



Effect of soil nutrient heterogeneity on the symmetry of belowground competition

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Abstract

Size variability in plant populations has been extensively studied and much of this inquiry has focused on the types of competition that are involved in increasing or decreasing size inequality. It is often assumed that competition for light is size-asymmetric, meaning that a plant can potentially dominate a competitive relationship through shading if it is taller than its competitor. The light resources obtained by the taller plant are thus disproportionate to its size. In contrast, competition for soil resources may be more size-symmetric, the amount of soil nutrients obtained seems to be in direct proportion to a plant's size. Most studies examining belowground competition have used homogeneously distributed nutrient resources. Soil homogeneity could make size-asymmetric belowground competition unlikely, but homogeneity is not often found in nature. In this study I use a greenhouse pot experiment utilizing *Ipomoea tricolor* to examine the hypothesis that size-asymmetric competition for soil nutrients may result when soil resource distribution is spatially heterogeneous. The results did not support the hypothesis of belowground size-asymmetric competition. Differences between experimental treatments and controls were not statistically significant suggesting size-symmetric competition. Implications of these results are discussed.

Introduction

In nature, many mechanisms increase size variation among plants. One potential mechanism that has been investigated is the effect of resource competition on size variation. Although extensively studied there is no universal agreement on this relationship. However, because size is directly related to resource acquisition, certain predictions can be made about the effect of different types of competition on size variation.

Competition for resources (i.e., light, water, and soil nutrients) among plants is often divided into size-symmetric and size-asymmetric forms (Weiner and Thomas 1986; Schwinning and Weiner 1998). Size-symmetric competition requires that competition results in resources being distributed in direct proportion to the size of the individual plant (Weiner and Thomas 1986; Weiner 1990). Size-asymmetric com-

petition occurs when larger plants acquire proportionally more of the available resources relative to their size (Weiner and Thomas 1986; Weiner 1988; Silvertown and Lovett Doust 1993; Schwinning and Weiner 1998). While size-symmetric competition will not increase the relative size inequality of a plant population over time, competition of the size-asymmetric type translates into greater relative growth for larger individuals. Over time, under this scenario, relative size inequality will increase.

Although, several studies have shown that competition for light is size-asymmetric due to the effects of shading (Benjamin 1984; Weiner 1986, 1990; Schwinning and Weiner 1998), competition for soil resources is generally assumed to be size-symmetric (Weiner 1990; Casper and Jackson 1997). The few studies that have looked directly at belowground competition support this hypothesis (Newberry and

Newman 1978; Wilson 1988; Casper and Cahill 1996; Weiner et al. 1997).

While this conclusion seems reasonable given the context of controlled experiments, other variables present in nature, such as nutrient heterogeneity, might result in size-asymmetric competition for soil resources. Weiner (1990) tentatively suggests that if soil resources are patchily distributed competition for these resources may be size-asymmetric. Consider the case where soil resources are localized in patches in a way that all plants experience the same initial environment. Here, individual plants that reach richer areas first can potentially dominate them by increasing their nutrient uptake (St. John 1983; Hutchings and Wijesinghe 1997; Wijesinghe and Hutchings 1997). This increased uptake can be accomplished by increasing root growth (Robinson 1994; Einsmann et al. 1999) and turnover (Pregitzer et al. 1995), increasing uptake kinetics (Robinson 1994) or changes in root architecture (Fitter and Strickland 1991). The more successful 'foragers' that are able to most effectively increase their nutrient uptake could obtain more than their size-proportional share of soil resources. In this case size-asymmetric competition could result.

Of the studies examining belowground competition, only Casper and Cahill (1996) specifically include a heterogeneous soil resource. In their study size hierarchies in populations of *Abutilon theophrasti* are examined. While they found no evidence for belowground size-asymmetric competition they did not eliminate light competition, which could have obscured belowground effects on population structure.

The objective of this study was to test the hypothesis that belowground competition in soil with patchily distributed nutrients can be size-asymmetric. This was tested using the annual *Ipomoea tricolor*. This is an ideal plant for this type of study due to its twining growth form that allows for the minimization of aboveground light competition by training plants on individual stakes (Weiner 1986).

