

## 22 The Use of Functional as Opposed to Phylogenetic Systematics: A First Step in Predictive Community Ecology

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### I. Introduction

"That the plant-species may be classified not only according to their taxonomical relationship into genera, families etc., but also according to their types, has been clear to botanists ever since the childhood of botanical science".

du Rietz 1931

Plant classification could have two objectives: constructing groups with similar evolutionary histories in order to construct phylogenies, or constructing groups with similar ecological traits for predictive ecology. The former approach has had a major impact upon the historical development of ecology: many of the most high profile research questions in ecology can be traced back to the phylogenetic basis of species taxonomy. The objective of this paper is to argue for an increased emphasis upon the latter approach and to illustrate both some procedures and possible consequences for biosystematics and ecology. A re-direction of emphasis towards ecological classification could have a major impact upon the future development of ecology. I will offer a general research strategy for the latter approach, illustrate its application in the study of wetland plant communities, and then briefly discuss its broader implications for predictive ecology and the management of the biosphere.

### A. Two views of reality

To return to the dichotomy presented in the first paragraph, let us consider the two contrasting approaches to classifying plants. In one case we could emphasize traits that are conservative to allow us to postdict -- that is, to reconstruct the history of life on this planet. For whatever reasons, this has been the major emphasis of recent systematics. The alternative approach is to emphasize traits that have to do with function: nutrient uptake, competitive ability, stress tolerance, dispersal ability, etc, in order to classify species according to their function in ecological communities. There are two reasons why Kyoto is a particularly auspicious city in which to initiate discussion of this dichotomy and its consequences.

First, Kyoto is a city closely associated with the world's Zen Buddhist heritage. One of the axioms of buddhist psychology is that human beings become caught in habitual ways of interpreting reality, and begin to confuse these habitual views with reality itself. This bears directly upon the above point about biosystematics: there are two (at least) models for organizing biological classifications, but a majority of work has concentrated upon one view. While neither view is 'right', in that both are merely human thought systems imposed upon nature, each view may have intrinsic value.

Second, a recent international symposium in Kyoto (Kawano *et al.*, 1987) illustrated the logical endpoint of the phylogenetic, postdictive approach to biosystematics (Figure 1). The logic appears to go in the following manner. We begin with species classifications. One of the most dramatic results of enumerating the species composition of the biosphere is the discovery of the planet's biological diversity. This leads to the first major question: how did so many species arise? Darwin provided an answer, and stimulated a century of research into the mechanisms and consequences of evolution through natural selection. This leads to the second major question: how do all these species co-exist (May, 1986)? This of course, raises the question of coexistence, which has been a central theme of ecology at least since the Hutchinson's 1959 paper entitled 'Homage to Santa Rosalia'. It is not at all obvious that this is the most important or the most tractable question for ecologists to address. Its popularity may arise in part from the logical sequence described above, and equally from the human fascination with collections, be they lists of species or shelves of Elvis Presley memorabilia. Connell (1987) in Kawano *et al.* (1987) reviews the mechanisms of co-existence as they are currently understood and marks the end point of this logical progression of investigation. Another paper in Kawano *et al.* (1987), Raven (1987), marks the other logical end point -- the applied problem of protecting this biological diversity from the ravages of human population growth and overconsumption of resources.

Where does this path lead next? Actually, it seems that both of these endpoints can be dealt with best by returning to the starting point. That is, the problems they

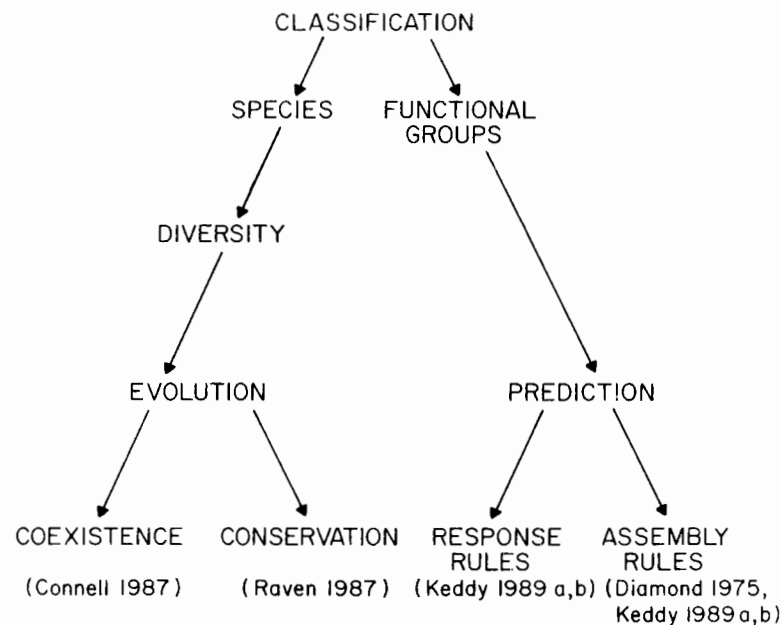


Fig. 1 Two research paths growing out of classification. The well-travelled left hand path (phylogenetic classification) leads to questions of diversity and coexistence. The less-travelled right hand path (functional classification) leads to predictive community ecology.

raise for ecology are inherent in the view that is chosen, and cannot be addressed by technical tinkering. Rather, it is necessary to fundamentally re-structure our research strategy. Let me illustrate why this is the case.

