

Competitive Hierarchies and Centrifugal Organization in Plant Communities

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I. Introduction

A. Choosing Research Goals

If we are going to study plant competition, we need to have some long-term research objectives. Otherwise, with at least a quarter of a million species of angiosperms on this planet, and a vastly larger number of possible interactions among them, our discipline could turn into simply a collection of special cases. Choosing long-term goals and the right questions is simultaneously the most important and most subjective part of scientific research programs (Keddy, 1989). Perhaps this is the reason why long-term goals are often neither explicitly stated nor extensively discussed. The long-term objective I propose is as follows: To be able to predict measurable aspects of competition and their effects on populations and communities from a knowledge of environmental conditions and the traits of the species involved.

I propose this goal for three main reasons:

1. It indicates the measurable state variables which will comprise a body of theory (e.g., Lewontin, 1974; Rigler, 1982; Keddy, 1987). These include state variables describing both mechanism (e.g., competition intensity, degree of asymmetry) and pattern (e.g., biomass, species richness, life form).
2. It emphasizes prediction as an essential element of understanding (Peters, 1980a,b; Rigler, 1982).
3. Such objectives, if met, would allow plant ecologists to make useful contributions to the three goals of the World Conservation Strategy (International Union for the Conservation of Nature and Natural Resources, 1980).

Other goals, are of course, possible. This particular goal has two basic assumptions about motivation for research. First, I assume that we have an interest in building theory (Austin, 1986). Second, I assume that the research and theory should apply in some way to real problems of living organisms, which is why I included reference to the World Conservation Strategy. Whether these assumptions are justified is open to discussion. One could argue that other motivations are both possible and reasonable. They could include visiting exotic locales, appreciating natural beauty, building one's reputation, keeping one's job, providing entertainment, filling in time, and so on.

One way of approaching the above goal would be to divide it into two components: The first would be "assembly rules" for plant communities. Although some of Diamond's (1975) methods have been justifiably criticized (e.g., Connor and Simberloff, 1979; Weins, 1983), the objective of producing rigorous rules for community assembly is still useful. A sec-

ond related goal would be to develop "response rules" to predict accurately changes in plant communities after specified perturbations (e.g., Nobel and Slatyer, 1980; van der Valk, 1981). I have discussed these objectives in more detail elsewhere (Keddy, 1989). In this chapter, I cover three topics: (1) The obstacles to general theory, and some possible antidotes to these obstacles. (2) Some general rules about plant competition which we already possess. (3) The implications of these general rules for the way in which wetland plant communities (and perhaps other plant communities) are organized.

B. Obstacles to the Development of Theory

I assume that the objective of science is the detection, testing, and refinement of general principles. This is not a new idea in plant ecology. Tansley (1914) stated in his Presidential address to the British Ecological Society that "Quantitative results are of no use . . . unless they have some kind of general validity." The large number of species and environments makes the search for generality essential. Suppose we make two simplifying assumptions: (1) that communities can be reconstructed from pairwise interactions, and (2) that these interactions do not change with changing environments (including herbivores and mycorrhizae). The number of interactions we need to study is then simply $\binom{S}{2}$ where S is the number of species in the pool. In wetlands near Ottawa we can easily locate 160 species, which would require $\binom{160}{2} = 12,720$ comparisons. Wilson and Keddy (1986a) explored $\binom{5}{2} = 21$ comparisons in 1 year. At this rate, it would take approximately 600 years to run the necessary experiments to characterize interactions in one comparatively small region of the planet, and Colinvaux (1986) estimates there are more than 250,000 angiosperms on the planet. Rigler (1982) and Wimsatt (1982) provide two similar illustrations. There are, of course, many other obstacles to the development of rigorous competition theory, as I have discussed elsewhere (Keddy, 1989). The obsession with collecting special cases, whether multivariate descriptions of site x or autecological studies of species y , is, however, probably the greatest obstacle faced by plant ecology.

C. A Path to General Theory (Antidotes to the Obstacles)

How do we search for general principles? We could still try to justify collecting observations of special cases. We could optimistically assume that if we patiently record enough such observations, generalizations will eventually emerge through induction. This is, however, more a statement of faith than a demonstrable fact. While we may count on later scientists to carry out reviews such as those of Schoener (1983) and Connell (1983) and put together the pieces, the least damning criticism

of this approach is its inefficiency. Clement's pioneering work (e.g., Clements *et al.*, 1929) showed countless examples of competition; in 1933 he attempted syntheses of his own experiments noting that, in general, "the taller grasses enjoyed a decisive advantage over the shorter." Yet 50 years later, we are still adding up the examples.

We could take a more visionary approach by designing our work to detect trends and test principles right now. Instead of emphasizing differences, we could pay more attention to similarities. Once we find similarities and make predictions using them, we can concentrate on improving our predictions by exploring the deviations from the general principles. The context of theory would then guide the selection of critical case studies. Peters (1980a,b) has elaborated on these arguments and argued in favor of "predictive ecology."

There are several tools which now exist to allow us to pose important general questions here and now (Keddy, 1989). I briefly consider four here.

1. Using Gradients in Comparative Studies Instead of studying allegedly homogeneous patches of vegetation, we could seek out natural environmental gradients. These gradients provide opportunities for "comparative studies" (*sensu* Keddy, 1989) or "natural experiments" (*sensu* Diamond, 1983) where vegetation characteristics, plant traits, and species composition all covary. By comparing such variables across a range of vegetation types, we can test for general patterns and detect exceptions from them.

2. Empiricism There is still little agreement about the choice and measurement of state variables for describing plants and plant communities. As a consequence, plant ecologists have pursued sterile debates such as the community unit–continuum controversy. Such controversies are unresolvable precisely because they are stated and debated in unfalsifiable form with nonoperational state variables (Shipley and Keddy, 1987). Proper choice of measurable state variables is one step toward rigorous theory (Lewontin, 1974; Peters, 1980a; Rigler, 1982; Keddy, 1987, 1989), as is illustrated by the clear relationships between α diversity and biomass (e.g., Grime, 1973, 1979; Al-Mufti *et al.*, 1977; Silvertown, 1980; Tilman, 1982; Morre *et al.*, 1989; Wisheu and Keddy, 1989a).