Materials and methods

Patch fertilization treatments were used to create a heterogeneous soil environment in which roots had to compete for limited nutrient-rich areas. A combination of nutrient and planting density treatments were utilized. Seeds of *Ipomoea tricolor* var. "Heavenly Blue" were planted at two densities: individually, and

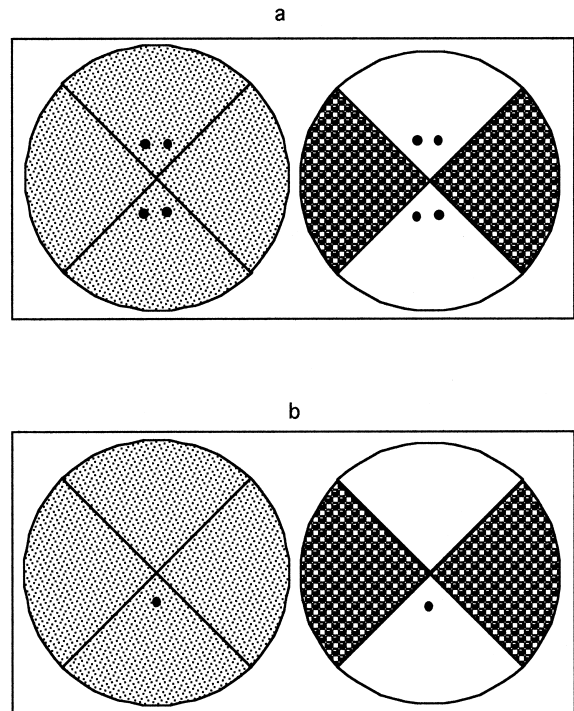


Figure 1. Diagrammatic representation of four-plant pots (a) and single-plant pots (b) with even and patch fertilization treatments. Shaded regions represent areas of fertilization and straight lines represent gravel walls. Intensity of shading indicates intensity of fertilization. Initial seed placement is represented by large black dots.

in groups of four plants per pot (8-inch pan). In order to minimize light competition, once plants were of sufficient size they were trained on stakes (one stake per individual) spaced 30cm apart. The individual plants were used as a control treatment to determine what size variability arises naturally in a competition-free environment. Parts of this experimental design were adapted from Weiner (1986).

The growing medium was potting soil (Sunshine-mix[®] 4) and gravel. Gravel walls (1.5 cm thick) were constructed, using a cookie cutter-like aluminum mold, to divide every pot (regardless of treatment) into four quadrants. The coarse grained barrier between the finer grained potting soil was used to reduce water and nutrient flow (through reduced capillary action) between quadrants without impeding root growth (Figure 1).

Osmocote[®] 12-12-12 100-day slow release fertilizer was used for nutrient treatments. The treatments included even low-concentration fertilization and patch high-concentration fertilization. The high-concentration mixture was twice that of the low-concentration mixture. This design ensured that both the

Table 1. The effect of root competition on the aboveground dry weight and size variability of *Ipomoea tricolor*. All comparisons were done using ANOVA based on within-pot statistics, except for CV and G in the single-plant treatment. For these the bootstrap technique was used (results not shown). No differences were statistically significant.

Fertilization treatment	Multi-plant treatment				Single-plant treatment			
	N (Pots)	Mean bio-mass $\pm$ SE df = 1 (F = .849)	Mean CV $\pm$ SE df = 1 (F = 1.973)	Mean Gini $\pm$ SE df = 1 (F = .197)	N (indiv.)	Mean bio-mass $\pm$ SE df = 1 (F = .295)	CV	Gini
Even	9	16.92 $\pm$.33	21.4 $\pm$ 3.5	.135 $\pm$.02	33	27.5 $\pm$.96	21.1	.121
Patch	7	16.46 $\pm$.37	28.7 $\pm$ 3.9	.180 $\pm$.03	34	28.24 $\pm$.95	18.5	.104

even and patch fertilizer treatments received the same absolute amount of nutrients. The sites of fertilization in the nutrient patch treatment were in opposing quadrants (Figure 1).

Seeds were planted 3 cm from the center of the pots. In pots containing four plants, two seeds were placed in each of two opposing quadrants, equidistant from adjacent quadrants. In the nutrient patch treatment, seeds were placed in the two unfertilized quadrants. For the single plant pots a seed was planted in one quadrant equidistant from adjacent quadrants. (Figure 1).

The number of plants per pot (1 or 4) was crossed with the fertilization treatments (even or patch) for a total of four treatment combinations: (1) evenly-fertilized pots with single plants; (2) patchily-fertilized pots with single plants; (3) evenly-fertilized pots with 4 plants; and (4) patchily-fertilized pots with 4 plants. Each of the individual treatments (1 and 2) was replicated 36 times. Each 4-plant treatment (3 and 4) was replicated nine times for a total of 36 plants per treatment.

