Asymmetric Competition in Plant Populations

Jacob Weiner

Recently there has been much interest in the hypothesis that competition between individual plants is asymmetric or one-sided: larger individuals obtain a disproportionate share of the resources (for their relative size) and suppress the growth of smaller individuals. This has important implications for population structure, for the analysis of competition between plants at the individual, population and community levels, and for our understanding of competition as a selective force in the evolution of plant populations.

Competition in plants ultimately occurs between individuals. Competition at higher levels, e.g. between species, is the summation over time and space of many such interactions, and has commonly been studied in terms of density–yield relationships and self-thinning trajectories. Ecologists have now begun to look at interactions between individuals in terms of mechanisms of interference.

How do competing individuals

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consume and divide up limiting resources? One concept that bears on this question is that of asymmetric competition. The term 'asymmetric competition'[1,2] is synonymous with, or overlaps, several other terms, including 'one-sided competition'[3,4], 'dominance and suppression'[5,6], 'resource pre-emption' and even 'snowball competition'[7]. Not only do all these terms overlap in meaning, but few have been clearly defined.

Symmetry versus asymmetry

The basic concept of competitive asymmetry is that larger plants have a competitive advantage over small plants. Similarly, 'symmetric' competition ('two-sided competition' or 'resource depletion') implies that competitive effects of larger and smaller individuals are, in some sense, equal. From basic principles, one would expect the effect of a plant on its neighbors to be related to its size. For example, plants have modular construction, such that a larger individual consists of more modules than a smaller one. Since these modules represent physiological units, it is to be expected that a larger individual (which is a larger population of modules) will have a greater competitive effect than a smaller one. How much or what type of an advantage is necessary if we are to consider competition 'asymmetric'?

Here, I use the term 'absolute symmetry' to refer to the case in which all individuals have the same effect or use the same amount of resources, irrespective of their size[8], and 'relative-size symmetry' (per-unit-size symmetry) to refer to situations in which the competitive effect or resource acquisition is proportional to some measure of size. Thus, the fact that a larger individual has a competitive advantage over a smaller individual does not necessarily mean that competition is asymmetric; it may be relative-size symmetric. For competition to be asymmetric, the larger individual must have a disproportionate effect or obtain a disproportionate share of the resources, for its relative size. Thus, if a plant that is twice as large as another has twice the effect or obtains twice the amount of resources, this would be considered relative-size symmetric competition. For competition to be asymmetric, the individual that is twice as large as another must have *more* than twice the competitive effect, or obtain more than twice the amount of resources as its smaller neighbor.

The opposite extreme of absolute symmetry would be absolute asym-

metry: in this case, a larger individual (even if it were only slightly larger than its competitors) would not be affected at all by competition from smaller individuals. This would mean that the largest plants in a crowded stand would be the same size as totally uncrowded plants. While such an extreme form of asymmetry has been modelled[9], we might expect the real world to reflect a continuum of possibilities between absolute symmetry and absolute asymmetry. Competitive asymmetry versus symmetry is similar to the concepts of 'contest' and 'scramble' competition in the animal ecology literature, but asymmetry focuses on the issue of the relative size of the contestants, rather than other factors.

Evidence for asymmetric competition
Size variability and density dependence

The first type of evidence that is relevant to competitive asymmetry is the relationship between density and size variability in crowded populations. The study of density dependence in plants has traditionally addressed the relationship between mean plant size and density. Most models of density dependence do not address the issue of variability in the population around this mean value. To develop hypotheses about the relationship between competitive symmetry and size variation, we must look to models that also address the distribution of sizes within the population[10,11], including those that model the growth of individual plants within a competing stand[12–14]. In such models, implicit or explicit assumptions are made about the symmetry or asymmetry of the competitive interactions.

In spatial models in which size or growth is a function of positional information only, competition is absolutely symmetric, because the size of neighbors is not a variable. This includes models in which plant size is a function of 'available area'[12], defined as the two-dimensional area that is closer to the plant than to any other individual, and 'neighborhood models', in which the size or growth of each plant is a function of the number[13], or number and distance[15], of its neighbors. Neighborhood models in which the size of neighbors influences size or growth of an individual[16,17] assume that

competition is relative-size symmetric. Competition is asymmetric in models in which the growth of a plant is disproportionately affected by larger neighbors[10,11,18], or where the areas of overlapping 'zones of influence' between competing individuals are disproportionately available to the larger individual[14,19].