3. Plant Traits Instead of using species nomenclature, we could build our theories on plant traits. One may not be able to generalize from the ecology of *Sabatia kennedyana* in the Tusket River valley, Nova Scotia (Keddy, 1985) to other situations. One may, however, be able to draw generalizations about the distribution of evergreen rosette species on shorelines (e.g., Keddy, 1983; Boston and Adams, 1987; Day *et al.*, 1988;

Wisheu and Keddy, 1989a) or, even more importantly, evergreen species in general (Grime, 1977; Chapin, 1980). The importance of theory built on plant traits is increasingly accepted (e.g., Grime, 1974, 1979; Box, 1981; Rorison *et al.*, 1987; Gaudet and Keddy, 1988; Tilman, 1988; Keddy, 1989). Rereading Clements *et al.* (1929) or du Rietz (1931) shows that this is hardly a new idea, yet theories built on plant traits have been slow to arise.

4. Nested Hierarchies of Models We can recognize that general models need more specific models nested within them, and explore our data using a continuum of models from the site-specific to the most general. For example, Grime's (1973, 1974, 1979) theories about plant strategies were criticized by Grubb (1985) as being incorrect, but a re-reading of Grubb's paper will show that, instead of a criticism of Grime, it could have been presented positively as the need for and an enumeration of some system-specific submodels. Table 1 illustrates this concept by presenting one possible hierarchical organization of ecological models describing plant communities in wetlands.

Table 1 One Possible Nested Hierarchy of Models for Plant Communities, Ranging from General (Top) to Most Specific (Bottom)^a

Level of Organization	Gradients	Plants
State variables	Biomass Species richness	Traits (e.g., growth rate, height)
General process and pattern	Fertility (stress, adversity) ← Disturbance	Functional groups, strategies (e.g., ruderals, stress tolerators)
Vegetation type (riverine wetlands)	Loss on ignition ← Ice damage Soil nutrients ← Wave damage	Wetland functional groups (e.g., annuals, reeds, isoetids)
Region (Ottawa River Valley)	DCA axes 1 and 2	Species nomenclature (e.g., <i>Phalaris arundinacea</i> , <i>Eriocaulon septangulare</i>)
Site (Westmeath)	Points in DCA space	Species nomenclature (e.g., <i>Phalaris arundinacea</i> , <i>Eriocaulon septangulare</i>)

^a A majority of work occurs at the very lowest levels. The concrete examples come from riverine wetlands (Day *et al.*, 1988; Shipley *et al.*, 1989).

II. Evidence for Predictable Patterns in Plant Competition

Are there general principles about plant competition which would take us in the direction of the goal stated above? In this section, I review some of the experimental data showing that competition varies in a predictable manner in plant communities. I then explore two sets of consequences for the organization of plant communities. The first set of consequences are some questions these data raise about the generality and significance of competitive hierarchies. The second consequence is the implications of such data for larger scale patterns of plant community organization along competition gradients. This yields a model of "centrifugal organization" which predicts changes in life form, α diversity, and species pools along biomass gradients.

A. Competition Intensity

Competition intensity can be defined as the combined (negative) effects of all neighbors on the performance of an individual or population (Keddy, 1989). The reason for measuring competition intensity is that an individual plant experiences the negative effects of all neighbors simultaneously; pairwise designs measuring each interspecific interaction separately measure something very different. Competition intensity can be measured by comparing the performance of plants in cleared plots with the performance of those surrounded by neighbors. One could either introduce phytometers (*sensu* Clements, 1935) into cleared and uncleared plots or else remove all plants but one from the cleared plots.

Wilson and Keddy (1986b) used this design to test whether competition intensity varied along a natural environmental gradient. Given the many species in the vegetation, they assumed, but did not test, that they had measured diffuse competition, the effects of many species combined. Individuals of three different plant species ("phytometers") were exposed to both above- and below-ground competition along a standing crop gradient. In some plots, phytometers were planted in pots containing intact cores of soil and plants which were inserted into established vegetation; in other plots, both pots and surrounding vegetation were weeded regularly so that above- and below-ground competition was minimized. Three general results emerged (Fig. 1). (1) Competition varied from one site to the next. (2) The intensity of competition increased with standing crop. (3) The intensity of competition increased with soil organic content. Therefore, not only did competition intensity change from site to site, but it was predictable from both biotic and abiotic factors. This competition bioassay is probably the most direct approach to asking questions about the predictable variation in competition intensity in nature.

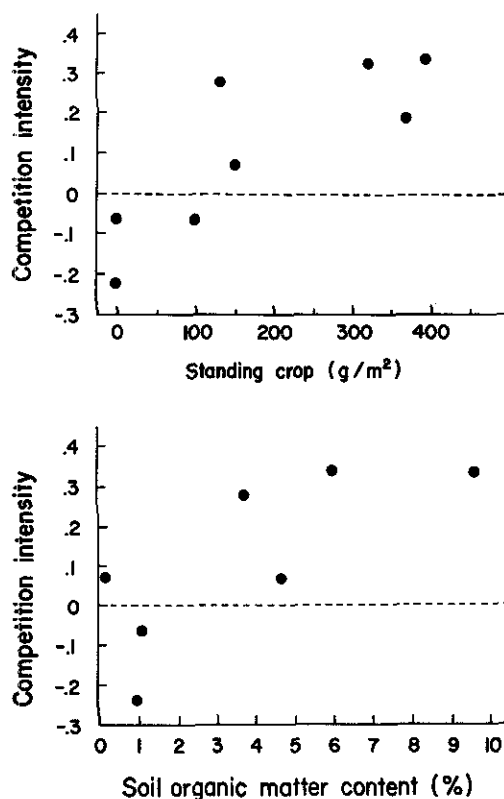


Figure 1 Competition intensity plotted against standing crop (top) and soil organic matter content (bottom) on lake shores. Competition intensity was measured as the total effects of neighbors on three species of phytometer. From Keddy (1989); data from Wilson and Keddy (1986b).