### B. Classification and prediction

Suppose we take a simple plant community with  $S$  species, and make two simplifying assumptions (1) that this community can be reconstructed from knowledge of pairwise interactions and (2) that these interactions do not change as the environment changes. The number of interactions we need to study is then simply  $\binom{S}{2}$  where  $S$  is the number of species. In wetlands in the Ottawa Valley, a very small part of the world, we can easily find 160 species, which yields 12,720 pairwise interactions. Assume we run a large experiment each year to look at 100 pairwise interactions. At this rate, it would take more than a century to develop simple predictions for this single vegetation type. If we assume following Colinvaux (1986) that there are more than 250,000 species of vascular plants on the planet, models for sustainable development will be very far off indeed (unless ecologists wait until a sufficient number are extinct, not a pleasing prospect). Rigler (1982)

and Wimsatt (1982) provide other examples of the limitations of models built upon species nomenclature. Species oriented models therefore cannot succeed in providing general prediction. The question, therefore, is how do we devise models that are both accurate and simple enough to be tractable? This directs attention to the second path in Figure 1.

This second path of inquiry (Figure 1, right) has a different logic. While on one hand there is the overwhelming species diversity of the biosphere, there is also dramatic and obvious repetition of certain themes. That is, there are recurring melodies as well as different notes. The convergence in plant growth forms representing very different families in deserts is but one example: 'succulents' occur in groups including the Cactaceae, Liliaceae, Euphorbiaceae, Crassulaceae, and Asclepidaceae. At the opposite extreme, in wetland habitats, 'mud flat annuals' are found in families including the Juncaceae, Cyperaceae, Asteraceae and Polygonaceae. If we develop this view, it is the convergence we emphasize. It is of course of interest to know what constraints phylogeny places upon convergence (Hodgson and Mackey, 1986; Givnish, 1987). But from the point of view of predictive ecology, the important questions start with what are the major convergent groups and how many are there? How many do we need recognize for a specific level of precision in our models? Growing out of this are other questions. What are the traits which they share? How do we use a knowledge of these traits to predict how a particular plant community will change after an external perturbation (response rules, Keddy, 1989a,b)? How can we use a knowledge of these traits to predict the group of species that will be present in a specified environment (assembly rules, *sensu* Diamond 1975, but modified according to Box (1981), Haefner (1981) and Keddy, 1989a,b)? These two endpoints represent two important questions facing ecologists today. On the theoretical side the question is whether we know enough to be able to develop rules to put communities together from their constituent pieces. On the applied side the question is whether we can predict state changes in ecological systems.

From the perspective of biosystematics, it would appear that biosystematists could stimulate this entire research path. This might generate a development for ecology as significant as species classifications did for evolution. The remainder of this paper therefore explores three aspects of this process: (1) a review of some recent ideas about functional classifications of plants, (2) a discussion of the sorts of traits necessary for recognizing functional groups, and (3) results from applying this approach to wetland plants.

## II. Functional Groups

The idea that organisms fall into functional groups is not a new one. The idea is particularly well-developed in the zoological literature, where the term 'guilds' (Root, 1967) is used to describe groups of functionally similar species in a com-

munity (Pianka, 1983). This terminology is particularly well-established in the study of bird and mammal communities (e.g. Severinghaus, 1981; Pianka, 1983; Diamond and Case, 1986; Terborgh and Robinson, 1986). Similarly, the concept of 'functional feeding groups' has been successfully applied to aquatic invertebrates (Cummins, 1973; Cummins and Klug, 1979). This approach is less well-established in the study of plant communities (but see Platt and Weiss, 1977; Beattie and Culver, 1981; Cody, 1986; Fitter, 1987; Givnish, 1987; Day *et al.*, 1988). The use of guilds in plant communities has often been primarily to split off one group of species from the rest of the community, such as the ruderal species which colonize animal mounds in herbaceous prairie vegetation (e.g., Platt and Weiss, 1977) or species which are dispersed by ants in deciduous forest (Beattie and Culver, 1981). The limited application to plants probably is the result of one major obstacle: functional groups of animals are recognized largely by the different foods they consume. In stream invertebrates, for example, functional groups include 'shredders', 'collectors', 'scrapers' and 'piercers'. This approach cannot be extrapolated to plants since all plants use the same few basic resources, light, water and mineral nutrients. This has been a principal reason why concepts of niche-differentiation have been so difficult to apply to plant communities (Harper, 1977; Grubb, 1977). There have been some attempts to apply concepts of niche-differentiation to resources such as the regeneration-niche hypothesis (Grubb, 1977) and resource ratio-hypothesis (Tilman, 1982, 1986), but these do not lead easily to functional classifications either. Are there some general procedures for constructing functional groups in plants? Before answering this, let us look at attempts that have been used to date.