Models of plant competition in which competition is asymmetric predict that populations grown at higher densities (without mortality) should show greater size variability or inequality (see Box 1) than populations grown at lower densities over the same period[2]. Simply put, although size variability will increase in the absence of competition if plants vary in their relative growth rates (RGRs)[25], asymmetric competition acts to increase the variation in relative growth rates and therefore to exaggerate relative size differences over what they would be without, or with reduced, competition. The higher the density, the sooner these asymmetric interactions begin, and the more intense they will be.

On the other hand, symmetric models of competition, whether absolute or relative-size symmetric, predict that populations grown at higher densities will have the same or lower levels of size inequality than populations grown at lower densities or without competition. This is because symmetric competition acts to slow the growth of all plants, and thus slow the divergence in size that occurs when plants are not interacting. So far, one exception to this theoretical generalization has been published[19]. In a spatial model in which the spatial pattern of plants is not uniform, size inequality will be lower at very low density (few or no plants competing) than at low density (most plants experiencing competition), even if competition is completely symmetric. Increasing density above that at which all plants are competing does not result in further increases in size inequality. It is unclear how important this exception is in natural or agricultural situations, since, at most densities and in most experimental and field studies, all plants have some neighbors.

To test the two alternative hypotheses, Weiner and Thomas[2] reviewed the published experiments on monocultures in which (1) den-

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Box 1. The measurement of size variability

One type of evidence for asymmetric competition is the effect of density on the variability in size or 'size hierarchy' within a population, but it is not always clear what is meant by these ambiguous terms. The classical measures of variation are the variance (s^2) and its square root, the standard deviation (s).

$$s^2 = \frac{\Sigma\,(\overline{x} - x_i)^2}{n - 1}$$

However, since these measure absolute variation, they do not allow us to compare populations of very different mean size, or the same population as its mean size increases. We would not expect a population of plants with a mean size of a few grams to have the same variance as a population with a mean size of many kilograms. What is needed is a measure of relative variation, such as the coefficient of variation (CV), which is simply the standard deviation divided by the mean (usually expressed as a percentage):

$$CV = \frac{s}{\overline{x}} \times 100$$

The observation that plant populations consist of many small individuals and few large ones led many ecologists to look at the skewness (g_1) of the size distribution as a measure of 'hierarchy'.

$$g_1 = \frac{n\Sigma\,(\overline{x} - x_i)^3}{(n - 1)\,(n - 2)s^3}$$

Weiner and Solbrig[20] argued that skewness is misleading in that it only measures the asymmetry of the distribution without reflecting its spread. Thus, a population could have a highly skewed distribution while having very low relative variation. They argued that 'size hierarchy' or size variability is synonymous with size inequality or concentration, as defined by economists to study inequality in wealth or income, and that the inequality of the size distribution, not its skewness, reflects what is important biologically. Their conclusions have been supported by an extensive study by Knox et al.[21] on population size structure of *Pinus taeda*. Knox et al. looked at the behavior of several of the summary statistics that have been used to describe size distributions, and found that measures of inequality provided robust indicators of density effects on growth and size-selective mortality, whereas skewness was less well-behaved. The most commonly used measures of inequality are the coefficient of variation[22] and the Gini coefficient (G)[20,21],

$$G = \frac{\sum\limits_{i=1}^{n} \sum\limits_{j=1}^{n} |x_i - x_j|}{2n(n-1)\overline{x}}$$

although there are also several others[23]. The choice of a measure of inequality ultimately depends upon the question being addressed and the underlying distribution of the data[24].

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sity was the independent variable, (2) mortality was not greater than 20%, and (3) size inequality was measured or could be calculated from published data or original data supplied by the researcher. Despite the hundreds of density studies on plants, they found only 16 studies that met these criteria. Of these, 14
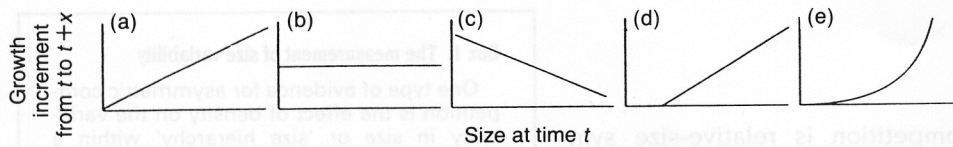
Fig. 1. Five types of relationship between growth increment (AGR) and size: (a) AGR proportional to size; (b) AGR independent of size; (c) AGR negatively related to size; (d) threshold size for additional growth; (e) increasing, convex relationship between AGR and size. (a)–(c) are consistent with symmetric competition or no competition; (d) and (e) are consistent with asymmetric competition.

showed increased size inequality at higher densities. The two cases that did not show this effect were the shortest of the 16 experiments, where the plants were grown from seed for less than 45 days. They concluded that early competition between seedlings was symmetric, whereas later competition becomes asymmetric.