B. Asymmetric Competition

There is a tendency among ecologists to compare competition within pairs of species that are very similar (e.g., Harper and Chancellor, 1959; Harper *et al.*, 1961; Harper and McNaughton, 1962; Harper and Clatworthy, 1963; Werner, 1979). In fact, similarity in size is an important assumption of the replacement series design (de Wit, 1960; Harper, 1977) to ensure that density and biomass are not confounded. There is consequently a tendency to assume that competitive interactions between species in general are symmetric (Keddy, 1989), that is, that each species is more or less capable of suppressing the growth of the other. In nature, however, plant communities may be made up of species having very different morphologies and life histories. Are interactions symmetric in such cases?

To explore this, we need a measure of asymmetry. Let Y_{ii} be the yield of an average individual of species i grown in monoculture, and Y_{ij} be the yield of an average individual of species i when grown in mixture with species j . Further, let $RYP_{ij} = Y_{ij}/Y_{ii}$. Pairwise asymmetric competition can be said to exist when $RYP_{ij} > 1$ and $RYP_{ji} < 1$. That is, species i grows better in mixture with species j but species j grows worse in mixture with species i . Therefore species i should eventually exclude species j .

Keddy and Shipley (1989) used this definition to examine asymmetry in eight published competition studies including species from sea cliffs, lake shores, and chalk grassland. In seven of the eight examples, the matrices were dominated by asymmetric interactions, that is, in pairwise interactions there was consistently a winner and loser. The sole exception was the study by Harper (1965) of competition among different varieties of the same species. This exception is entirely consistent with the prediction that the degree of asymmetry in competitive interactions is lowest when species are nearly identical. But few real plant communities consist of nearly identical species, suggesting that asymmetric interactions are the exception rather than the rule. I have agreed elsewhere that this has important implications for studies of coexistence and the competitive exclusion principle (Keddy, 1989).

C. Competitive Hierarchies

The usual way of approaching the organization of plant communities is to explore pairwise interactions by growing (or removing) component species in all possible pairwise combinations. While the replacement series (de Wit, 1960; Harper, 1977) is the most widely used design, it is not the only one possible. However, this is the design which has been used in many recent studies of natural communities, including sea-cliff vegetation (Goldsmith, 1978), lakeshore vegetation (Wilson and Keddy, 1986a), and chalk grassland (Mitchley and Grubb, 1986). What evidence of community structure or effects of competition can be extracted from such matrices? Keddy and Shipley (1989) have proposed a quantitative measure of transitivity for exploring such matrices, and have found a highly significant pattern of transitive community structure in seven of eight published matrices. That is, in most cases, there was a significant tendency for plant communities to be organized in a competitive hierarchies. Again, the single exception was not a plant community, but intraspecific interactions among genotypes of a single species (Harper, 1965; Keddy and Shipley, 1989).

Of course, all pot experiments are subject to the criticism of any laboratory experiment: that the results cannot be extrapolated to real plant communities. One way out of this difficulty is to test whether predictions from the laboratory are consistent with patterns in the field. Wilson and

Keddy (1986a) found that position in the competitive hierarchy was correlated with field distributions along lakeshore exposure gradients, and that the field distributions were consistent across many study sites. Similarly, Mitchley and Grubb (1986) found that the position in the competitive hierarchy was positively correlated with abundance of species in chalk grassland, and that these patterns of abundance were consistent across many study sites. Goldsmith (1978) did not perform any statistical tests, but similarly observed that the competitive dominants in his pot experiments tended to occupy least exposed sites with lower salinities.

D. Traits Conferring Competitive Ability

If plant communities tend to be organized in competitive hierarchies, and if there are competition intensity gradients, we may well ask about plant traits associated with positions higher in the competitive hierarchy, or equally, about plant traits associated with habitats having higher competition intensity. There are two ways to explore this: to review the literature, or to design experiments specifically to test for empirical relationships. Consider these approaches in turn. Clements (1933) summarized the results of hundreds of transplant and removal experiments in prairie vegetation (e.g., Clements *et al.*, 1929) and concluded that, in general, "the taller grasses enjoyed a decisive advantage over the shorter." Goldsmith (1978) studied sea-cliff plants and showed that the larger species suppressed the smaller (Fig. 2). Wilson and Keddy (1986b) experimentally derived a competitive hierarchy for seven shoreline species. The dominant was a tall species whereas the subordinate was a small rosette species. Keddy and Shipley (1989) reanalyzed the Wilson and Keddy data and showed that more than one-third of the competitive ability of these species in mixture could be predicted from knowledge of their heights ($r^2 = 0.37$). Similarly, in the chalk grassland study, Mitchley and Grubb (1986) derived a dominance hierarchy for six plant species and found a significant correlation between position in the hierarchy and mean turf height in monocultures; Mitchley and Grubb noted that "the plants with the tallest leaves were the most effective in interference." Mitchley (1988) has since shown that there is a positive correlation between the height of grassland species and their relative abundance. Givnish (1982) has presented a general model for the evolution of leaf height in herbaceous plants that are competing for access to light.

Since diallele designs increase in size by the square of the number of species examined, there are obvious upper limits on the number of species which can be studied to relate traits to competitive ability. To overcome this problem, Gaudet and Keddy (1988) used a modified additive design to measure competitive ability of 44 wetland plant species. Each

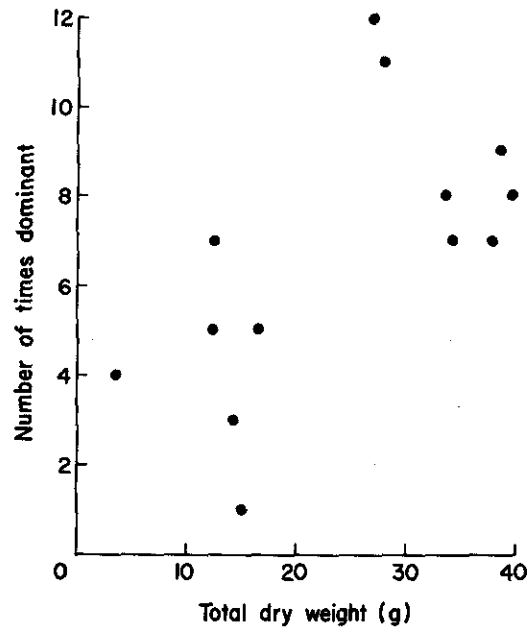


Figure 2 Position in competitive hierarchy (measured as number of times dominant in mixture) plotted against plant size in pure stand for sea-cliff plants. From Keddy (1989); data from Goldsmith (1978); $r = 0.61$, $p < 0.05$.

