with neighbors, belowground competition reduced growth more in the unfertilized than in the fertilized blocks (fertilization × belowground, $P < 0.05$, Table 3). With fertilization, there was a greater dissimilarity between predicted and actual TCR values of plants grown with full aboveground interactions (Treatment $\mathrm{IV}_{\mathrm{AG}}$) than occurred in the unfertilized treatments. However, for the other two aboveground treatments (I_{AG} and $\mathrm{III}_{\mathrm{AG}}$), the actual and predicted CR values differed by similar amounts in the two fertilization treatments (Table 4), contributing to a significant fertilization × aboveground × method interaction (Table 3).

DISCUSSION

Interactions between above- and belowground competition

The primary findings from this study demonstrate that (1) above- and belowground competition can interact to affect plant growth, and (2) there was a shift from no interaction to a positive interaction with fertilization. Both of these findings contradict assumptions made in recent studies investigating shifts in the intensities of aboveground and belowground competition along natural and artificial productivity gradients (Wilson and Tilman 1993, 1995, Belcher et al. 1995, Twolan-Strutt and Keddy 1996, Peltzer et al. 1998).

A positive interaction likely occurred in the fertilized blocks, due to a decreased ability of the target plants to compete in asymmetric competition for light, when their initial growth was reduced due to root competition. In the absence of root competition, initial growth was rapid, and plants in all four aboveground treatments were approximately the same size (Fig. 1); there was no aboveground competition. Shading by neighbors increased plant height after 4 wk, which likely increased the ability of target plants to obtain a dominant position in the size hierarchy, even though they were initially shaded by neighbors. However, with root competition, this morphological adjustment to shading was not great enough to compensate for decreased growth caused by competition belowground. Target plants competing belowground had a decreased probability of overtopping the surrounding vegetation, and

TABLE 4. Mean competitive response (CR) when target plants interact simultaneously with neighbors above- and belowground. Both the actual and predicted values (assuming no interaction) are presented as a function of fertilization (FERT), aboveground (AG), and belowground (BG) treatments.

FERT	BG treatment	AG treatment	Actual CR (lower and upper CL 95%)	*N*	Predicted CR (lower and upper CL, 95%)	*N*
Unfertilized	no plastic (IV_{BG})	None tied (IV_{AG})	0.05 (0.02–0.12)	9	0.08 (0.01–2.68)	2
		1/3 tied (III_{AG})	0.06 (0.02–0.14)	9	0.06 (0.02–0.16)	6
		2/3 tied (II_{AG})	0.15 (0.08–0.29)	15	0.11 (0.03–0.33)	7
	5 uncovered (III_{BG})	None tied (IV_{AG})	0.15 (0.07–0.31)	11	0.15 (0.01–1.60)	5
		1/3 tied (III_{AG})	0.27 (0.11–0.66)	12	0.28 (0.03–2.33)	6
		2/3 tied (II_{AG})	0.21 (0.08–0.54)	12	0.49 (0.13–1.88)	9
	2 uncovered (II_{BG})	None tied (IV_{AG})	0.17 (0.07–0.40)	13	0.26 (0.03–1.91)	5
		1/3 tied (III_{AG})	0.25 (0.12–0.52)	12	0.30 (0.06–1.63)	4
		2/3 tied (II_{AG})	0.31 (0.22–0.43)	12	1.25 (0.26–5.93)	7
Fertilized	no plastic (IV_{BG})	None tied (IV_{AG})	0.06 (0.02–0.18)†	11	0.49 (0.11–2.17)	8
		1/3 tied (III_{AG})	0.10 (0.05–0.22)	12	0.15 (0.03–0.68)	11
		2/3 tied (II_{AG})	0.13 (0.06–0.32)	14	0.22 (0.05–0.91)	11
	5 uncovered (III_{BG})	None tied (IV_{AG})	0.05 (0.01–0.21)	11	0.56 (0.17–1.86)	7
		1/3 tied (III_{AG})	0.14 (0.07–0.27)	12	0.20 (0.06–0.69)	10
		2/3 tied (II_{AG})	0.21 (0.10–0.43)	16	0.23 (0.08–0.69)	12
	2 uncovered (II_{BG})	None tied (IV_{AG})	0.02 (0.01–0.12)	6	0.87 (0.19–4.05)	7
		1/3 tied (III_{AG})	0.19 (0.07–0.54)	13	0.34 (0.11–1.09)	12
		2/3 tied (II_{AG})	0.31 (0.10–0.95)	12	0.61 (0.26–1.45)	13