This conclusion was supported by a study by Edmeades and Daynard[22] on size variability in sequential harvests of maize (*Zea mays*) grown at four densities. Early in the course of the experiment there was no clear relationship between the coefficient of variation (CV) in plant weight and density. By the end of the experiment (130 days), the CV in plant weight increased directly with density. Several more studies with data on size inequality and density have since been published. With one notable exception[26], they show results that are consistent with the previous studies.

Relationships between size and growth rate

Another type of evidence in support of the notion that plant competition is often asymmetric is the relationship between the size of an individual and its growth in a crowded population. Several plant

ecologists have independently developed the idea of examining the relationship between a plant's size at time *t* and its growth increment (which is the same as absolute growth rate, AGR) from time *t* to *t+x* as a way of studying how size distributions change over time[27–29]. Some AGR–size relationships are incompatible with the hypothesis of asymmetric competition, while others are inconsistent with symmetric competition.

Consider, first, AGR–size relationships in plants that are not competing. Plant growth is sigmoidal, with a period of increasing AGR (i.e. exponential growth), a period of relatively constant AGR (linear growth), and a period of declining AGR (growth levelling off)[30]. If most plants are in their exponential growth phase, we would expect AGR to be directly proportional to size (Fig. 1a). If most plants are in their linear growth phase, then AGRs will be similar for all plants, with no clear relationship between size and AGR (Fig. 1b). If plants are in their levelling-off phase, then AGR will decrease with size (Fig. 1c). Now, suppose that plants are crowded and competition is symmetric. The general types of predicted AGR–size relationships may be similar, although the actual growth rates will be lower, and the lengths of the different phases and the sizes achieved within them will be changed.

Asymmetric competition should result in very different types of AGR–size relationships. Specifically, a threshold size for additional growth (Fig. 1d) or a convex relationship between AGR and size (Fig. 1e) is consistent with asymmetric, but not symmetric, competition. To see why this is the case, it may be useful to translate the above arguments about AGR–size relationships into RGR–size relationships. Simply, sigmoidal growth means that a plant's RGR decreases as it grows, although AGR increases during the early near-exponential phase of growth. Similarly, we might expect larger plants in a stand to have higher

AGRs if plants are in the exponential phase of growth, but we would never expect a positive relationship between size and RGR if competition is symmetric: smaller plants should still be able to grow, and their RGRs (although not their AGRs) should be as large as those of their larger neighbors. Thus a positive relationship between RGR and size within a crowded population provides evidence in support of competitive asymmetry. This is what occurs if there is a threshold size for further growth (Fig. 1d, Fig. 2), or if there is a convex positive relationship between AGR and size (Fig. 1e). Relationships of this type have been observed in crowded populations of *Impatiens capensis*[6], *I. pallida*[31], *Polygonum* spp.[32] and *Pinus radiata*[33]. If plants below a certain threshold size are not able to grow further, some of them die (density-dependent mortality or self-thinning).

One must be cautious in using a single observed AGR–size relationship to determine the symmetry of competitive interactions, since there may be alternative hypotheses to explain a given AGR–size relationship. Much stronger inferences can be made by comparing AGR–size relationships for crowded and uncrowded plants of similar sizes or over similar periods of growth.

Extreme initial advantage in plant competition

A third, although similar, type of evidence for asymmetric competition between plants comes from the observation that plants that have a 'head start', i.e. germinate earlier than their neighbors, often have a tremendous advantage in competition[4,34–36]. If competition is symmetric, the initial advantage in competition should be limited to the additional time for growth and the resources acquired before the other competitors appear[7]. Of course, if growth is exponential, a slightly longer period of growth can result in large differences in size, but in most of the studies showing an extreme initial advantage, the populations were well past their exponential growth phase. Because of the AGR–size relationships discussed above, only asymmetric competition can account for the manyfold size difference between
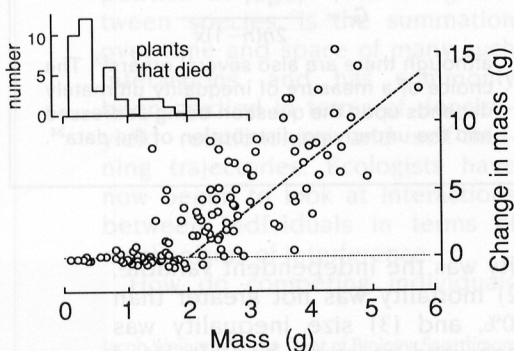
Fig. 2. The relationship between growth increment (AGR) and size for a naturally occurring crowded population of *Impatiens pallida* (jewelweed, touch-me-not), and the size distribution of plants that died during the period of observation[31]. The *x*-axis is the same for both graphs.

plants that germinate just a few days apart in these experiments.