species was grown with a phytometer (*Lythrum salicaria*), and competitive ability measured as the ability to suppress this phytometer (competitive effect sensu Goldberg and Fleetwood, 1987; Goldberg, this volume). We showed that simple traits such as biomass, height, and canopy diameter could account for 74% of the measured competitive ability. Above-ground biomass was the best predictor ($r^2 = 0.62$). Height also was significant ($r^2 = 0.43$). A subset of the species was tested against a different phytometer and similar results were obtained. Figure 3 plots percent reduction in the phytometer biomass plotted against the above-ground biomass for 44 species.

E. A Possible Mechanism for the Above Patterns

The above evidence comes from patterns detected in experimental studies. Are such patterns consistent with our understanding of mechanisms by which pairs of plants interact? If two plants are growing close enough to one another to interact, the taller plant will not only have access to incoming light for its own growth, but it will simultaneously reduce the growth of the smaller plant by setting up a positive feedback loop where the larger plant continually improves its access to light and the smaller

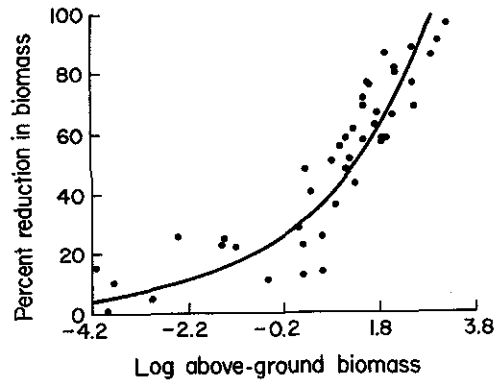


Figure 3 Screening for competitive ability across 44 plant species. Percent reduction in the biomass of a phytometer (*Lythrum salicaria*) when grown with each species of neighbor is plotted against mean above-ground biomass of the neighbors. [44 species, each point is the mean of $n = 5$ replicates, $y = \exp(3.34 + 0.44x)$, $r^2 = 0.69$.] Points on the left are small evergreen species while points on the right are from one large leafy species. The remaining 31% of variation includes both experimental error and the contribution of other plant traits. From Keddy (1989); data from Gaudet and Keddy (1988).

plant is increasingly denied access to it (Givnish, 1982; Keddy and Shipley, 1989).

This will in turn influence ability to forage for nutrients. Reduced access to light will reduce carbohydrates available for root growth, thereby reducing rates of nutrient uptake. It is therefore a mistake to treat roots and shoots as separate entities, since they are part of one physiologically integrated unit. Caldwell *et al.* (1987) illustrated this by showing that shading or defoliation can reduce root growth and mineral uptake within 24 hr.

The taller plant will therefore not only deny light to its shorter competitor, but will also reduce the ability of its neighbor to forage for nutrients. Simultaneously, the increased energy reserves of the larger plant should increase resources for root construction, which will increase the depletion zone of nutrients around the larger plants. The result is that the smaller individual will likely be trapped in an asymmetric interaction in which positive feedback loops operating above and below ground are confining it within light and nutrient depletion zones created by the larger plant. A situation like this has been studied using the vine *Ipomea tricolor*, where above- and below-ground competition can be neatly separated. Weiner (1986) has shown that when above- and below-ground effects are separated, above-ground interactions (competition for light) are asymmetric, whereas below-ground effects (competition for nutrients) are symmetric. When above- and below-ground effects occur, interactions are again asymmetric.

An alternative approach which arrives at the same conclusion begins with a consideration of the characteristics of two classes of resources: light and nutrients. There is a fundamental distinction between them. Nutrient gradients can occur in the absence of neighbors since soil fertility varies along natural environmental gradients. In contrast, light gradients are almost invariably produced by the presence of neighbors. Species responses to gradients in soil fertility might therefore be considered part of their fundamental niches, whereas species responses to light gradients may be a part of their realized niches. This difference would generate a situation where species' field distributions along fertility gradients could be determined at one end by their fundamental niche (physiological tolerance limits) and at the other end by their realized niche (ecological tolerance limits determined by ability to compete for light). That is, ability to tolerate low fertility may produce a special "physiological response curve," whereas ability to forage for light or tolerate low light may produce a species' "ecological response curve." Inclusive fundamental niche structure (*sensu* Miller, 1967; Colwell and Fuentes, 1975) for nutrients combined with a hierarchy of abilities to compete for light could produce the dominance hierarchies described above, as well as the zonation patterns observed along natural environmental gradients. I have called this the "competitive hierarchy model," and have contrasted it with traditional resource partitioning models elsewhere (Keddy, 1989).

F. New Questions

The above examples illustrate the insights into plant communities which can be gained by looking for experimental designs that avoid traditional pairwise approaches, by explicitly considering plant traits, and by testing for patterns using operationally defined state variables. The potential for such approaches has barely been explored, and many new questions can be raised. These include the following.

1. Are competition intensity gradients found in most vegetation types? If so, what environmental variables and plant traits are correlated with competition intensity gradients?
2. Are competitive hierarchies a general feature of plant communities?
3. For a given plant community, are hierarchies invariant across the range of environmental conditions occupied by that community?
4. What plant traits predict positions in competitive hierarchies?
5. Do the traits conferring competitive ability vary among vegetation types?

The approaches for answering some of these questions are straightforward. Question 3 poses some more difficult issues, so I will briefly ex-

pand on it below. Two kinds of experiments are possible to answer this question. Let us consider them in turn.