Plants were grown on greenhouse benches at the Mathai Botanical Gardens in Ann Arbor, Michigan for the two month period of July and August in 1996. Plants were kept moist at all times. During watering the two quadrants without fertilization (treatments 2 and 4) were watered first followed by the quadrants with fertilizer. In this way leaching of water from the fertilized to unfertilized quadrants was minimized. Pots with one or more plants adversely affected by insect damage were removed, these included: three pots from treatment 1 (three individual plants), two pots from treatment 2 (two individual plants), and two pots from treatment 4 (8 individuals). After the designated period plants were cut at soil level, dried at 70 °C and weighed.

Size variability was measured by the Coefficient of Variation (CV = standard deviation / mean), and the

Gini Coefficient (G):

$$G = \frac{\sum_{i=1}^n \sum_{j=1}^n |x_i - x_j|}{\{2\bar{x}n(n-1)\}},$$

where n is the number of individuals and x_i and x_j are the sizes of individuals. Both measures were calculated for plant aboveground dry weights. To evaluate the effects of the fertilization treatment on size variability within the multi-plant density treatment, and mean size within and between density treatments, one-way ANOVAs were conducted on within pot statistics. To evaluate the fertilization treatment within the single plant density treatment comparisons were made by calculating the confidence intervals for CV and G for each treatment with bootstrapped estimates of each statistic (Dixon et al. 1987). This method allows error estimates to be calculated for the sample statistics without assumptions (Weiner and Solbrig 1984).

Results

The number of individuals per pot had a significant effect on the mean dry weight of the plants ($P < .0001$). Individuals in the multi-plant pots (treatments 3 and 4) were significantly smaller than those in either of the two single plant treatments (1 and 2) (Table 1). This suggests that competition for soil resources was present within the four plant treatments. Further, the distribution of fertilizer (patch or even) did not affect plant dry weight, suggesting that the gravel walls did not inhibit root growth (Table 1).

When the Coefficient of Variation and Gini Coefficient were used to compare nutrient treatments no statistically significant effects were found (Table 1). This suggests that size-symmetric competition was the dominant form of competition during this experi-

ment. However, in the multi-plant pot treatments there was a statistically non-significant trend towards greater variability in the nutrient heterogeneous treatment.

Discussion

The results of this study do not support the original hypothesis and suggest that soil heterogeneity does not influence the size-symmetry of belowground competition. Other experiments examining the symmetry of belowground competition have had similar results (Newberry and Newman 1978; Weiner and Thomas 1986; Casper and Cahill 1996; Weiner et al. 1997).

Theoretically, size symmetric belowground competition may occur if soil resources are localized in patches and individual plants that reach richer areas first are able to dominate them through increased nutrient uptake. However, there are reasons to believe that this may be a rare occurrence. First, unlike the light resource which is disproportionately absorbed by taller plants, the three spatial dimensions of a nutrient patch make it less likely to be completely usurped by one individual. Further, even if a plant is able to dominate a particular nutrient patch, other patches may be dominated by its competitors. Secondly, it appears that patch size may influence whether a plant is able to respond to nutrient heterogeneity. In a spatially heterogeneous nutrient environment, if nutrient patches are too large a plant's root system may not be able to span beyond an individual patch, and if patches are too small a plant may not be able to discriminate between patches of differing nutrient availability (Wijesinghe and Hutchings 1997).

If asymmetric competition exists its most likely mechanism would be increased rooting density into nutrient-rich patches. Here, size or random factors will determine which plant gets to a resource patch first and after discovery this first colonizer will be able to limit the benefits of the patch to other plants by physically limiting access and by reducing the patch's available nutrient stores. The size of the nutrient patch, speed of root growth, and the lag period before a competitor discovers the resource will determine how much of the resource is physically dominated and depleted by the first plant. An assumption in the current design was that naturally arising competition-independent size variability would be sufficient to induce asymmetric belowground competition.

One way to exacerbate these size differences would be to allow plants of different ages to compete. With such a design random factors would be less important and the domination of nutrient rich areas by the larger individual would be more likely.

In this study, factors relating to nutrient availability and the ability of *Ipomoea tricolor* to forage for nutrients may have also influenced the results. The potting soil used was composed primarily of Sphagnum peatmoss (55–60%) which may have contaminated the 'nutrient free' areas of the patch treatments as it decayed. This supply of nutrients may have been sufficient to eliminate (or reduce) the belowground size-asymmetric effect.

