

Symmetry of below-ground competition between *Kochia scoparia* individuals

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Competition among individual plants is usually asymmetric, i.e. larger plants are able to obtain a disproportionate share of the resources (for their relative size) and suppress the growth of smaller individuals. There is evidence that the asymmetry of competition is primarily due to shading, but there is very little information about the symmetry of competition below ground. We grew *Kochia scoparia* individuals singly and in pairs in containers for 54 d with dividers above ground so that competition could occur only below ground. Initial size differences were generated by a 10-d difference in sowing date.

There was no evidence that larger individuals had a disproportionate effect on smaller individuals; the effect of a small neighbor on the growth rate of a plant was similar for large and small plants, as was the effect of a large neighbor. The results demonstrate that competition for resources below ground can be symmetric. When competition is symmetric, it will not exacerbate initial size differences.

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There has been much recent interest in the role of size and relative size in competition among individual plants (Weiner 1990). Plant competition is usually asymmetric, i.e. larger plants are able to obtain a disproportionate share of resources (for their relative size) and suppress the growth of smaller plants¹. Four basic types of competitive symmetry can be defined:

- (1) absolute symmetry – contested resources divided equally, irrespective of the size of the competing plants
- (2) relative-size symmetry – contested resources divided in proportion to size or “under-proportionally” with respect to size
- (3) (relative-size) asymmetry – contested resources divided “over-proportionally” with respect to size
- (4) absolute asymmetry – larger plant obtains all the contested resources.

¹ Some researchers (e.g. Goldberg 1990) use the term “asymmetry” to simply mean any competitive advantage for a larger individual or species. We follow the terminology of Begon (1984) and Weiner (1990) to distinguish size-proportional from “over-proportional” effects, and reserve the term asymmetry for the latter case. The term “asymmetry” has also been used more generally to describe any unequal effects of competition between two individuals or species (e.g. Johansson and Keddy 1991) without reference to size differences.

(1) and (4) represent theoretical end points of a continuum; (2) and (3) cover the continuum between them. We can also imagine “negative asymmetry” in which smaller plants obtain a disproportionate share of resources.

Weiner (1990) describes several types of evidence for competitive asymmetry among plants. Over the past 20 years there have been numerous experiments that have

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produced data more or less relevant to this question of competitive asymmetry. In the great majority of cases, the data support the hypothesis that competition is asymmetric [(3) above]. However, competition appears to be size-symmetric when plants are grown for a very short period of time (Rabinowitz 1979, Turner and Rabinowitz 1983), or at relatively low density (Stoll et al. 1994). The conclusion that early plant competition tends to be symmetric, and that it becomes more asymmetric as plants grow, gave rise to the hypothesis that competition below ground is symmetric, whereas competition above ground is asymmetric (Weiner 1988). Crowded plants can compete for soil resources immediately after germination, as their radicles emerge and take up nutrients and water, but they can only compete for light after they have grown large enough to shade one another. The unidirectional nature of the light resource suggests asymmetry: leaves are shaded only by those above them, so lower leaves do not reduce the amount of light reaching higher leaves at all.

While the asymmetry of competition for light is quite well established, the symmetry of competition below ground is still speculative. We know of only three studies which have attempted to directly address the symmetry of competition below ground. Weiner (1986) grew *Ipomoea tricolor* vines (a) without competition, (b) with roots only competing, (c) with shoots only competing, and (d) with roots and shoots competing, to see which mode of competition causes an increase in size variability (which is considered to be evidence of competitive asymmetry). Although competition below ground was much more intense than competition above ground, size variation increased with competition only when plants were competing above ground. Root competition alone did increase size variation, but the increase was not significant. This suggests the possibility that root competition is asymmetric but that statistical power was insufficient to detect a significant effect.