Very little or no local competitive effect of smaller neighbors

Perhaps the strongest evidence for asymmetric competition has come from the few cases in which ecologists have looked at the effects on subject plants of neighbors that are larger or smaller than the subject individual. It is observed that larger neighbors have a depressing effect on the growth rate, whereas smaller neighbors have little or no effect[3,8]. Often, plants that are only slightly smaller than the subject plant still seem to have very little effect on the subject's growth.

The mechanism of competitive asymmetry

What are the mechanisms that give rise to asymmetric or symmetric competition? One hypothesis is that competition for light is asymmetric and competition for soil nutrients is symmetric. This was suggested by the observation (discussed above) that in even-aged populations competition seemed to be symmetric at first, and became asymmetric later on. Competition for light can only occur when plants are large enough to shade one another, but competition for soil resources can begin soon after plants germinate[2].

This hypothesis was tested with an experiment on morning-glory vines (Ipomoea tricolor) in which root and shoot competition were separated (Fig. 3)[37]. While root competition was much more severe than shoot competition, in that the former reduced plant weight much more than did the latter, it did not result in a significant increase in size inequality. Shoot competition had a smaller (although significant) effect on mean plant size, but it did significantly increase size inequality. In the case where plants were competing both above and below ground, the mean plant weight was not significantly smaller than when competition occurred only below ground, yet the size inequality was the highest of the four treatments. When the plants were competing both above and below ground, the reduction in mean plant size (i.e. the intensity of competition) was due to competition for soil resources, whereas the increase in size variation was due to competition for light. Thus, it ap-
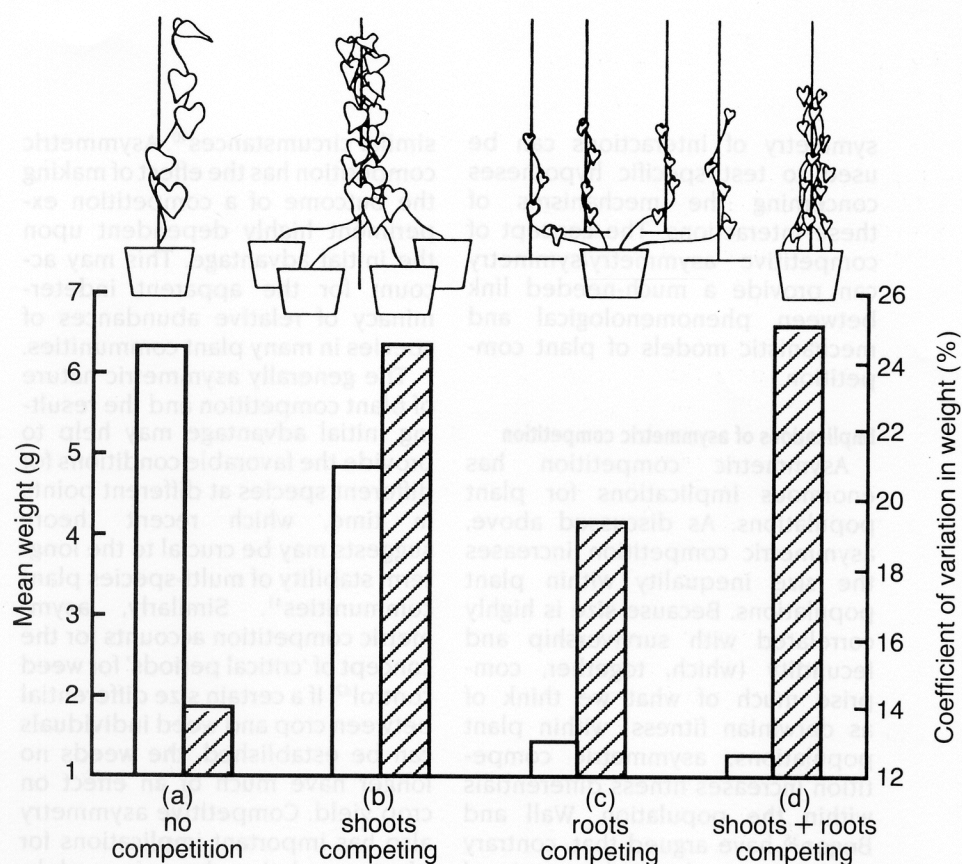
Fig. 3. An experiment on vines (Ipomoea tricolor), in which root and shoot competition were separated[37]. Mean weight (open bars) was significantly different ($P<0.01$) for all comparisons between treatments except (c) and (d). The CV in weight (shaded bars) was significantly different for the comparison of treatments (a) and (b) ($P<0.05$), and for (a) and (d) ($P<0.01$).

