

COMPETITION AMONG PLANTS

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Curs CIRIT celebrat a Bellaterra els dies 29, 30 i 31 de maig de 1991.

RESUM

Gairebé totes les plantes pateixen una influència negativa de les plantes del voltant. Encara que la paraula *competència* suggereix que aquests efectes negatius es deuen a l'esgotament d'alguns dels recursos disponibles, hi ha organismes que exerceixen la seva acció negativa mútua mitjançant diferents mecanismes, a més de la utilització dels recursos. En aquest treball es descriuen tres nivells de competència en plantes: competència interpoblacional, competència asimètrica i competència interespecífica.

MOTS CLAU: *competència, dependència de la densitat, competència asimètrica, monocultius, interferència.*

SUMMARY

Almost all plants are negatively affected by neighboring plants. Although the word «competition» suggest that the negative effect is due to the depletion of some limiting resources, organisms can have mutually negative effects on each other through different mechanisms, in addition to resource utilization. This article describes competition within populations, asymmetric competition and interspecific competition in plants.

KEY WORDS: *competition, density-dependence, asymmetric competition, monocultures, interference.*

INTRODUCTION

What is competition?

Competition is ubiquitous in its influence on plants. It is rare to find a plant which has not been affected negatively by neighboring plants. While there has been much study of competition between individuals and populations, the role of competition in nature is still a mystery. Indeed, the word «competition» appears to have different meanings to different ecologists.

Competition can be defined as an interaction between individuals or populations which is negative for both. While the word «competition» suggests that this negative effect is due to the depletion of some limiting resource, organisms can have mutually negative effects on each other through mechanisms in addition to resource utilization. For example, it has been shown that some plants release chemicals into the environment which reduce the growth and survivorship of other plants (allelopathy). Also, organisms can physically interfere with each other. Harper (1977) developed a terminology for discussing interactions between plants which, although not widely accepted, is helpful in clarifying the interactions between plants. Because plants are sessile and interact only with nearby individuals, Harper suggested the term «neighbor effects» as the general term to refer to all effects of plants on one another. Observed neighbor effects are the sum of many positive and negative interactions. He suggested that negative neighbor effects be referred to as «interference». Negative effects of neighbors include:

- i. Shortages of light, water or mineral nutrients
- ii. Release of harmful chemicals (allelopathy)
- iii. Greater susceptibility to epidemic disease or other hazards (e.g. grazing)
- iv. Greater susceptibility to lodging
- v. Decreased availability of pollinators
- vi. Changed ability of the environment to

provide special triggering mechanisms (e.g. for breaking dormancy)

Harper said that the term competition is perhaps best reserved for those negative neighbor effects which are mediated by resource consumption (i. and v. above), although I will follow the generally-accepted use of «competition» to refer to all negative neighbor effects.

Positive effects of neighbors which have been observed include:

- i. Protection against epidemic disease, grazing, wind or lodging
- ii. Increased availability of specific resources (e.g. nitrogen provided by nitrogen-fixing symbionts may become available to neighbors)
- iii. Reduction in over-abundant resources which are harmful

While positive neighbor effects exist and may be important in specific situations, neighbor effects are usually negative and most often due to resource utilization and limitation, so competitive interactions have been the focus of most research.

It has become apparent over the past few years that discussions and debates about competition between organisms have been plagued by confusions between different scales and levels of organizations. Competition between what? individuals? —parts of one individuals? —species? According to the reductionist approach, competition between species is the sum of numerous interactions among individuals over space and time. But it seems that this summation is not a simple extrapolation. For example, suppose species A will out-perform species B if they are grown from seed in a competition experiment, because species A can put a canopy above species B and reduce the growth of B. However, over long term, after vegetation has been established, it is the ability of seedling to compete with other seedlings. Similarly, fast-growing early successional trees will dominate over slower-growing late successional trees in the short run, but late successional trees are shade tolerant and will come to dominate after

the first generation. In a recent experiment by Bergelson (1990) in which plants were grown for more than one generation, it was the ability of plants to germinate and establish in the litter of dead plants from the previous generation that was most important in determining the outcome of competition. This example makes several important points. First, it emphasizes the importance of time scale in the study of competition. The outcome of competition between two species over the long term is not the same as that over short term. Second, there may be critical points in the life cycle of the organisms which determine the long-term outcome of competition, and these may not be the points that are usually studied. This is not an argument against the reductionist program. Rather, it sounds a cautionary note about making inferences from one level of biological organization to another level. Successful reductionism usually occurs in small steps, and we cannot leap over many levels of analysis in one step.