Notes: The potential intensity of neighbor interactions increases from two uncovered (Treatment II_{BG}) to no plastic (Treatment IV_{BG}), or from two-thirds tied (Treatment II_{AG}) to none tied (Treatment IV_{AG}). Targets experienced full interactions both above- and belowground. Values did not vary with fertilization (PLSD > 0.05). Means were back-transformed from the logarithmic scale in which they were calculated and analyzed; 95% confidence limits (CL) are also presented.

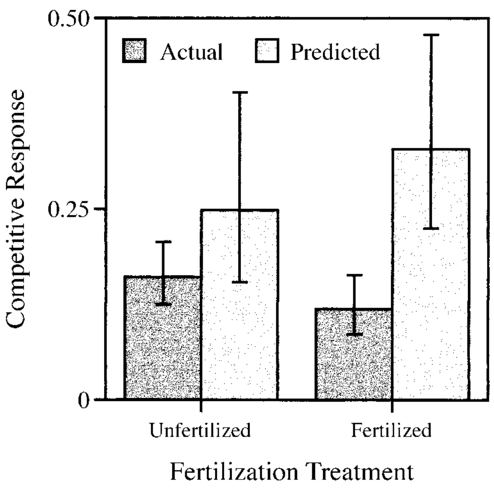

FIG. 3. Graphical representation of the significant fertilization × method of calculation interaction term in ANOVA of competitive response (Table 3). Total competitive response was calculated using two methods: (1) actual determination from the experiment (difference in ln[biomass] between plants interacting with neighbors both above- and belowground and those grown with no neighbor interactions), and (2) predicted, assuming no interaction between above- and belowground competition. In unfertilized plots, the actual and predicted values did not differ significantly (Fisher's PLSD, $P = 0.06$). In the fertilized plots, plants were significantly smaller than that predicted assuming an additive interaction (Fisher's PLSD, $P < 0.0001$). Means are back-transformed from the logarithmic scale used to calculate and analyze the data. The asymmetrical error bars represent CL (95%).

they were delegated to subordinate positions in the size hierarchy. Since <10% of the available light reached below the canopy, and *A. theophrasti* has a high light compensation point (Bazzaz 1979), once a plant obtained a subordinate position, it was unable to recover. As a result, the effects of belowground competition were compounded through the asymmetry of aboveground competition, resulting in a positive interaction between the two competitive forms. In asymmetric competition, initially small size differences will become exaggerated during the growing season. In this study, even modest reductions in initial plant size (from belowground Treatments II_{BG} or III_{BG}) were enough to reduce initial aboveground competitive ability and therefore resulted in a positive interaction between competitive forms.

In the unfertilized blocks, there was no evidence of any interaction between above- and belowground competition (Fig. 1), which was likely the result of a reduction in the asymmetry of competition. In the absence of competition, plant size was slightly <40% of that obtained when fertilized (Fig. 1). Additionally, >25% of available sunlight reached the soil surface. Since not all of the light was pre-empted by the canopy plants, subordinate plants did not experience as severe a light environment as did those in the fertilized blocks. As a result, belowground competition did not reduce aboveground competitive ability to the extent found in the fertilized blocks, and no significant interaction was found between above- and belowground competition.