Wilson (1988) grew *Festuca ovina* plants of initially different sizes with dividers above ground to see if the extreme "initial advantage" in competition, which is a manifestation of competitive asymmetry, exists when competition occurs only below ground. Because Wilson's experiment was designed to address a specific field situation in which there was grazing, plants were repeatedly clipped when they overtopped the relatively short (7 cm) dividers, and he used the amount of biomass removed as the measure of performance. Using a similar design, Newberry and Newman (1978) grew four species of grassland plants, *Plantago lanceolata*, *Holcus lanatus*, *Lolium perenne* and *Rumex acetosa*, in monocultures and pairwise mixtures, with and without dividers above ground to prevent competition for light. Different initial plant sizes were generated by using plants of different ages. Plants were clipped regularly to a height of 3, 4 or 8 cm, and the biomass of clippings was used as a measure of growth. There was no initial

advantage in Wilson's or Newberry and Newman's experiments, and the difference in size between large and small plants actually decreased over time. However, their conclusions that below-ground competition is symmetric must be tentative because of the clipping regime. If larger plants are taller as well as wider, as in Newberry and Newman's experiment, clipping above a certain height will disproportionately affect the larger plants (because they will lose a larger proportion of their biomass), and will in itself reduce any initial advantage in size by making the plants more equal in size (Weiner 1988, Crawley and Weiner 1991). Also, since competition at a given density increases with plant size, clipping biomass repeatedly will reduce competition, below as well as above ground, keeping it weak. If asymmetry appears as competition increases in intensity, continued clipping to a given size may prevent competition from becoming intense and therefore prevent asymmetry from appearing. Thus, Newberry and Newman found no initial advantage without, as well as with, dividers above ground. On the other hand, regrowth following clipping sometimes results in increased uptake of soil resources, and therefore in some situations clipping could increase competition for these resources. Despite these limitations, these previous studies have been important in raising the possibility that there is no size advantage in competition below ground.

We performed an experiment in which *Kochia scoparia* plants of two different initial sizes were grown with competition occurring only below ground, to see if we could find evidence of competitive asymmetry.

Materials and methods

Three-liter, 160-mm diameter black plastic pots were filled with a mixture of 12 parts potting soil (Metromix 500 by Sierra Horticultural Products) to 3 parts coarse sand to 1 part fine sand. The soil mixture was put through a coarse sieve to increase soil homogeneity. To prevent shoot competition, 16 cm × 38 cm Plexiglas dividers were attached to the pots at the upper edge, dividing the area above the pot into two equal halves. The dividers were covered with opaque white contact paper. When plants exceeded the dividers in height, a cardboard extension was added to the dividers.

Kochia scoparia (L.) Schrad (Chenopodiaceae), known commercially as *Kochia trichophylla* (Schmeiss) Schinz and Thell or "burning bush" is an annual herb with a tree-like growth form (Franco and Harper 1988) that allows for good non-destructive measures of plant size (Weiner and Fishman 1994). Seeds (purchased from Thompson and Morgan Co., NJ, USA) were planted on two separate days. "Old" ("large") plants were planted on 31 March, 1994, and the "young" ("small") plants were started 10 d later. When planting, five seeds were placed close to the center of the semicir-

cular area defined by the pot edge and the divider. The seeds were lightly covered with soil and watered.

There were five types of experimental units: (1) old plants growing with younger plants, (2) old plants growing with old plants, (3) young plants growing with young plants, and both (4) old plants and (5) young plants growing without neighbors on the other side of the divider. Twelve replicates were maintained for the old/young treatment and seven replicates for all others.

Multiple seedlings were thinned to one plant 10 d after sowing. The plant closest to the center point was chosen unless it had any growth anomalies, such as a very crooked stem or signs of pathology. If two or more plants were equally close to the center, one was randomly selected to remain.

The pots were spread approximately 60 cm apart on benches in the glasshouse at Martin Biological Laboratory at Swarthmore College. The dividers were oriented at 15° from N-S to approximately equalize the sunlight reaching both sides of a plant while compensating for morning shading from neighboring buildings. Pots were rotated 180° daily and their locations re-randomized every three d. Watering was done as needed to keep the soil moist.

Measurements of the plants were taken weekly for diameter, height, and branch lengths. Diameter was measured half-way between the cotyledons and the first leaves using a digital caliper (± 0.005 mm). Height measurements were taken from the cotyledons to the tip of the apical meristem. Branches greater than 5 mm were measured in 5-mm size classes. Plants began to flower during the last weeks of the experiment. There was no apparent loss of reproductive parts other than some pollen, and plants continued growing. At day 54 all plants were measured again and then harvested at ground level, dried, and weighed.