G. Constraints on Competitive Hierarchies

1. Pairs of Species along Gradients One approach would be to take a pair of species and allow them to interact along an environmental gradient. If we measured the performance of each species in mixture relative to pure stand, we could ask whether or not competitive outcome varied with environment. There are some difficulties with this approach. The design incorporates only two species. Communities are made up of large numbers of interacting species, and there is no reason why a pair of species selected ad hoc will necessarily provide inferences about the community as a whole.

There are also significant problems in the interpretation of such experiments. One good example illustrating the difficulty in testing for reversals in competitive ability comes from Goldsmith (1973). The experiment involved a small rosette species found in saline habitats (*Armeria maritima*) and a rapidly spreading, taller perennial grass (*Festuca rubra*) found in less saline habitats. Goldsmith grew them in a replacement series design, with two replicates receiving fresh water and two receiving salt water (Fig. 4). Reference to the pure stands shows that both species

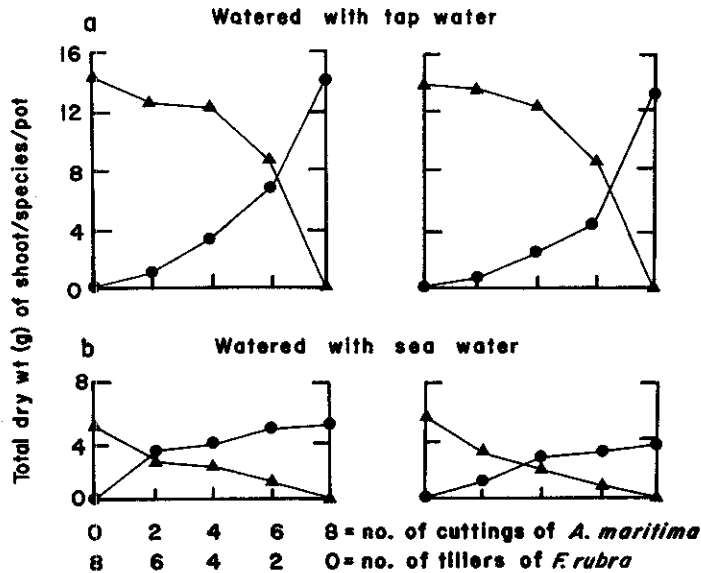


Figure 4 The interaction between *Festuca rubra* and *Armeria maritima* grown for 1 year in a replacement series watered with tap water (a) and sea water (b). Both replicates are shown. After Goldsmith (1973).

showed dramatic declines in performance at high salinity. Comparison of the degree to which the lines deviated from linearity reveals that with fresh water (Fig. 4a) interspecific competition was more intense than with salt water (Fig. 4b). *Festuca rubra* was clearly the competitive dominant with fresh water. The key question is whether *Armeria maritima* became a better competitor under saline conditions, or was simply better able to tolerate the saline conditions. It appears from inspection that *Armeria* shows little ability to suppress *Festuca* at high salinities (as judged by the weak skewing of the *Festuca* line at high salinity).

Let us assume that in fact *Festuca* was significantly suppressed by *Armeria* at high salinities. Two facts remain. *Festuca* shows more than a 50% reduction in performance in this environment in the absence of competition (pure stand); the added reduction (if any) due to competition is very small by comparison. The salinity reduced *Festuca*'s performance far more than competition. Therefore, on one hand we might argue that a reversal took place. On the other hand, the pure stands show that these species have inclusive niches, and that interspecific competition was more intense in the more productive environment.

2. Diallele Experiments An alternative approach to choosing a pair of species would be to examine the structure of community matrices in large diallele experiments. Two questions could be asked: (1) Do transitivity and asymmetry vary among experiments? (2) Does the rank order of species in the hierarchy vary among experiments? The measures proposed by Keddy and Shipley (1989) provide the means to test these hypotheses, but practical constraints are the main problem.

Experiments examining many pairwise interactions increase in size as the square of the number of species considered. Thus, practical problems of research budgets and space may discourage people from creating diallele designs in different environments. Presumably, this is why studies such as those of Goldsmith (1978), Wilson and Keddy (1986a), and Mitchley and Grubb (1986) have all looked at only one environment.

The largest test to date was done by Fowler (1982), who looked at hierarchies among four weedy species in a North Carolina grassland. Let us look at her results in some detail. First, consider the constraints. Only four species were used. Second, the species were all small herbaceous species (weights in pure stand: *Anthoxanthum odoratum* 5.98, *Plantago lanceolata* 5.84, *Poa pratensis* 3.73, *Rumex acetosella* 5.22 g/pot in watered and fertilized treatments). Fowler created dry, unfertilized, and dry and unfertilized treatments in addition to moist and fertilized treatments, and explored variation in hierarchical organization. Given the initial similarity of the species, this is a strong test for invariance because these are precisely the conditions where asymmetry would be expected to be

small, and therefore variance in the hierarchy might be expected. Nonetheless, Fowler found remarkably invariant ordering: in all environments *Anthoxanthum* was competitively dominant to *Poa* and *Rumex*. *Rumex* and *Poa* were the two species lowest in the hierarchy (as predicted from pure stand biomass) and for these species outcome was dependent on environment. Fowler's data support the contention that hierarchies are relatively invariant.

3. Relationship to Real Communities Two aspects of experiments need to be considered here: the environmental conditions used, and the similarity of the species, since the outcome of a particular experiment and its applicability to real communities will likely depend on both.

First, consider the environmental conditions. Experiments enable us to create environments which may be rare or absent in natural systems. If we observe changes in competitive hierarchies in experiments, this may or may not be relevant to real communities. The question is therefore not whether (or where) hierarchies can reverse in theory, but whether reversals occur within the range of conditions actually found in real communities. If, following the Goldsmith (1973) example, reversals occurred only at salinity levels higher than those normally found in the field, the pot experiment would not necessarily tell us anything about real sea-cliff vegetation. If, in general, reversals occur only at very low fertilities where plants have very low growth rates, normal levels of natural disturbance could eliminate both species from real communities. This could have major consequences for field distributions, but is something we would not detect in experiments where biomass removal (loss rates) is kept to a minimum. In the studies by both Goldsmith (1973) and by Fowler (1982), we could ask how much the results would have differed if different treatments had been used.