Another factor could be that *Ipomoea tricolor* does not forage for nutrients. To date this species has not been specifically studied for its foraging ability and while root data were not collected casual observations suggested rooting density in nutrient rich and poor patches was similar. Root foraging is common and most species studied thus far have shown some degree of morphological or physiological response to increased nutrient availability. However, it is not a universal occurrence (Jackson and Caldwell 1992; Robinson 1994).

Unlike light competition, which is generally size-asymmetric, soil resources might be competed for in different ways under different circumstances. The present study rejects the hypothesis of size-asymmetric competition for nutrient resources under the conditions tested. However, there are several untested variables that may affect the way nutrient resources are competed for. These include, the patch size of the soil resource, the plant's root foraging ability and, if present, the type of root foraging involved.

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References

- Benjamin L. 1984. Role of foliage habit in the competition in the competition between differently sized plants in carrot crops. *Annals of Botany* 53: 549–557.

- Casper B. and Cahill J. 1996. Limited effects of soil nutrient heterogeneity on populations of *Abutilon theophrasti* (Malvaceae). *American Journal of Botany* 83: 333–341.
- Casper B. and Jackson R. 1997. Plant competition underground. *Annual Review of Ecology and Systematics* 28: 254–70.
- Dixon P., Weiner J., Mitchell-Olds T. and Woodley R. 1987. Bootstrapping the Gini-Coefficient of inequality. *Ecology* 68: 1548–1551.
- Einsmann J., Jones R., Pu M. and Mitchell R. 1999. Nutrient foraging traits in 10 co-occurring plant species of contrasting life forms. *Journal of Ecology* 87: 609–619.
- Fitter A. and Strickland T. 1991. Architectural analysis of plant root systems. 2. Influence of nutrient supply on architecture in contrasting plant species. *New Phytologist* 118: 383–389.
- Hutchings M. and Wijesinghe D. 1997. Patchy habitats, division of labour and growth dividends in clonal plants. *Trends in Ecology and Evolution* 12: 390–394.
- Jackson R. and Caldwell M. 1992. The scale of nutrient heterogeneity around individual plants and its quantification with geostatistics. *Ecology* 74: 612–614.
- Newberry D. and Newman E. 1978. Competition between grassland plants of different sizes. *Oecologia* 33: 361–380.
- Pregitzer K., Zak D., Curtis P., Kubiske M., Teeri J. and Vogel C. 1995. Atmospheric CO₂, soil nitrogen and turnover of fine roots. *New Phytol* 129: 579–585.
- Robinson D. 1994. The responses of plants to non-uniform supplies of nutrients. *New Phytologist* 127: 635–674.
- Schwinning S. and Weiner J. 1998. Mechanisms determining the degree of size asymmetry in competition among plants. *Oecologia* 113: 447–455.
- Silvertown J. and Lovett Doust J. 1993. *Introduction to Plant Population Biology*. Blackwell Scientific Publications, New York.
- St. John T. 1983. Response of tree roots to decomposing organic matter in two lowland Amazonian rain forests. *Canadian Journal of Forestry Research* 13: 346–349.
- Weiner J. 1986. How competition for light and nutrients affects size variability in *Ipomoea tricolor* populations. *Ecology* 67: 1425–1427.
- Weiner J. 1988. Variation in the performance of individuals in plant populations. In: Davy A., Hutchings M. and Watkinson A. (eds), *Plant Population Ecology: The 28th Symposium of the British Ecological Society*. Blackwell, New York, pp. 59–81.
- Weiner J. 1990. Asymmetric competition in plant populations. *Trends in Ecology and Evolution* 5: 360–364.
- Weiner J. and Thomas C. 1986. Size variability and competition in plant monocultures. *Oikos* 47: 211–222.
- Weiner J., Wright D. and Castro S. 1997. Symmetry of below-ground competition between *Kochia scoparia* individuals. *Oikos* 79: 85–91.
- Weiner J. and Solbrig O. 1984. The meaning and measurement of size hierarchies in plant populations. *Oecologia* 61: 334–336.
- Wijesinghe D. and Hutchings M. 1997. The effects of spatial scale of environmental heterogeneity on the growth of clonal plant: an experimental study with *Glechoma hederacea*. *Journal of Ecology* 85: 17–28.
- Wilson J. 1988. The effect of initial advantage on the course of plant competition. *Oikos* 51: 19–24.