There is an apparent discrepancy between the results from the biomass ANOVA (Table 1) and the ANOVA comparing measures of actual vs. predicted total competitive response (TCR) (Table 3). In the biomass ANOVA, the fertilized × aboveground × belowground interaction was not significant (P = 0.10, Table 1), suggesting that the interaction between competitive forms did not vary with fertilization. However, in the analysis of competitive response, the form of interaction between above- and belowground competition varied with fertilization (Fig. 3, Tables 3 and 4). Possible explanations for this are as follows:

1) There was substantial variation in plant size, even in the absence of competitive interactions (unfertilized, CV = 58%; fertilized, CV = 67%), some of which is certainly due to heterogeneity within the field site. The reasoning behind the use of a randomized block design is to remove this source of variation (Underwood 1997) and reduce the error term in ANOVA. By not incorporating blocks into the analysis of plant biomass, the error term is inflated, reducing the ability to detect a three-way interaction. In contrast, blocks are indirectly incorporated into the measures of competitive response, increasing the ability to detect a significant interaction term (method × fertilization). Since competitive response values were calculated separately within each block, competing plants and the no-competition control (to which their growth was compared) were never separated by >4 m. This likely had the effect of reducing the variability in competitive response between blocks due to field heterogeneity, facilitating the detection of a significant interaction term.

2) Although not significant, there was a trend towards a positive interaction in the unfertilized blocks (Fig. 3, P = 0.06). Since the trend was in the same direction as in the fertilized blocks it suggests that the fertilization × aboveground × belowground interaction would not be a large term and would be difficult to detect with an inflated error term, as is found in the biomass ANOVA. It is important to note that the shift in the interaction with fertilization found in the competitive-response data was not a function of the underlying assumption of a multiplicative, rather than an additive, interaction between above- and belowground competition. Analysis of the data calculated as competitive intensity and assuming an additive interaction also found a shift to a positive interaction with fertilization (Cahill 1997).

Measures of competition and prior models of plant competition along productivity gradients

Two main models of the relationship between competition and productivity have been proposed in the literature. (1) Grime (1973, 1979) has suggested there should be an increase in the strength of competition (both above- and belowground) with increased productivity, and (2) Tilman (1982, 1988) has suggested that the strength of competition should not vary, due to an increase in aboveground and a decrease in belowground competition with increased productivity.

TABLE 5. Aboveground competitive response (ACR) when (1) calculated directly through experimentation (TRUE), (2) estimated assuming multiplicative effects of proportional growth reductions (MUL), and (3) estimated assuming additivity (SUM).

Fertilization treatment	ACR_{TRUE}	ACR_{MUL}	ACR_{SUM}
Unfertilized	0.714	0.422	0.932
Fertilized	1.204	0.205	0.768

Notes: Aboveground competitive response (ACR) values reported correspond to the proportional plant growth (compared to control) that either occurred or would be predicted to occur when target plants grew with full aboveground interactions with neighbors. These values are back-transformed into the arithmetic scale for presentation and for calculation of the predicted values. ACR_{MUL} (aboveground competitive response assuming a multiplicative relationship between above- and belowground competition) was calculated as follows: (mean total competitive response [TCR] when plants experienced full competition [Treatments IV_{AG} and IV_{BG}])/(mean belowground competitive response [BCR] when plants experienced full belowground competition [Treatment I_{AG} and IV_{BG}]). ACR_{SUM} (aboveground competitive response assuming an additive interaction between above- and belowground competition) was calculated by converting mean CR measures to competitive intensity, and then estimating aboveground competitive intensity (ACI) as TCI − BCI. ACI was then converted back to aboveground competitive response, so that all values could be presented in the same form.

As previously stated, experimental tests of these models have been founded upon the assumption that aboveground and belowground competition do not interact. This assumption is implicit in the estimation of aboveground competitive intensity (ACI = relative growth reduction due to aboveground interactions) as the difference between total competitive intensity (TCI = relative growth reduction due to above- and belowground interactions) and belowground competitive intensity (BCI = relative growth reduction due to belowground interactions). Such studies often find ACI increases with productivity, which corresponds to a decrease in aboveground competitive response (ACR) as measured in the present study (Wilson and Tilman 1991, 1993, 1995, Twolan-Strutt and Keddy 1996). Another important difference between this study and the previous ones is the underlying assumption of a multiplicative, not an additive, relationship between above- and belowground competition. The estimate of ACR, assuming no interaction (with a multiplicative relationship), is much lower than when estimated assuming an additive relationship (Table 5). This suggests two important problems with the estimation of ACI in prior studies. First, assumptions of no interaction between above- and belowground competition can result in the appearance of a positive relationship between aboveground competition and productivity in conjunction with a negative correlation between above- and belowground competition, even if such a correlation does not exist (Table 5). Second, if an assumption of no interaction must be made, an additive assumption underestimates the negative effects of aboveground competition, compared to a more realistic multiplicative assumption.

