

Competition and coexistence in plant communities

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It is useful to distinguish between two different, though often overlapping, approaches in studies of plant competition. One is to examine the proximate mechanisms of competition, by focusing on the acquisition and use of resources and on the traits that determine competitive ability¹⁻³. The other is to focus on the results of competition, i.e. to analyse community structure and the maintenance of diversity⁴⁻⁶. Often the latter approach stimulates an interest in the mechanisms that prevent plant species with similar niches from excluding each other through competition.

Ten years ago, Schoener⁷ and Connell⁸ reviewed field experiments on competition. They were mainly interested in the question whether interspecific competition could be detected or not. Although they differed slightly in their interpretations of the data, their results agreed on the main issue – interspecific competition may indeed occur in natural communities. In retrospect, this may not seem a very exciting conclusion, but at that time it was sometimes questioned whether or not ecologists could provide any evidence at all for the operation of competition in the field.

Two recent reviews of competition experiments by Goldberg and Barton⁹ and Gurevitch *et al.*¹⁰ can be used to decide whether or not ecologists have come any further during the past decade than merely demonstrating that competition occurs. However, both reviews selected a rather limited number of journals (seven by Goldberg and Barton, six by Gurevitch *et al.*), and surveyed the past decade only. Hence many relevant studies were not included. Also, the highly uneven quality of field experiments on competition makes the results of these reviews less conclusive.

A major problem is that many studies of competition have not analysed the results in ways that can answer many recently raised questions, such as whether or not competition intensity varies along productivity or herbivory gradients. Often, only main effects of neighbour removals are analysed. However, to investigate if competition varies in space and time, interaction terms in ANOVAs (or equivalents) must be examined⁹. Future comparative studies of competition and other biotic interactions would be greatly facilitated if the standard procedures and statistical comparisons suggested by Goldberg and Barton⁹ were followed (see Table 1).

Few ecologists today doubt that competition is an important structuring factor in plant communities, but researchers disagree on the circumstances where it is most intense, and on which traits can be considered to contribute to competitive ability in different species. The distinction between a species' effect on resources and its response to reduced resource levels might help to solve these questions.

Whereas classical competition theory predicts competitive exclusion of species with similar requirements, recent ideas stress that species diversity may be explained by a multitude of processes acting at different scales, and that similarities in competitive abilities often may facilitate coexistence.

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The two reviews agree on the main points, despite their use of largely non-overlapping data-sets and different criteria for including studies. Competition is frequent among plants, influencing both fitness components of individuals and the abundance of populations in most experimental studies. However, a surprising observation is that positive interactions were also quite frequent⁹, in spite of the fact that most experiments were designed to examine negative interactions. Several possible mechanisms for positive interactions can be suggested (see the article by Bertness and Callaway in the May issue of *TREE*¹¹). For example, even if two species use the same nutrient resources, a species producing litter that is rapidly decomposed may enhance nutrient availability for its neighbours. Apparent mutualism¹² may be observed if one species increases the performance of a target species by suppressing a common competitor. These kinds of indirect positive interactions have received little attention, and they are common

enough to deserve more investigation⁹.

Competition also influences the distribution and abundance of plant species, and so community composition^{9,10}. Furthermore, abundant or dominant species often have negative effects on diversity, supporting the assumption that species richness increases when dominants are removed. Several of the hypotheses for species coexistence discussed below, such as the 'intermediate disturbance hypothesis', rest on this assumption.

Both reviews concluded that intraspecific competition may not be more intense than interspecific competition, which is contrary to the popular notion of classical competition theory. Among plants, asymmetry in competition for nutrients and light is mainly a result of size differences, rather than of species differences, because acquisition of these resources usually depends more on plant size than on species identity. This means that classical resource partitioning, whereby species coexist through niche differentiation, may not be of major importance in plant communities.