Since competition occurs only after plants have grown large enough to interact, and the intensity of competition increases over time thereafter, asymmetry is more likely to be found later in growth. Therefore our analysis emphasized the last 12 d of growth. To estimate growth of individual plants one needs good non-destructive measures of plant size. *Kochia scoparia* was chosen because previous research has shown robust, simple allometric relationships between some non-destructive measurements (total branch length, stem diameter) and biomass, even when plants are crowded (Weiner and Fishman 1994). Plant biomass was estimated from the measurements using simple prediction equations based on the final measurement at harvest. There was a linear relationship between log total branch length and plant mass ($\log \text{mass} = 0.979 + 0.953 \log [\text{total primary branch length}]$; $r^2 = 0.93$; Fig. 1). A prediction equation using both total branch length and diameter ($\log \text{weight} = 1.167 + 1.096 \log \text{diameter} + 0.664 \log [\text{total branch length}]$) accounted for 96% of the variation in final plant mass, and the

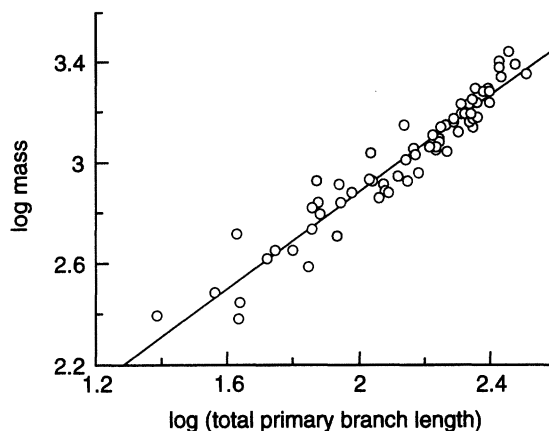


Fig. 1. Relationship between log (total primary branch length) and log dry mass for all plants at harvest; $r^2 = 0.93$.

residuals fit the assumptions of normality and homoscedasticity. Results were similar for analyses using total branch length and those using the estimate of weight based on total branch length and diameter. Data were analyzed with analysis of variance and analysis of covariance.

The null hypothesis is that competition is symmetric, i.e., the effect of large (older) versus small (younger) neighbors is the same for large and small subject plants (Fig. 2). If competition is asymmetric, the effect of a

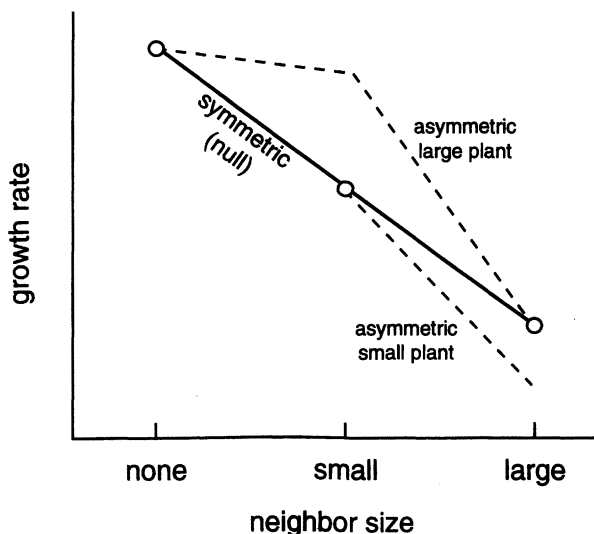


Fig. 2. Prediction of results of the experiment under the null hypothesis of symmetric competition (solid line) and under the hypothesis of asymmetric competition (dashed lines). The null hypothesis of symmetric competition is represented by a straight line for convenience; all that is required is that the growth rate decrease monotonically from none to young to old neighbor. Similarly, a single line is used to represent the null hypothesis for simplicity, assuming that the growth rate has been standardized with respect to other factors. The null hypothesis could also be represented by two parallel relationships, one for old and one for young plants.

Table 1. Analysis of variance of plant dry mass of *Kochia scoparia* individuals competing below ground. Independent variables are plant age (old, young) and neighbor age (none, old, young).

factor	df	MS	P
plant age	1	15.57	<0.0001
neighbor age	2	1.52	<0.0001
interaction	2	0.09	0.379
residual	60	0.09	

large plant on a small plant would be greater than that of a larger plant on a large plant. Similarly, under asymmetric competition the effect of a small plant on a large plant would be less than that of a small plant on a small plant. The significance of such evidence of asymmetry can be tested as the significance of the plant age \times neighbor age interaction term in an analysis of variance on a measure of growth (e.g. absolute or relative growth rate). Since plant growth, however measured, is size-dependent, it is important to include size at the beginning of the growth interval as a covariate (e.g. Stoll et al. 1994, Duncan 1995).