Second, natural plant communities contain a wide array of plant morphologies, but given the current paradigms (*sensu* Kuhn, 1970) of plant ecology, the choice of species is not likely to represent this reality. There is an overwhelming tendency to select pairs of "similar" species, often congeners, for competition experiments. Such similar pairs of species are exactly those where asymmetry and hierarchies may be least important, and therefore where switches in competitive ability are most likely (Keddy, 1989). Switches in competitive ability among very similar species may tell us little about hierarchical organization among very different species. Such studies will therefore need to include objective means for testing how similar the pairs of species are (Green, 1980; Legendre and Legendre, 1983; Keddy, 1989).

4. A Potential Reconciliation Dichotomies are part of our Western intellectual heritage, but undoubtedly there are cases where the search

for a synthesis is more appropriate than struggling for a yes/no answer. As Dayton (1979) observed, "Many of my own hypotheses were carefully designed to force yes or no answers from nature when, in fact, nature may have been crying out *mu*. . . ." "Mu" is the only response possible when both yes and no are wrong (Watts, 1958).

Competitive hierarchies may be the rule along gradients of resource quantity, or where one environmental factor alone is of overwhelming importance. In wetlands, for example, major soil nutrients are often correlated along gradients from sand beaches to organic bays (Wilson and Keddy, 1985, 1986a,b); this would be a gradient of nutrient availability (see Chapin *et al.*, 1986). On sea cliffs, salinity is the major factor controlling plant community structure (Goldsmith, 1973, 1978). In contrast, resource partitioning may occur along gradients of resource quality. If soil nutrients levels are relatively constant, ratios of two resources may be opportunities for species to partition resources along a ratio gradient (Tilman, 1982). The critical question may turn out to be, How many communities are organized along each kind of gradient? Critical tests will be necessary to resolve such points.

III. Large-Scale Patterns and Long-Term Goals

A. Patterns in Wetland Vegetation

At this point it is important to return to our long-term objectives. If we lose sight of clear goals, it is easy to be side-tracked into collecting natural historical detail (Peters, 1980a) or distracted by unresolvable arguments about untestable concepts (Shiple and Keddy, 1987). As stated in the Introduction, I think our long-term goals should be nested models which allow us to make quantitative predictions about the structure of plant communities and their responses to perturbations. As well as doing intellectually satisfying science we should be able to say something useful about global environmental problems. Unfortunately, our intellectual training is usually to dissect our problems into smaller and smaller sub-problems. The regrettable result can be a loss of perspective—with negative consequences for development of general theory and for our own biosphere. I therefore deliberately end this chapter not by listing a series of more precise questions which need to be addressed (see the list in Section II,F), but instead by considering how the empirical relationships reviewed here suggest a general community model with both theoretical and applied relevance.

Let us return to the search for general principles. There is good evidence that plant communities are structured by competitive hierarchies.

There is also evidence that competition is most intense in high-biomass sites and that such sites are occupied by plants occurring at the top of hierarchies. These general patterns are consistent with natural patterns in wetland vegetation. Fertile undisturbed sites are usually dominated by *Typha* spp.; *Phragmites communis*, *Phalaris arundinacea*, *Calamagrostis canadensis*, or *Carex* spp. can also form dense, nearly monospecific stands. These species all share certain traits: height and clonal spread. These traits are recognized in other published studies as traits which allow plant species to dominate communities (Grime, 1973, 1979; van der Valk, 1981; Givnish, 1982; Day *et al.*, 1988; Gaudet and Keddy, 1988; Shipley *et al.*, 1989).

The remarkable morphological convergence suggests only one type of morphology is appropriate to fertile undisturbed sites with high biomass. This occurs at ecological time scales (competitive exclusion) and evolutionary time scales (selection for size). In contrast, a vast array of life forms and morphologies is found in disturbed and/or infertile sites: annuals (van der Valk, 1981; Keddy and Reznicek, 1986), isoetids (Boston, 1986; Boston and Adams, 1987; Wisheu and Keddy, 1989b; Day *et al.*, 1988; Moore *et al.*, 1989), and carnivorous plants (Keddy, 1983; Wisheu and Keddy, 1989a,b). Thus, once the constraints of intense competition are released, a wide array of life forms apparently becomes possible. Table 2 lists, for a few representative sites, the morphological and ecological diversity of plants in wetlands that are infertile or exposed to damage from waves and flowing water.

Figures 5 and 6 attempt both to portray these patterns in wetlands accurately and express them in a testable form. The variation in life form types has already been discussed, but Fig. 6 emphasizes that increasing biomass may produce changes in other state variables such as the total species pool, α diversity, and number of vegetation types. Although the species pool may decrease with increasing biomass, α diversity has different patterns. Grime (1973) proposed that species density (α diversity) reaches a maximum at intermediate levels of community biomass. It is important to recognize the distinction between the total species pool and α diversity. The latter has received most emphasis in conservation management (e.g., Grime, 1973), but when planning nature reserve *systems* to maintain biodiversity, it is the species pool which is most important. Since the number of kinds of vegetation and species increases with decreasing biomass, any reserve system representing wetlands must include this array of low-biomass environments. Moore *et al.* (1989) have recently explored one part of this model by testing whether there was a negative relationship between the number of nationally rare plant species on wetlands and standing crop. They found that nationally rare species occurred only in peripheral habitats (less than 500 gm⁻²).