None of these conclusions is very surprising, rather almost expected. What is surprising is that, despite some decades of intensive studies of plant competition, there are so few studies explicitly examining the issues raised in Table 1 and by Ref. 9. It is clearly premature to draw any

Table 1. Necessary treatments and statistical comparisons for analyses of competition in field experiments^a

Question	Necessary treatments	Statistical comparison
Consequences for individuals, populations and communities		
(1) Does competition affect (a) individuals, (b) populations, or (c) community composition within sites?	Differences in absolute abundance of neighbours, monitoring (a) individuals of the examined (target) species, (b) population size (biomass) of the target species, or (c) all species in the community.	Main treatment effects of neighbour abundance on (a) fitness components, (b) population size (biomass), or (c) some measure of community composition (relative abundances, diversity, etc.).
(2) Does the occurrence/magnitude of competition vary (a) over time, (b) over space, or (c) along productivity or herbivory gradients?	As in (1), but repeated (a) more than once at the same site, (b) at several sites at the same time, or (c) crossed with productivity/herbivory treatment (alternatively using sites differing in productivity/herbivory).	Neighbour abundance × (a) time, (b) site, (c) productivity/herbivory treatment interaction.
(3) Does competition affect the distribution and abundance of the target species among sites?	Neighbour abundance treatments repeated on sites differing in abundance of the examined (target) species; cf. (2).	Neighbour abundance × site interaction.
(4) Does the effect of competition on community composition differ among sites (e.g. along gradients)?	As in (2), but abundances of all species in the community monitored.	Neighbour abundance × site interaction on some measure of community composition, cf. (2) and (3).
Competitive ability		
(5) Does competitive ability differ between species? (a) competitive effect. (b) competitive response.	(a) Neighbour abundance treatment using different neighbour species, but one target species only. (b) Different target species crossed with neighbour abundance treatment of a single neighbour species (or group of species).	(a) Main effect of neighbour species on target species. (b) Target species × neighbour abundance interaction.

^aThe most important questions that can be analysed with field experiments concern whether or not competition varies among sites or along gradients of, for example, productivity or herbivory. However, many experiments on plant competition did not include the necessary experimental treatments needed to answer these questions, or they included the treatments but the authors did not perform the statistical analyses required to answer them. The compilation should be used for designing future experiments on competition. *Based on Table 1 in Ref. 9.*

conclusions about how competition intensity may vary in time and space from these studies. Explicit examinations of these issues in different communities and ecosystems are badly needed.

Competitive effect and response, plant traits and competitive ability

The study of competition in plant communities would be greatly simplified if competitive ability could be predicted from easily measured plant traits. We would then be able to predict community composition without performing a large number of time-consuming experiments. Hence, several plant ecologists have made attempts towards this goal^{1-3,13,14}, but there is no agreement between them on which plant traits should be included in order to arrive at such a measure of competitive ability¹⁵.

Goldberg¹⁶ made the distinction between competitive effect (the ability to suppress resource levels for other species) and competitive response (the ability to tolerate suppression or low resource levels). This is an important conceptual advance which is applicable not only to plants. For example, these concepts would have been useful in the literature on zooplankton competition¹⁷.

Grime^{1,13} based his definition of successful competitors on a triangular scheme for plant life strategies, in which plants trade-off the abilities to capture resources, to tolerate stressful environments and to survive disturbances. Thus (as stressed by Goldberg¹⁶), good competitors are those species with traits that maximize resource capture (competitive effect), while species tolerant to low resource levels belong to the stress-tolerators. Tilman^{2,3}, on the other hand, identifies superior competitors by their ability to deplete resources to a low level and to tolerate the low resource levels created. Hence, both competitive effect and response seem to be involved. However, it turns out

that the superior competitor is the species which requires the lowest resource levels to maintain a population; that is, traits that contribute to competitive response in both seedlings and adults should be most important in the long run (see Refs 15,16). Different traits may contribute to the rankings of competitive effect and competitive response. Thus, the controversy regarding plant traits and competitive ability can be partly resolved by adopting these concepts^{9,15,16}.

Studies carried out along natural or experimental productivity gradients are relevant to the controversy between Grime and Tilman. Grime^{1,13} hypothesized that competition should be more intense and have larger effects on species composition on productive sites. Indeed, in studies using natural gradients the magnitude of competition seems to increase with productivity⁹, in support of Grime's proposition. However, this is not the case along experimental gradients⁹, which is in accordance with Tilman's suggestion³ that the intensity of competition does not change with productivity. This discrepancy may be because experimental additions of inorganic nutrients do not correspond to patterns of nutrient mineralization in natural ecosystems, and because productivity along natural gradients may be confounded with other factors such as grazing pressure or disturbance⁹. A further complication is that it has been recognized only recently that a distinction must be made between absolute and relative competition intensity, which has consequences for the resolution of this conflict¹⁸.