The possibility of an interaction between above- and belowground competition has not been incorporated into any current model describing the role of competition in plant community dynamics (e.g., Grime 1979, Tilman 1982, 1988, Keddy 1989, Belcher et al. 1995, Twolan-Strutt and Keddy 1996). For this reason, an alternative model for the relationships between productivity and the competition is presented below.

A new model of changes in competition along a productivity gradient

If the form of interaction between above- and belowground competition changes with the symmetry of competition, then it is necessary to incorporate the relationship between competitive asymmetry and productivity into any new model of competition in plant communities. Several studies have shown an increase in the asymmetry of competition with increased density and plant size (e.g., Weiner and Thomas 1986, Connolly and Wayne 1996, Schwinning 1996). Often, this asymmetry is measured as an increase in the skewness of the population (CV or Gini Coefficient; e.g., Weiner 1986, 1990, Weiner and Thomas 1986), or it appears as an experimentally derived parameter of a growth model (e.g., Schwinning and Fox 1995, Connolly and Wayne 1996). However, when competition is primarily belowground, it appears to be symmetric (Wilson 1988*b*, Stoll et al. 1994, Gerry and Wilson 1995, Cahill 1997, Weiner et al. 1997). I hypothesize that in low productivity sites, plant size and density will be low, with competition predominately occurring belowground, and therefore being symmetric. As productivity increases, plant density and size increase, resulting in an increase in the asymmetry of competition (Fig. 4A). After productivity is high enough to create great disparity in light availability between dominant and subordinate plants, competition becomes strongly asymmetric. Further increases in productivity should not result in greater disparity in light availability between dominant and subordinant plants, and, thus, the degree of asymmetry no longer increases. This relationship is purely speculative; field studies measuring asymmetry along productivity gradients are lacking. Schwinning (1996) has argued that if resources are distributed heterogeneously, belowground competition may be asymmetric. However, Casper and Cahill (1996, 1998) found no increase in the CV of populations of *A. theophrasti* when grown on heterogeneous soils (compared to that grown on homogeneous soils), raising doubts about that prediction. Nonetheless, it is likely that under some circumstances belowground competition may be asymmetric and/or aboveground competition may be symmetric (Schwinning and Weiner 1998), and therefore it is essential to understand the mechanisms of competition when addressing questions of interactions in a particular community.

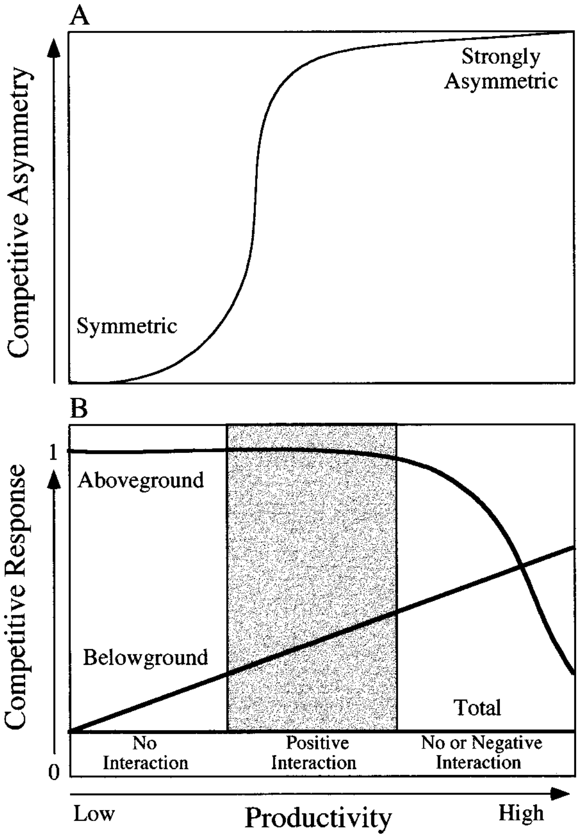

FIG. 4. (A) Hypothesized relationship between productivity and asymmetry of competition. (B) Hypothesized relationship between competitive response (total, above- and belowground) and productivity. The shaded region corresponds to the range of productivities that are likely to result in positive interactions between above- and belowground competition. At high productivity, either no interaction or a negative interaction may occur, depending upon the relationship between belowground competition and productivity.