Another way to obtain evidence of asymmetry is to look at the effect of neighbors as a function of their size. If the effect of a neighbor on the growth of a subject plant is a function of the neighbor's absolute size, this supports the hypothesis of competitive symmetry. If competition is asymmetric, we would expect the relative sizes of the subject and neighbor plants to be important (Thomas and Weiner 1989, Schwinning and Fox 1995). Thus, in the present experiment, if competition is asymmetric we would expect large and small neighbors to have significantly different effects on large versus small subject plants.

Results

Competition was significant, i.e. plants with neighbors were smaller than plants without neighbors. Large neighbors had more of an effect than did small neighbors on the final biomass of both large and small plants, but there was no significant interaction between the two factors (Table 1, Fig. 3). Plant growth over the last 12 d of the experiment, when competition became detectable, was closer to linear than to exponential (Fig. 4), so analyses based on the absolute growth rate are more appropriate than those based on relative growth rate, and the distribution of residuals support this conclusion. Log absolute growth rate was used because it had the best residual structure. Plant age, plant size (on day 42), and neighbor age all had highly significant effects on the log of the change in size (absolute growth rate) from day 42 until day 54, but there were never significant age \times neighbor age (Table 2) or size \times neighbor age (Fig. 5) interactions. These

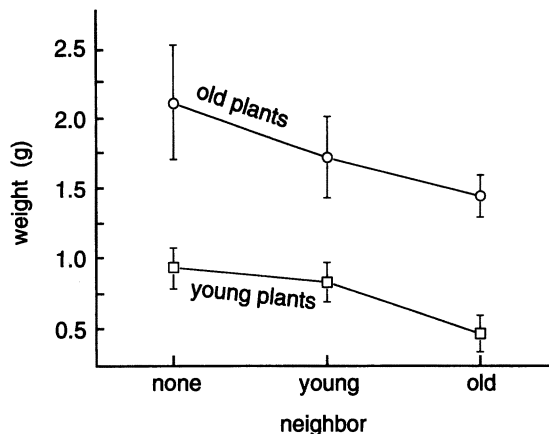


Fig. 3. Mean dry mass of old (above) and young (below) plants with no, young and old neighbors. Both plant age and neighbor age had highly significant effects ($P < 0.0001$) but their interaction term was not significant ($P = 0.38$).

results are very similar using any of the measures of plant and neighbor size (total branch length, or estimates of size based on diameter and/or total branch length). If relative growth rate is used as the dependent variable, plant age does not always have a significant effect, but plant size at the beginning of the interval does. Again, there is never a significant interaction between age and neighbor age, or size at the beginning of the interval and neighbor age (Table 3).

There was a negative relationship between the growth of a plant and the size of its neighbor, and the slope of the relationship was the same for both large and small plants (Fig. 6). A plant's age, its size and its neighbor's size all had significant effect on plant growth rate, and there was never a significant interaction between neighbor size and any other variable (Table 4).

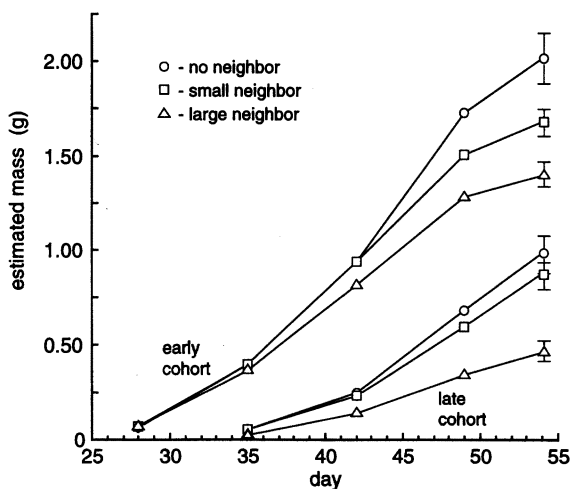


Fig. 4. Mean growth in estimated weight for old (above) and young (below) plants with outneighbors (○), with young neighbors (□), and with old neighbors (△).