Several shortcomings of most studies of plant competition are evident. One is that most experiments do not last long enough – usually less than a year^{9,10} – to give conclusive results. To measure population-level responses to competition, and to include indirect effects of, for example, litter decomposition and nutrient release, experiments must be carried out for much longer periods. Another

shortcoming is the lack of attention to the dynamics of resource renewal. Variation in nutrient mineralization rates may create conditions under which different plant species with different traits are superior competitors. Some causes of this variation are environmental conditions such as temperature and moisture, plant litter quality¹⁹, activity of microbial decomposers, grazing on microbes²⁰ and grazing by herbivores²¹⁻²³. Recognition of these mechanisms will change our views of plant competition substantially in the future.

The coexistence of plant species

Historically, the questions of species coexistence and diversity have been strongly linked to that of competition. Three recent reviews on processes affecting plant species diversity by Wilson⁴, Aarsen⁵ and Zobel⁶ indicate how the views have broadened during recent years. The understanding of how different mechanisms act depends very much on the appreciation of spatial and temporal scales (Box 1).

Large-scale processes

Whereas most literature on species diversity deals with mechanisms that prevent competitive exclusion, Zobel⁶ also discusses how diversity is created, and includes evolutionary and historical processes on large spatial scales in addition to ecological processes in local communities. Calcicolous grasslands in Europe are an example. These hold more species than acidic grasslands, a fact that can be attributed to the large areas of dry steppe on base-rich soil which have a long evolutionary history for speciation²⁴. All species that have evolved traits enabling them to survive in a habitat type represent a species pool, a 'null community', the size of which is a function of the commonness and geological age of the biome or habitat type (cf. Refs 25,26). Not all species in this null community have evolved traits to cope with the local conditions in a given region. In Zobel's example from Estonia, the climate of the boreo-nemoral zone is outside the tolerance range of some dry-steppe species. Historical factors, such as limited dispersal after glaciation, will further reduce the local species pool. Finally, ecological processes such as competition determine the actual number of species coexisting in a community. Changing habitat conditions causes one local species pool to replace another; that is, succession takes place. Zobel argues that such replacement is mainly due to asymmetric light competition, and in grasslands, the process is often initiated by increased soil fertility or cessation of grazing or mowing. Contrary to Gause's principle, which predicts competitive exclusion among similar species, this replacement is caused by species dissimilarity in plant height.

The fact that plant communities are not isolated is stressed in some theories that invoke immigration from nearby communities as a means of compensating for local extinctions. In models of metapopulation dynamics, the species are assumed to have reproducing local populations in all or most patches of a habitat, and may coexist regionally even though competitive exclusion in each patch is common²⁷. Coexistence is based on either close similarity in competitive ability, or a trade-off between dispersal and competitive ability. The mass effect²⁸ suggests that some species may persist in habitats where they can survive but not reproduce, providing there is a compensatory inflow of diaspores.

Box 1. Scale-dependence of processes affecting species richness and coexistence in plant communities

The explanations for coexistence and diversity in plant communities operate on different temporal and spatial scales. The evolutionary time-scale is the time needed for macroevolution and speciation, and corresponds to a large spatial scale of entire biomes (continental). The historical time-scale refers to a few to several thousand years (e.g. the time since the last glaciation), the spatial scale is also large. The ecological time-scale is shorter and often related to the generation time of the species involved. Regional and local spatial scales refer to processes among and within communities, respectively. Often the processes affecting diversity on different scales may act simultaneously (cf. Ref. 6).

Essentially the same set of mechanisms have been listed under twelve, five and seven headings in three recent reviews (Refs 4, 5 and 6, respectively), indicating that the mechanisms are related and overlapping (almost 30 additional synonyms were listed by Wilson⁴), and that a strict classification is impossible.