Competition within populations: density-dependence in monocultures

The study of competition in plants starts with the analysis of density-dependence in single species populations. There are three possible reactions of a plant to interference (Harper, 1977). A plant may:

- 1) fail to germinate while retaining viability
- 2) die
- 3) survive and grow to an extent or for a time, as limited by the environment (including its neighbors)

One of the most important types of experiments on competition are density/yield experiments. Looking at the plant as a population of modules, competition can decrease the birth rate and increase the death rate of plant parts (e.g. leaves, buds or branches). Thus, competition decreases the rate of growth and/or increases the probability of death of an individual from what

it would be in the absence of neighbors. It can be shown for a great variety of plants that, if one looks at a wide range of sowing densities, yield per unit area after a given period of growth increases with density at low densities. At the low end of the density continuum, yield increases linearly with density, but at higher densities further increases in density produce progressively smaller increases in yield. Eventually, a maximum yield per unit area is achieved, and further increases in density do not result in further increases in yield, because the whole population is limited by the available resources. This represents a «carrying capacity» for the whole population, and the levelling off of the density-yield curve has been called «the law of constant final yield» (Kira, Ogawa and Shinozaki, 1953). If perennial ryegrass (*Lolium perenne*) is sown at low density, most plants will produce many tillers. If the density is high, crowding will reduce the number of tillers produced by each individual. There is a carrying capacity for tillers, and the same density of tillers area will result from a wide range of sowing densities.

There have been numerous studies of the relationships between density and mean plant size (or total yield) within a crop population, and quantitative relationships between these density and yield have been developed. (Willey and Heath, 1969). One widely applicable formulation is the «reciprocal yield» relationship (Bleasdale and Nelder, 1960; Holliday, 1960):

$$1/w = ad + b$$

where w is the mean yield per plant, d is the density, a and b are constants. A more general formulation has been developed by Vandermeer (1984):

$$w = w_m / (1 + cd^e)$$

where the constants have the following biological interpretation: w_m is the mean yield of isolated plants, c is a measure of competition including its intensity and the area within which

it operates, and e is a measure of the rate at which the effect of competition decays as a function of the density between plants.

The relationship between yield and density varies with environmental conditions, e.g. addition of a limiting resource such as nitrogen can change the optimal density as well as the maximum yield (Snaydon, 1980). This results in a change in the constant in the above formulations, but not a change in the general form of the relationship.

Although increases in density above that for maximum yield per unit area result in corresponding decreases in mean plant weight such that total yield remains constant, several important changes in the population do occur at higher densities:

a) At some point on the density continuum, further increases in density are absorbed, in part, by mortality as well as plasticity. The fraction of plants surviving decreases as density increases. Concurrent changes in density and size of surviving plants as a dense population grows and undergoes density-dependent mortality («self-thinning») have been studied quantitatively (Westoby, 1984; White and Harper, 1970). Since crop plant density is usually below the threshold for extensive density-dependent mortality because maximum crop yield is usually achieved at such densities, we will not focus on self-thinning here.

b) Size variability within the population increases with density. Not only is mean plant size smaller at higher densities, but the distribution of plant sizes around the mean becomes more skewed and unequal, and a larger percent of the total yield is to be found within a smaller percent of the population (Weiner and Thomas, 1986).

c) The relative contribution of yield components to the total yield changes with density. Specifically, at higher densities more of the total yield is to be found in structural tissues, and less in reproductive tissues or other harvestable components.

Observations *b)* and *c)* are related, and it is not clear how much of the change in the population's harvestable components is due to changes in the behavior of all plants, and how much is due to the behavior of the smallest individuals (Weiner, 1988). For example, if there is a minimum size for flowering, a smaller fraction of the population will be above that minimum at higher densities.