Table 2 Variation in Life Form and Life History Type in Five Wetlands with Low Standing Crop^a

Low Standing Crop Areas	Annual Species	Reeds ^b	Isoetids ^c	Insectivorous Species ^d
Nova Scotia Gillfillan Lake ^e (n = 114)	<i>Eleocharis smallii</i>		<i>Eleocharis acicularis</i>	<i>Drosera intermedia</i>
	<i>Eleocharis tenuis</i>		<i>Eriocaulon septangulare</i>	<i>Drosera rotundifolia</i>
	<i>Equisetum arvense</i>		<i>Gratiola aurea</i>	<i>Sarracenia purpurea</i>
	<i>Equisetum fluviatile</i>		<i>Isoetes acadensis</i>	<i>Utricularia cornuta</i>
	<i>Juncus filiformis</i>		<i>Juncus pelocarpus</i>	<i>Utricularia geminiscapa</i>
			<i>Lobelia dortmanna</i>	<i>Utricularia subulata</i>
			<i>Lycopodium inundatum*</i>	<i>Utricularia vulgaris</i>
			<i>Ranunculus reptans</i>	
			<i>Sabatia kennedyana</i>	
			<i>Xyris difformis*</i>	
Wilson's Lake/ (n = 67)	<i>Elatine minima</i>		<i>Eleocharis acicularis</i>	<i>Drosera intermedia</i>
			<i>Eriocaulon septangulare</i>	<i>Drosera rotundifolia*</i>
			<i>Isoetes tuckermanni</i>	<i>Utricularia cornuta</i>
			<i>Juncus pelocarpus</i>	<i>Utricularia purpurea*</i>
			<i>Lobelia dortmanna</i>	<i>Utricularia resupinata</i>
			<i>Lycopodium inundatum*</i>	<i>Utricularia vulgaris*</i>
			<i>Myriophyllum tenellum</i>	
			<i>Ranunculus reptans</i>	
			<i>Sabatia kennedyana</i>	
			<i>Xyris difformis*</i>	
Ontario Axe Lake ^e (n = 65)	<i>Bidens sp.</i>		<i>Eriocaulon septangulare</i>	<i>Drosera intermedia</i>
			<i>Juncus pelocarpus</i>	<i>Drosera rotundifolia*</i>
			<i>Lobelia dortmanna</i>	<i>Utricularia cornuta</i>
			<i>Lycopodium inundatum*</i>	<i>Utricularia gibba</i>
			<i>Myriophyllum tenellum</i>	<i>Utricularia intermedia</i>
		<i>Xyris difformis*</i>	<i>Utricularia purpurea</i>	
				<i>Utricularia resupinata</i>
				<i>Utricularia vulgaris</i>

Ottawa River^a
(n = 55)

Eleocharis calva
Eleocharis smallii
Equisetum fluviatile
Scirpus acutus
Scirpus americanus

Eleocharis acicularis
Eriocaulon septangulare
Isoetes echinospora
Juncus pelocarpus
Myriophyllum tenellum
Potamogeton gramineus
Ranunculus reptans
Sagittaria graminea
Eleocharis acicularis
Eriocaulon septangulare
Juncus pelocarpus
Ranunculus reptans

Westmeathⁱ
(n = 75)

Bidens cernua
Bidens frondosa
Fimbristylis autumnalis
Gratiola neglecta
Impatiens capensis
Ludwigia palustris
Polygonum lapathifolium
Polygonum neglectum
Polygonum persicaria
Sporobolus vaginiflorus

Eleocharis elliptica
Eleocharis smallii
Equisetum fluviatile
Scirpus acutus
Scirpus americanus

*Drosera intermedia***
*Utricularia cornuta***
*Utricularia vulgaris***

^a All have uncommon vegetation types. Wetlands with high biomass are dominated by one life form, large leafy rhizomatous perennials (e.g., *Typha angustifolia*, *Phalaris arundinacea*, *Calamagrostis canadensis*).

^b As defined by Day *et al.* (1988); species with a single "leafless" aerial shoot.

^c From Table 1 in Boston and Adams (1987); * indicates two similar species I have added.

^d Species not in cited sources but * added from personal observations or ** added from unpublished report.

^e Unpublished data analyzed by Keddy (1984a,b).

^f From Wisheu (1987); see also Keddy (1985).

^g From Keddy (1981); see also Keddy (1983).

^h From Day *et al.* (1988).

ⁱ Unpublished data of C. Gaudet, D. Moore, and P. Keddy.

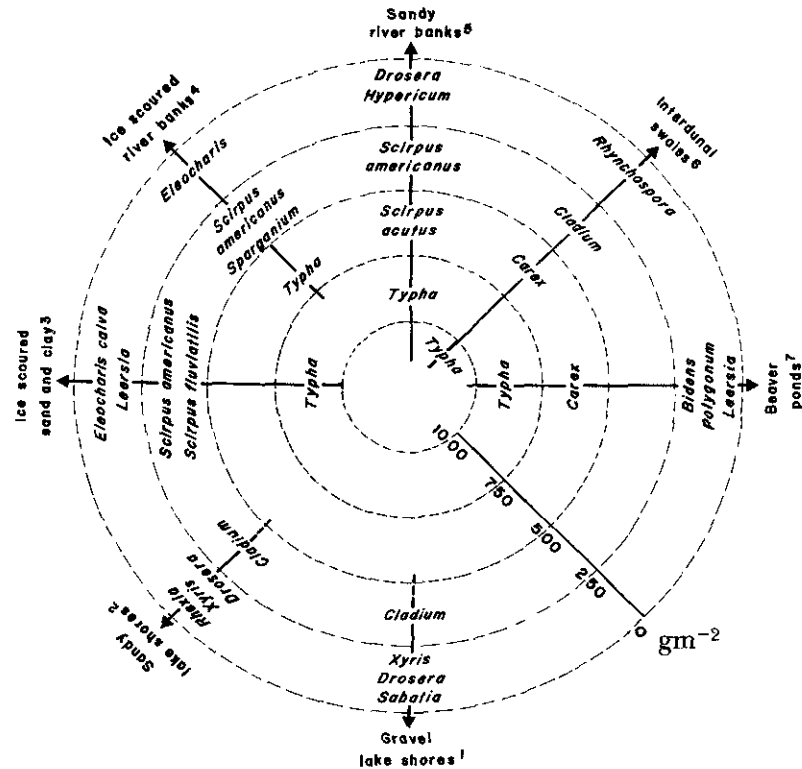


Figure 5 Community organization along biomass gradients in some wetlands. 1, Wilsons Lake (Wisheu and Keddy, 1989a,b); 2, Axe Lake (Keddy, 1981); 3, Luskville, Ottawa River (Moore *et al.*, 1989); 4, Ottawa River at four locations (Day *et al.*, 1988); 5, Westmeath, Ottawa River (Moore *et al.*, 1989); 6, Presqu'île Park, Lake Ontario (Moore *et al.*, 1989); 7, Beaver ponds, Lanark County, Ontario (P. A. Keddy, field observations). From Moore *et al.*, 1989, by permission of Elsevier, Applied Science Publishers, Ltd.