The relationship between productivity and asymmetry is incorporated into a model of a putative relationship between competition and productivity in Fig. 4B. Most studies measuring competition in natural systems (including the current study) have found it to be invariant along productivity gradients (Wilson and Tilman 1991, 1993, Wilson 1993*a*, Reader et al. 1994, Belcher et al. 1995, Peltzer et al. 1998; but see Reader and Best 1989, Reader 1990). Additionally, belowground competitive intensity generally decreases (Putz and Canham 1992, Wilson 1993*b*, Wilson and Tilman 1993, 1995), or competitive response increases (as seen in the current study), with productivity. As previously stated, I found no change in aboveground competitive response with increased productivity, predominantly due to the fact that, in the absence of belowground competition, *A. theophrasti* was able to obtain a dominant position in the size hierarchy, regardless of the aboveground treatments. However, if the high-productivity site had significantly more biomass featuring a perennial size hierarchy (e.g., shrubland), then *A. theophrasti* would not have been able to reach the top of the canopy, regardless of the belowground treatments. Therefore the negative growth effects of aboveground competition would have increased with productivity (as found in Putz and Canham 1992).

Based upon these relationships between aboveground, belowground, and total competition, I hypothesize the following (Fig. 4B): (1) In low productivity sites, where competition is primarily belowground and symmetric, there should be no interaction between the two competitive forms. (2) As long as the target plant has the potential to reach the canopy, the interaction between above- and belowground competition should become increasingly positive as productivity increases, due to an increase in the asymmetry of competition and positive feedback. (3) Eventually, with further increases in productivity, target plants will be unable to reach the canopy, even in the absence of root competition. As a result, belowground competition will *not* decrease aboveground competitive ability, since target plants will lose aboveground competition, regardless of the belowground treatments. Therefore, with further increases in productivity, there should be a shift back toward no interaction between the two competitive forms. If, however, belowground competition remains constant with productivity (Belcher et al. 1995, Twolan-Strut and Keddy 1996, Peltzer et al. 1998), then a plant growing in a high-productivity site may experience intense interactions above- and belowground simultaneously. As a result, a negative interaction may occur. The actual form of interaction is likely to be species specific. I hypothesize that in sites of intermediate productivity, ruderals, which have high growth rates and high light compensation points, are more likely to show positive interactions than would plants adapted to more stressful conditions (e.g., forest understory species, small prostrate species in old fields).

CONCLUSIONS

By focusing solely on changes in the relative importance of aboveground and belowground competition with fertilization, and ignoring potential interactions, researchers may miss the more complicated (and interesting) dynamics that are actually occurring. The effects of belowground interactions between plants can either be direct (e.g., competition for limiting soil resources) or indirect (e.g., reduction of plant growth rates, which reduces aboveground competitive ability). Since this study was conducted on only one species, it would be imprudent to assume the findings in this study will be the same for all species in all habitats. The important finding in this study is not that above- and belowground competition always interact to affect plant growth, rather it is that the two competitive forms *can* interact; an a priori assumption of no interaction is unjustifiable. Future studies should be conducted to determine how the interaction between above- and belowground competition varies among species.

The failure to incorporate the potential effects of competitive asymmetry into community models may result in an incomplete understanding of community dynamics. To better understand the role of competition in natural plant communities requires stepping away from the traditional view that competition occurs in two discrete locations: belowground and aboveground. This study suggests that understanding the interactions between roots and shoots, as well as the mechanisms of interactions between competing individuals within a community, may be the best approach to a better understanding of the role of competition in natural systems.

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