pears that the asymmetry of the interaction can be determined by competition for a resource that is not the one limiting the growth of the population.

Wilson[7] separated root and shoot competition between pairs of plants to see if the extreme initial advantage occurred in both cases. He found asymmetry only when there was competition above ground, although his result of symmetric below-ground competition can be questioned because the plants were clipped to keep the shoots from overtopping the above-ground barriers. Removal of above-ground biomass is known to reduce below-ground as well as above-ground competition. More tests of hypotheses concerning the mechanisms of competition for specific resources are necessary.

Clearly, competitive interactions between plants are the result of combined effects of competition for several resources, which may vary in their degree of asymmetry. The degree of asymmetry of competition for a specific resource will be determined by the distribution of the resource in space (e.g. distributed uniformly or patchily), the nature of

the resource's renewal (continual or episodic flow, or a depletable pool), and the mobility of the resource. The morphology of the plant with respect to uptake of the resource in question will also play a role in determining the asymmetry of the interaction[32]. Since a leaf shades only leaves below it, competition for light seems to be almost inherently asymmetric[2]. But in the rare situations in which plants grow in only one dimension, becoming taller but not wider[26], even competition for light can be symmetric. If a soil nutrient is distributed throughout the soil matrix, and if nutrient uptake is proportional to the size of the root mass, then we would expect competition for this nutrient to be relative-size symmetric, as a smaller plant will get its 'share' of the contested resource. On the other hand, if soil resources are distributed in large patches that can be reached and usurped by larger individuals, then this would result in an asymmetric interaction.

The close relationship between the concept of asymmetry/symmetry and mechanistic interpretations of plant–plant interactions means that data on the

symmetry of interactions can be used to test specific hypotheses concerning the mechanisms of these interactions. The concept of competitive asymmetry/symmetry can provide a much-needed link between phenomenological and mechanistic models of plant competition.

Implications of asymmetric competition

Asymmetric competition has enormous implications for plant populations. As discussed above, asymmetric competition increases the size inequality within plant populations. Because size is highly correlated with survivorship and fecundity (which, together, comprise much of what we think of as darwinian fitness) within plant populations, asymmetric competition increases fitness differentials within the population. Wall and Begon[38] have argued that, contrary to the commonly used operational definition of competition as an interaction between two individuals that is negative for both, asymmetric competition can actually increase the fitness of individuals. This is because fitness is defined in relative, not absolute, terms within a population. If an individual's fecundity is decreased by 50% by competition but, because of asymmetry, most of the other individuals within the population show a greater decrease in fecundity, then the fitness of the individual in question has actually increased. If there are correlations between competitive dominance and genotype, this will result in natural selection; if there are not, asymmetric competition will decrease effective population size and increase genetic drift[39].

Competitive asymmetry also accounts for the sensitivity of the outcome of competition experiments to initial conditions. Competition coefficients calculated to summarize the competitive interactions between pairs of species often vary enormously, even when the experiments are conducted under very

similar circumstances[40]. Asymmetric competition has the effect of making the outcome of a competition experiment highly dependent upon the initial advantage. This may account for the apparent indeterminacy of relative abundances of species in many plant communities.

The generally asymmetric nature of plant competition and the resulting initial advantage may help to provide the favorable conditions for different species at different points in time, which recent theory suggests may be crucial to the long-term stability of multi-species plant communities[41]. Similarly, asymmetric competition accounts for the concept of 'critical periods' for weed control[42]. If a certain size differential between crop and weed individuals can be established, the weeds no longer have much of an effect on crop yield. Competitive asymmetry also has important implications for plant population dynamic models. For example, asymmetry means that a crowded population will still have large plants, and these will contribute most of the seeds to the next generation; therefore seed yield will not, as some symmetric models predict, decrease at high densities.

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