Table 2. Analysis of covariance of log absolute growth rate (change in total branch length from day 42 until day 54). Independent variables are plant age (old, young), neighbor age (none, old, young), with plant size (total branch length) at the beginning of the interval as covariate. Interactions not shown were not significant ($P > 0.3$) and were removed from the analysis.

factor	df	MS	<i>P</i>
plant size	1	0.209	0.0022
plant age	1	0.233	0.0013
neighbor age	2	0.140	0.0021
(age × size) interaction	1	0.241	0.0011
(age × neighbor age) interaction	2	0.024	0.67
residual	53	0.020	

Discussion

There was no evidence for competitive asymmetry in this experiment in which competition occurred only below ground. There are several possible explanations for this, which can serve as hypotheses for further research.

The first hypothesis is simply that below-ground competition is, by its very nature, symmetric. In competition, larger plants have larger root systems, and they are able to extract proportionately more nutrients from the soil than smaller plants, but not disproportionately more. This would support the hypothesis that the asymmetry of plant competition that is observed in the vast majority of studies is solely due to competition for light.

A weaker version of this hypothesis is that the results show that below-ground competition can be symmetric, but this may be due in large part to the homogeneous soil in our experiment. According to this hypothesis, when soil resources are distributed homogeneously, ac-

Table 3. Analysis of covariance of relative growth rate from day 42 until day 54 (based on estimated mass). Independent variables are plant age (old, young), neighbor age (none, old, young), with plant size (estimated plant mass) at the beginning of the interval as covariate. Interactions not shown were not significant ($P > 0.7$) and were removed from the analysis.

factor	df	MS	<i>P</i>
plant size	1	10.62	0.0001
plant age	1	5.82	0.0002
neighbor age	2	3.09	0.0005
(age × size) interaction	1	6.10	0.0001
(age × neighbor age) interaction	2	0.700	0.15
residual	53	0.353	

cess to these resources is directly proportional to some aspect of root size, and that corresponds to our definition of competitive symmetry. If soil resources are distributed heterogeneously, e.g. if resources occur in pools that large plants could reach and usurp before smaller plants could reach them, competition could be asymmetric. This hypothesis can be tested with experiments with heterogeneous soils environments.

Another hypothesis that has not received attention is that, while competition for light may tend to be more asymmetric than competition for soil resources, competitive asymmetry for many resources increases with the intensity or strength of competition for the resources. One example would be a resource that is available as relatively large quanta. In such a case competitive asymmetry will increase with the number of individuals competing for these quanta. If food is available to animals only as relatively large discrete particles, then as the number of individuals competing for a limited number of particles increases it will not be possible for them to be distributed proportionately: more and more individuals will get zero. This hypothe-

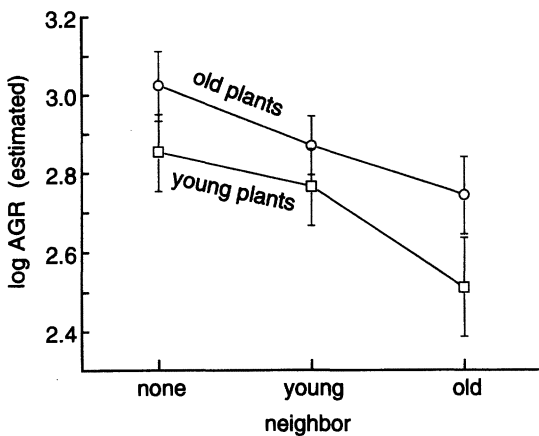


Fig. 5. Log of absolute growth rate (change in estimated biomass) from day 42 to day 54 old (above) and young (below) plants with no, young and old neighbors. Both plant age and neighbor age had highly significant effects ($P = 0.001$ and 0.002 , respectively; their interaction term was not significant).

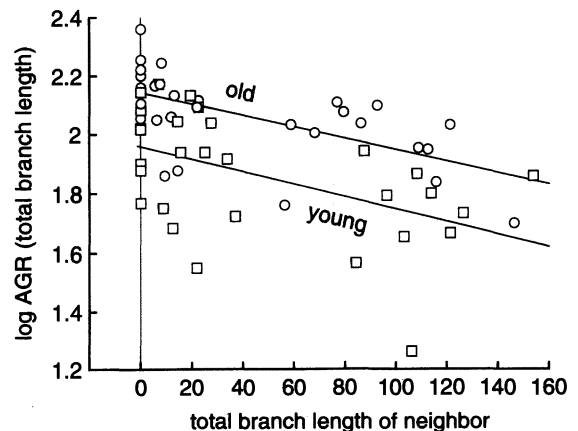


Fig. 6. Log of absolute growth rate (change in total branch length) from day 42 to day 54 versus neighbor size (total branch length) on day 42 for old (○) and young (□) plants. The slope of the relationship is the same for young and old plants.