Asymmetric competition

How do competing individuals consume and divide up limiting resources? One current concept which has great bearing on these questions is asymmetric competition. «Asymmetric competition» refers to a situation in which larger individuals have a disproportionate effect or obtain a disproportionate share of the resources (for their size) and suppress the growth of smaller plants. The fact that a larger individual has a competitive advantage over a smaller individual does not necessarily mean that competition is asymmetric. 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 which is twice as large as another has twice the effect or obtains twice the amount of resources, this could be considered «size-symmetric» competition. For competition to be asymmetric, the individual which is twice as large as another must have *more* than twice the competitive effect or obtain more than two times the amount of resources than its smaller neighbor.

There are several lines of evidence that competition among plants is asymmetric. The first type of evidence is the relationship between density and size variability in competing populations. Models of plant competition in which competition is asymmetric predict that populations grown at higher densities should show greater size variability (inequality) than

populations grown at lower densities over the same period (Weiner and Thomas, 1986). Simply put, although size variability will increase in the absence of competition if plants vary in their relative growth rates (RGRs) (Koyama and Kira, 1956), asymmetric competition acts to increase the variation in relative growth rates and therefore exaggerate relative size differences over what they would be at lower densities, or in the absence of competition. The higher the density, the sooner these asymmetric interactions begin, and the more intense they will be. Symmetric models of competition, on the other hand, 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.

To test the two alternative hypotheses, Weiner and Thomas (1986) reviewed the relevant published density experiments on monocultures in which 1) density was the independent variable, 2) mortality was not very high and 3) size inequality was measured or could be calculated. Despite the hundreds of density studies on plants which have been published, they found only sixteen studies which met these criteria. Of these, fourteen showed increased size inequality at higher densities. The two cases which did not show this effect were the shortest experiments studied: 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. Their conclusion was supported by a study by Edmeades and Daynard (1979) on size variability in sequential harvest of maize (*Zea mays*) grown at four densities. Early in the course of the experiment there was no clear relationship between the variability in plant weight and density, but by the end of the experiment (130 days) variability increased directly with density.

Another type of evidence in support of the notion that plant competition is asymmetric is the relationship between size and growth in crowded populations. 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 $t \rightarrow t+x$ as a way of studying the way size distributions change over time (Hara, 1984; Kira, 1978; Westoby, 1982). There are certain types of AGR-size relationships which are compatible with the hypothesis of asymmetric competition, whereas there are others which are not consistent with symmetric competition.

Consider first AGR-size relationships in plants which are not competing. Plant growth is sigmoidal, with a period of increasing AGR (i.e. relatively constant RGR), a period of relatively constant AGR (linear growth), and a period of declining AGR (growth is levelling-off) (Hunt, 1982). If most plants are in their exponential growth phase, we would expect AGR to be directly proportional to size. 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. If plants are in their levelling-off phase, then AGR will decrease with size. 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 minimum size for additional growth 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 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 is occurring if there is a minimum size for additional growth. Relationships of this type have been observed in crowded populations of *Impatiens capensis* (Schmitt, Eccleston and Ehrhardt, 1987), *I. pallida* (Thomas and Weiner, 1989), *Polygonum* spp. (Geber, 1989) and *Pinus radiata* (West and Borough, 1983).

A third, although similar, type of evidence for asymmetric competition between plants comes from the observation that often, plants which have a «head start», i.e. germinate earlier than their neighbors, have a tremendous advantage in competition (Black and Wilkerson, 1963; Firbak and Watkinson, 1987; Howell, 1981; Ross and Harper, 1972). 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 (Wilson, 1988). Because of AGR-size relationships discussed above, only asymmetric competition can account for the enormous size difference between plants that germinate just a few days in these experiments.

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 which 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 (Cannell, Rothery and Ford, 1984; Thomas and Weiner, 1989). Often, even plants that are only slightly smaller than the subject plant seem to have very little effect on the subject's growth.

What are the mechanisms which give rise to asymmetric or symmetric competition? The first hypothesis which has been proposed 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 (Weiner and Thomas, 1986). This hypothesis was tested with an experiment on morning-glory vines (*Ipomea tricolor*) in which root and shoot competition were separated (Weiner, 1986). While root competition was much more severe than shoot competition in that root competition had a much greater effect on mean plant weight, 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 asymmetry of the interaction can be determined by competition for a resource which is not the one limiting the growth of the population. Wilson (1988) found no evidence for competitive asymmetry when plants were competing only below ground. More tests of mechanistic hypotheses concerning the nature of competition for specific resources are in order.