This model therefore integrates a number of state variables of interest to plant ecologists. It summarizes apparent general patterns in wetland vegetation. It has patterns of plant traits consistent with our current empirical understanding of competitive hierarchies and plant competitive ability. It makes testable predictions about how species pools and vegetation types should change along biomass gradients. It also predicts the negative effects for biodiversity which would result from eutrophication. And finally, it guides managers of natural areas regarding the priorities for selection of sites for a comprehensive system of protected wetlands. It is therefore one preliminary attempt to provide some "assembly rules" and "response rules" for a plant community.

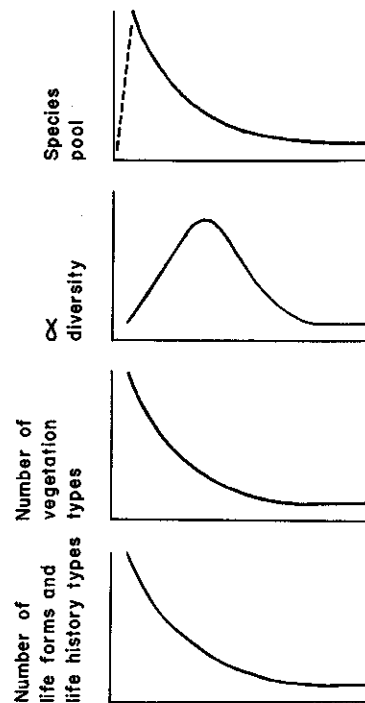


Figure 6 Predicted relationships between state variables of communities and landscapes as a function of biomass.

B. Centrifugal Community Organization in Wetlands

The graphical model in Figs. 5 and 6 appears consistent with the “centrifugal community organization” model proposed for desert rodents by Rosenzweig and Abramsky (1986). The essential element of their centrifugal organization model is that there is a central or core habitat which is preferred by all species, and a series of peripheral habitats with different species specialized upon each. Interspecific competition is therefore intense in this central habitat, but each species has a refugium from interspecific competition in its preferred peripheral habitat. The peripheral habitats therefore permit coexistence. The underlying mechanism is (1) that the species have shared preference (inclusive niche structure, sensu Colwell and Fuentes, 1975) and (2) that secondarily they have distinct preference for peripheral habitats.

This model appears to describe some aspects of the situation in wetlands. There is a central preferred habitat (high fertility, low disturbance) with species radiating out from it, each responding to different kinds of stress or disturbance. There is experimental evidence that these

species have shared preference for the central habitat (Wilson and Keddy, 1985) with competitive hierarchies excluding species different distances along radial axes (Wilson and Keddy, 1986a).

The application of this model to species-rich plant communities simultaneously suggests a number of possible extensions of and refinements to the centrifugal organization model.

1. In plant communities, it appears that a few species can dominate the central habitat without having refugia along another axis.
2. Rather than individual species radiating outward from a shared central habitat, entire niche axes radiate outward. Each axis appears to represent a different set of increasingly severe environmental constraints along which an entire group of species can be arrayed.
3. Rather than simple inclusive niche structure where all peripheral species prefer the central habitat, it may be that the end of the axis near the center has species with inclusive niche structure, but that species at the periphery tend toward distinct niche structure. In other words, as the environmental constraints become more severe at the margins, there is selection for distinct preference. In lake shores, there is evidence that stress tolerators, such as the evergreen rosette species *Lobelia dortmanna*, which occupy extremely infertile sandy shorelines, do not grow better in the central habitat (Wilson and Keddy, 1985, 1988).
4. There is the possibility of a niche structure that is neither shared nor distinct, but one sided. In such a case, species would have fundamental niches which overlap several adjacent species occurring toward the central habitat, but not toward the periphery. Competition would then displace such species down the axis toward the periphery; removal experiments would be predicted to show the possibility of competitive release in one direction but not the other ("competitive hierarchy model"; Keddy, 1989). The amount of competitive release toward the central habitat would then be predicted to be highest near the center (shared preference) and decrease through the middle of the axis (one-sided preference) to the margins (distinct preference).

Centrifugal organization is one possible model to provide assembly rules and response rules for communities. The degree to which one can generalize from the patterns and processes observed in wetlands is unclear, and can only be determined by testing for similar patterns and processes in other vegetation types.

IV. Summary

To illustrate the possibilities for general theory based on measurable state variables, I present evidence that some plant communities are orga-

nized along competition gradients with distribution and abundance controlled by asymmetric competition producing competitive hierarchies. The evidence comes from three sources. (1) A field experiment has tested for variation in competition intensity along an environmental gradient. (2) Published diallele experiments including sea cliff, grassland, and lakeshore vegetation have been analyzed to test for asymmetric competition and competitive hierarchies. (3) A comparative study using phytometers as a bioassay of competitive ability of 44 plant species has provided evidence of the direct relationship between plant size and competitive ability. These empirical relationships are probably a direct consequence of the fact that tall plants shade short plants but short plants cannot shade tall ones.

Two sets of consequences are explored. First, the presence of new state variables (e.g., competition intensity, transitivity) raises basic questions about general patterns of organization in plant communities. Some critical questions are suggested. Second, competition gradients and competitive hierarchies can produce large-scale patterns. An example is "centrifugal organization" in wetlands. In fertile undisturbed sites, a few large rhizomatous perennials dominate the vegetation. As fertility declines or disturbance increases, a much wider array of vegetation types radiates outward from the region dominated by clonal perennials. As biomass decreases, life form variation, the number of vegetation types, α diversity, and the total species pool change in a predictable manner.

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