Processes:

Temporal and spatial scale

Speciation:

Null communities

Evolutionary, continental

Migration:

Local species pool

Historical, continental

Immigration-extinction dynamics:

Metapopulation dynamics

Mass effect

Ecological, regional

Centrifugal community organization:

Competitive hierarchies

Species differences:

Resource niche

Phenological niche

Life-form niche

Regeneration niche

Resource ratios

Ecological, local

Species differences combined with:

Spatial heterogeneity

Temporal heterogeneity (gradual change hypothesis)

Disturbance (intermediate disturbance hypothesis)

Species similarities:

Competitive combining ability

Herbivory leading to competitive equivalence

Lotteries (often combined with disturbance and gap dynamics)

Positive interactions:

Mutualism

Apparent mutualism

Another explanation for regional coexistence of plant species is based on the fact that many species seem to be arranged in competitive hierarchies²⁹. Sites where competition is most intense may be monopolized by the species with the highest rank with respect to competitive ability. The intensity of competition can decrease towards more-peripheral sites for various reasons, such as increased disturbance or different types of abiotic limitations. Keddy³⁰ depicted these changes as radiating out in different directions from a central high-biomass habitat where competition is intense. In such a 'centrifugal organization of plant communities' there is a decreasing intensity of competition and an increasing diversity of species and life forms in the more-peripheral habitats.

Processes within the community

Mechanisms acting within the community can be placed into two categories: (1) those based on niche differences between coexisting species, and, paradoxically, (2) those based on similarities in competitive ability. In the latter case, species may either be similar with respect to relevant life history and physiological traits, or have different combinations of traits which acting together give rise to similar competitive ability.

In the category (1), coexistence is made possible because species avoid competitive exclusion through niche differentiation. This explanation requires environmental heterogeneity, so that competitive advantage varies spatially in the community. The gradual change hypothesis, on the other hand, assumes that competitive advantage shifts over time because of environmental variability. This idea can be traced back to Hutchinson's explanation for the paradox of the plankton³¹: how can so many species coexist in a seemingly homogeneous environment? The time-scale of environmental changes is crucial since competitive advantage must shift before the currently weaker competitor has been eliminated, for example, because of seasonal variation³².

Problems with the niche differentiation explanation for coexistence arise because all green plants have similar resource requirements, which makes resource partitioning less likely than in animal communities. The resource-ratio hypothesis^{2,3} expands the possible solutions by assuming trade-offs between competitive ability for different resources, for example, light and nitrogen, but heterogeneity is still required for many species to coexist.

Another approach has been to expand the niche concept beyond differences in resource use. Coexistence can be mediated by differentiation in life form or phenology. The most influential expansion was the concept of the regeneration niche²⁴, according to which the species differ in their requirements for seed production, dispersal, germination etc. A competitive disadvantage in vegetatively weaker species could thus be compensated during a year which is more favourable for regeneration. As defined, the concept describes differential responses to resources or conditions required for regeneration, but life-history differences could well be discussed under the same heading. A species with competitive disadvantage could avoid exclusion by having a greater seed production³³. Another extension is that if juveniles differ from the adults in their requirements, competitive advantage could shift with life stage. Such differences would be expressed more readily in systems where disturbances create gaps in the vegetation. Trampling in grasslands and storm-gaps in forests act differently from gradual change in that these processes cause a sudden killing of all species and a momentary release of

resources in a small area relative to the community. Since too much disturbance may be disadvantageous for all species, diversity tends to peak at intermediate levels of disturbance.

The second category of explanations for coexistence rests on the notion that if species are sufficiently similar in competitive ability, competitive exclusion may either not occur at all, or occur at such a low rate that compensatory processes (e.g. evolutionary change) have time to work. Similarity may be brought about by 'environmental filtering': only species that are reasonably similar can survive in a given abiotic environment³⁴. Alternatively, Aarssen's concept³⁵ of competitive combining ability can be invoked. This concept assumes that competitive equality is a result of ongoing coevolution in which selection for competitive ability is stronger in the species that is weaker at the time. Intermediate levels of grazing or mowing also increase the similarity between species, and can thus increase diversity by suppressing dominant light competitors.