Table 4. Analysis of covariance of log absolute growth rate (change in estimated weight from day 42 until day 54). Independent variables are plant age (old, young), with plant size and neighbor size (estimated weight on day 42) as covariates. Interactions not shown were not significant ($P > 0.5$) and were removed from the analysis.

factor	df	MS	P
plant size	1	0.227	0.0007
plant age	1	0.107	0.0165
neighbor size	1	0.469	0.0001
(age × size) interaction	1	0.201	0.0013
(age × neighbor age) interaction	1	0.014	0.37
residual	52	0.020	

sis is similar in some ways to the argument above concerning heterogeneity. Since the role of competition for light may increase with the intensity of competition in general (e.g. with density or size), it has not been possible to distinguish the hypothesis of light competition from the alternative (but not exclusive) hypothesis of competitive intensity. Our experiment concluded after 54 d and competition, although significant, was still weak, and it is possible that it would have become asymmetric as the intensity of competition increased with continued plant growth.

Ultimately, the asymmetry of competition is a function of the mechanism of competition. This includes factors such as the architecture and allometry of the uptake structures and the mechanism of resource uptake, as well as the mechanism of resource renewal (e.g. directionality) and the mobility of the resource.

Unlike competition above ground, competition below ground can potentially involve numerous resources, and the observed effects of below-ground competition may be the result of competition for more than one "limiting" resource. It is commonly assumed (e.g. Schmitt et al. 1986) that the more limiting a resource is, the more intense is competition for it, but this assumption does not withstand critical analysis. Competition ("interference" *sensu* Harper 1977) among individuals plants can be defined operationally as the reduction in some aspect of performance (e.g. size, growth or reproductive output) due to the presence of neighbors. If resources are in very short supply, plants will not grow large enough to interact. Seedlings will be limited by the resource supply independent of neighbors, not by the reduction in resource supply due to neighbors. While a continuous superabundance of a resource (e.g. water in an aquatic environment) can prevent competition for it, in general, addition of resources will increase growth and thus, after a period of additional growth, will increase competition for other resources, and for the resource which was added. For example, if there is no or very little light for seedlings they will not grow large enough to shade one another very much, so there can be no or very little competition for light. At higher light levels, competition will become important as shading limits

the light available to some individuals. If we increase the light levels further, we will increase the leaf area index that can be sustained. Competition, defined as the reduction in growth due to neighbors, can increase in importance as the resource level increases. Since a zero level of a resource means no competition for that resource, and an infinite abundance and availability of a resource also means no competition for that resource, the maximum intensity of competition for a resource must occur somewhere between those two extremes. This question of intensity is especially problematic in the experimental study of below-ground competition: if the level of soil nutrients is very low, plants will not grow enough to interact much, and if the level is very high roots will flourish to the point that plant roots will be limited by physical space (McConnaughay and Bazaz 1991) rather than soil nutrients.

Johansson and Keddy (1991) looked at competition between pairs of wetland plants that varied in their degree of ecological similarity: (1) plants of the same species, (2) plants of different species but within the same guild, and (3) plants from different guilds. They found that the effects of competition were more unequal when the individuals were of different species. (They use the term "asymmetry" to refer to any unequal effects of competition between two individuals, without reference to initial size differences.) While our results could be interpreted as evidence that intraspecific interactions are inherently more equal, even where there are initial size differences, an alternative explanation for their result could be that plants of the same species will certainly tend to be more similar in size when competition begins than will plants of different species. Unequal effects of competition between plants of different species in Johansson and Keddy's experiment may be in large part due to initial size differences and competitive asymmetry, which is to be expected in wetland species grown under high fertility conditions, as in their experiment.

The analysis of competitive symmetry can be a useful tool in helping us understand the mechanisms by which plants interact, and it has important implications for plant populations and communities. For example, contrary to the view that larger species will generally out compete and exclude smaller species (Gaudet and Keddy 1988), when competition occurs primarily below ground, individuals of smaller species may be able to obtain their "share" of contested resources, and "hold their own" against larger species. This may help explain the high plant diversity often found on low-nutrient soils in the temperate regions, e.g. chalk grasslands in Britain and Fynbos in South Africa.

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