Asymmetric competition has enormous implications for plant populations. As discussed above, asymmetric competition increases the size inequality within plants 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. Competitive asymmetry accounts for the sensitivity of the outcome of plant 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 (Law and Watkinson, 1989). 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.

Interspecific competition I: the analysis of species mixtures

In many ways interspecific competition is not fundamentally different from competition within a species. Plants all have the same general requirements, and the effect of a neighbor may be determined more by its size than by its species (Goldberg and Werner, 1983). While the analysis and qualification of intraspecific interference at the population level has been relatively successful (see above), modelling interspecific competition has been more problematic. The presence of more than one species increases the complexity of the analysis because the performance of each component will be influenced by the density of both components.

Two types of experiments, additive and substitutive, have been used to study the effects of interspecific interference. In the former case, a second species is added to a constant background density of another species. This can be an appropriate method for the study of weed interference, where the weed is an addition to the crop population. In substitutive experiments the overall density is kept constant but the relative

proportions of the two species are varied. The «replacement series» method has been used to look at the relative effects of interspecific and intraspecific competition in experiments with substitutive designs (Harper, 1977; Wit, 1960). Comparisons can then be made between the performance of each species in monoculture and in mixture. The replacement series approach has been much criticized recently because:

1) the overall density is kept constant. The effects of interference at one total density may be very different from interactions at a different density, and changes in total density are very common and important in nature (Inouye and Schaffer, 1981; Weiner, 1980). Another way of saying this is that mixtures are inherently two-dimensional in that the density of each species should be treated independently (Connolly, 1986).

2) replacement series analysis cannot be used to interpret or predict the results of additive experiments.

3) The comparison between intraspecific and interspecific interference in replacement series analyses is expressed in terms of relative competitive or yield coefficients, which can be difficult to interpret biologically (Firbank and Watkinson, 1985).

4) Replacement series have special difficulties when the species are of different sizes.

Alternative methods of analyzing interspecific interference in plants are greatly needed. The single-species density-yield equations, such as those presented in the second section, can be extended to model species mixtures (e.g. Firbank and Watkinson, 1985). In such a model, the size of an individual is a function of the densities of all species.

In many cases, greater total yield is obtained when two species are grown in mixture than when either species is grown alone. This phenomenon, called «complementation» or «overyielding» may be due to differential resource utilization by the two species. Thus, if the two species have different resource requirements, they may be able to utilize more of

the total available resources when they are grown together than when either is grown alone. In addition, there may also be positive neighbor effects that may counteract, to a greater or lesser extent, negative effects. For example, some of the nitrogen fixed by a legume may become available to nearby grass plants, increasing the yield of the grass component and the whole mixture. In some cases positive neighbor effects may outweigh interference effects (e.g., Weiner, 1980; Weiner, 1985) and a population may actually benefit from the presence of another population.

Interspecific competition II: competition in natural communities

Although most studies of competition in plants have looked at one or two species, most natural communities have more than two plants species. According to the approach of «limited reductionism» discussed at the beginning of this essay, we must look at competition in whole communities as well as small subsets of the community. Even if we could look at all pairwise interactions it would be impossible to predict what would happen in multispecies communities because of the numerous higher-order interactions.

The first question plant community ecologists have asked is whether competition is occurring in nature. While this question seems strange to botanists who feel intuitively that competition amongst plants is ubiquitous, there is evidence that competition in some groups of animals (e.g. phytophagous insects) may not occur in the field. Thus, establishing the importance of competition in nature is a necessary first step in the study of competition in real plant communities. The standard procedure is a removal experiment: neighbors around specific «subject» or «target» plants are removed, and the growth, survival or reproductive output of these plants is compared with that of control plants which are experiencing the normal level

of competition. It is very rare for such a study not to show a major effect of neighbor removal. A recent study by Montserrat Vilà of the Universitat Autònoma de Barcelona is an example (Vilà, 1991; Vilà *et al.*, 1993). Vilà studied the effect of competition on resprouting in *Arbutus unedo*, a common shrub in the Mediterranean communities of Catalonia. Fire is a common feature of these ecosystems, and many woody plants are able to resprout following fires from stumps or subterranean organs. Vilà clipped *Arbutus* plant at ground level. Neighbors within a 1.5 m radius were removed from some clipped individuals. She found significantly more and larger sprouts on plants which had neighbors removed, but the effect of competition appeared to be greater 2 months after treatment than it was 7.5 months after clipping.