An important recent advance is the finding that certain elements of stochasticity generally enhance coexistence and, hence, the degree of similarity between competitors that permits coexistence. The so-called lottery models^{33,36} typically assume that space is allocated to seedlings by chance processes (e.g. random seed dispersal in space) and that relative recruitment to the community from different species fluctuates over time due to stochastic fluctuations in seed set and/or seed germination. In communities where the component species obey these rules, interspecific differences can be arbitrarily small and yet indefinite coexistence is permitted, provided that the fluctuations in recruitment rates are not perfectly correlated between species. Indeed, Fagerström³⁷ claimed that no interspecific differences at all are required, i.e. that identical species can coexist, provided the system is of finite size and spatially heterogeneous. This result was later challenged by Chesson³⁸. Whatever the outcome of this controversy will be, it has limited practical importance since no one has seriously argued that any two species in nature are identical. The qualitatively important result – on which there appears to be general agreement – is the robust finding that if (1) recruitment rates of different species are temporally variable, and (2) these variations are at least to some extent asynchronous, then coexistence of arbitrarily similar species is permitted.

The fact that competition in plants is a neighbourhood phenomenon, rather than a Lotka–Volterra type of global interaction, may slow down the route to equilibrium also in the absence of any changes in the abiotic environment. Even if the outcomes of two-species interactions are predictable, each species may encounter and compete with different species combinations in different places^{5,35}. Clumped distributions are commonplace, and species aggregation may reduce rates of competitive exclusion³⁹.

A distinction has often been made between equilibrium and non-equilibrium coexistence. The former situation is assumed to involve cases where species coexist at fixed population densities, whereas the latter covers cases where exclusion is prevented by environmental changes or disturbances. Problems arise with this terminology, however, because stochastic population and community theories – such as lottery models – do not have the point equilibria which are characteristic of classical (deterministic) theories. Thus, when we say that a lottery model predicts indefinite coexistence, we do not imply that species abundances remain constant over time. Instead, they fluctuate continuously and coexistence prevails because

(1) the mean and variances of abundances do not change with time (in the terminology of stochastic theory, the system is stationary), and (2) an advantage is conferred to a species when it happens to become rare (the invasibility criterion³⁸).

A more lucid terminology would be to define a non-equilibrium mechanism as one which depends on there being fluctuations in the community (regardless of whether we invoke the mechanism to explain coexistence, succession or whatever), and an equilibrium mechanism as one which is not dependent on fluctuations^{37,40}. By this terminology, lottery models and the gradual change hypothesis are examples of non-equilibrium theories, but they can still be used to analyse conditions for coexistence^{33,36,40} as well as for succession generated by competitive exclusion^{37,41}. These mechanisms are sometimes, but not always, scale-dependent. Disturbances, such as storm gaps in forests, may kill the competitive dominants in patches of the size of square metres and create (non-equilibrium) conditions for ruderal species, but the whole forest may still be in an overall equilibrium regarding species composition and relative abundances.

An observation on species turnover in plant communities that is difficult to reconcile with several of the niche-differentiation models has been presented by van der Maarel and Sykes⁴². In short-turf, species-rich limestone vegetation on the island Öland in the Baltic Sea they observed that while species richness was relatively constant over time, species composition was not. Some species disappeared and others colonized, so that the average cumulative richness in 0.01 m² plots increased from 16.3 to 24.1 over six years. The authors conclude that most species would occur in any plot within a short time, and they introduce the 'carousel model' as a metaphor for this scenario. It was earlier described as 'drifting clouds of abundance'²⁴. This open limestone community is dominated by short-lived species which seem to have very similar habitat niches, and local disturbances that prevent competitive equilibrium to be reached are important. It would be interesting to know the extent of species mobility in vegetation types where species are long-lived and seed regeneration is less common.

Conclusions

The most important steps forward in understanding plant competition concerns the recognition of mechanisms, most notably the distinction between competitive effect and response. Further research in this area will be rewarding, but the emphasis should be put on long-term experiments and on analyses of statistical interactions (see Table 1). The finding that positive interactions are common is likely to change our views on how plant communities are structured.

As for species coexistence, most models discuss the maintenance of diversity, but we have highlighted hypotheses on the creation of diversity, and emphasized the consideration of spatial and temporal scales. The within-community mechanisms for coexistence are not mutually exclusive; it seems plausible that species coexist (or exclusion is prevented) for different reasons even within a community. We advocate studies that would reveal the relative importance of different mechanisms.

Acknowledgements

Peter Chesson, Lena Gustafsson and Eddy van der Maarel commented on the manuscript. We have been supported by the Swedish Natural Science Research Council.

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