The importance of competition among plants has led many ecologists to ask if there is such a thing as «competitive ability» in plants and, if so, what plant characteristics are associated with competitive ability. A few decades ago, Sakai (1961) hypothesized that competitive ability is a heritable trait. He looked without success for correlations between success in competition experiments and measurable plant traits such as height, seed number, time of flowering, etc. Other studies have found that success in mixture goes to species which establish first, e.g. germinate earlier, put up a canopy early, have the largest seed reserves, etc.. In competition studies with species of *Trifolium*, the species with the longest petiole always won (Black, 1957). These results suggest the importance of asymmetric interactions, which were discussed above.

Philip Grime of Sheffield, UK, is the major proponent of the concept of competitive ability in plants. He has outlined three basic plant strategies which he calls «stress toleration» (S), «ruderal» (R), and «competitive» (C) (Grime, 1979). He hypothesizes tradeoffs between these different strategies, such that a plant can pursue one of these strategies only at the expense of their abilities. Grime's approach assumes that

competitive ability is a useful concept, and that aspects of competitive ability will be positively correlated. Plants that are good competitors for one resource will also tend to be good competitors for other resources. This is because competition is not important in some environments (either because resources are so low that plants do not interact much (S), or because a disturbance occurs before plants begin to compete intensely). In environments in which competition is important, plants are competing for many resources at the same time. Plants in these environments evolve a suite of characteristics which enhance their ability to compete for all these resources. Support for this approach comes from Paul Keddy and his co-workers, who studied competitive relationships among numerous species of plants which live on lake shorelines in Canada (Gaudet and Keddy, 1988). He found that competitive relationships between species were transitive, i.e., if species A outcompetes species B, and if B outcompetes C, then A outcompetes C. He also presented evidence that competitive ability was correlated with plant size. Thus, Keddy's results are consistent with Grime's ideas.

An alternative approach has been developed by David Tilman from Minnesota, USA. Tilman has developed mechanistic models of plant competition in which the best competitor is the species which can tolerate the lowest levels of the limiting resource (Tilman, 1982; Tilman, 1988). This is because resource levels are reduced when plants compete. When resource levels become very low, the ability to survive and grow under these reduced resource levels becomes the important issue. Plants differ in their tolerances for low levels of different resources. A plant that is good at tolerating low light levels will not be good at tolerating low nitrogen levels. There is no single entity called «competitive ability». Rather, there is a competitive ability for each different resource, and competitive relationships will change depending on the levels of different resources.

Differences between the approaches of Grime and Tilman have been difficult to resolve or even clarify because of the differences in their assumptions and terminology. Part of the problem has to do with questions of scale discussed in the first section. For Grime, competition occurs between individuals in one generation, as in the classic competition experiments. For Tilman, competition is a long-term process which occurs over many generations. As discussed above, the factors determining the outcomes at these two different scales may be very different. Goldberg (1990) has made a significant contribution to the discussion by pointing out that there are two basic aspects of resource competition which have been confused:

- 1) An individual reduces the resources available to another individual («competitive effect»)
- 2) An individual responds to the reduced resource level («competitive response»)

Thus, a good competitor can be one which is effective at reducing the resources available to other plants (Grime), or a good competitor can be one that can tolerate low resource conditions created by its neighbors (Tilman). These two aspects of competitive ability may be related (as in the case of competition for some mineral nutrients), but this relationship is not inevitable. For example, when individuals are competing for light, the ability to reduce light available to other individuals is a function of the position of the leaves, but leaves that are higher in the canopy (competitive effect) may not be more tolerant of low light levels (competitive response).

In conclusion, while plant ecologists have been successful in documenting and, in some cases quantifying, the effects of competition among plants, the mechanism by which plants compete, and the implications of these interactions for the ecology and evolution of plants are still unknown. We have just scratched the surface of these exciting and important questions.

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