The idea that plants can be grouped naturally into functional groups is not a new one. Du Rietz (1931) traced the idea back to Threophrastos (ca. 300 B.C.). Du Rietz also provided an extensive review of early classification schemes, noting that some emphasized only 'morphological' traits, whereas others emphasized 'biological' ones. More recently, there has been a proliferation of ecological classification schemes (e.g. Grime, 1974, 1977, 1988; van der Valk, 1981; Grubb, 1985; Cody, 1986; Givnish, 1987; Day *et al.*, 1988). Some of the best examples of guild classification come from studies on the photosynthetic phenology of temperate woodland plants (Kawano, 1985; Givnish, 1987) where the seasonal patterns of leaf development can be used to build a classification of photosynthetic guilds.

There are three principal trends which these recent studies illustrate. The first is to place greater emphasis upon the ecological role of species in communities (e.g., Noble and Slatyer, 1980; Givnish, 1987; Day *et al.*, 1988). The second is to emphasize functional traits which can only be determined by screening (e.g. Grime and Hunt, 1975; Grime *et al.*, 1981). The last is a shift from using these schemes to describe vegetation to using them to predict future states of vegetation (e.g. van der Valk, 1981). Most of these recent trends seem to have been developed ad hoc for specific systems and the objective of the next section is to uncover the basic

principles. Figure 2 summarizes the process and these principles. It also presents the structure of the remainder of this paper.

### III. Trait Selection

Du Rietz reviewed the many traits considered in early classifications, including life form, life span, method of vegetative propagation and position of overwintering shoots. These are all traits which can be determined upon inspection of the plant form. However, if we consider the processes which occur in vegetation, such as nutrient uptake, competition, and interaction with agents of disturbance or stress,

**TABLE 1**

Some recent classifications which emphasize function of species in communities rather than their morphology

functional group (number)	types	reference
strategies (3)	ruderal competitor stress tolerator	Grime, 1977
life history type (12)	annual perennial <sup>1</sup> matrix	van der Valk, 1981
guild (7)	interstitial winter annual spring ephemeral early summer later summer wintergreen evergreen dimorphic	Grubb, 1985
functional group (6)	clonal dominants gap colonizers ruderals stress tolerators reeds ruderals	Day <i>et al.</i> , 1988

<sup>1</sup> van der Valk's system recognizes twelve different life history types by also considering whether or not the perennials vegetatively propagate, establishment requirements (flooded, unflooded) and propagule longevity.

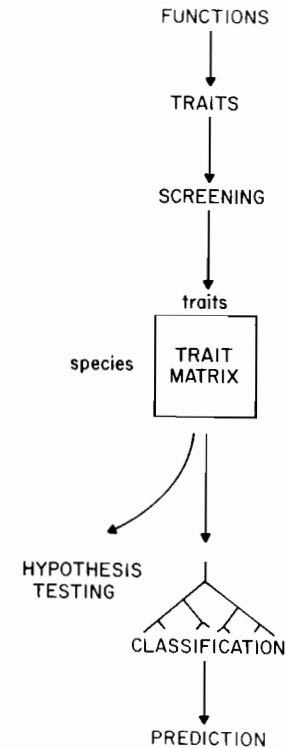


Fig. 2 A general research strategy for constructing functional groups (guilds). Key steps are selecting the traits which are related to different plant functions in communities, screening large numbers of species for these traits, constructing a trait matrix, and building a classification from the trait matrix. The classification of functional groups is then used to make simple predictive ecological models.

there are traits which may not be obvious upon inspection, but may be none-the-less closely related to the role the plant plays in a community. We could begin by looking for traits that measure performance in these three areas: (1) ability to forage for essential elements in the absence of neighbours, (2) traits associated with interaction with other plants and (3) traits associated with ability to withstand agents such as fire, flooding, grazing, etc. Table 2 illustrates some traits which have been measured to date.

Since many of these traits are not obvious upon inspection, we need to consider the process of screening (e.g., Grime and Hunt, 1975; Grime *et al.*, 1981). The objective of screening is to develop a simple bioassay for a particular attribute, and then apply it systematically to the entire flora of interest. There is still a great deal of opportunity to develop new and innovative bioassays for plant traits ranging from foraging ability to competitive ability to stress tolerance (Table 2).

TABLE 2

Some recent examples of traits which reflect plant function and for which screening has been conducted

trait	examples
germination	Grime <i>et al.</i> (1981) Shipley <i>et al.</i> (1990)
relative growth rate	Grime and Hunt (1975) Sheldon (1987) Shipley <i>et al.</i> (1990) Shipley and Peters (in press)
nutrient foraging	Crick and Grime (1987) <sup>1</sup>
shoot extension rates	Boutin and Keddy (ms)
evergreenness	Givnish (1987) Wisheu and Keddy (1989)
competitive ability	Gaudet and Keddy (1988)
stress tolerance	Shipley and Keddy (1989)
biomass partitioning	Shipley and Peters (in press)
drought tolerance	Raynal <i>et al.</i> (1985) Boot <i>et al.</i> (1986) <sup>1</sup>
palatability	Sheldon (1987) Southwood <i>et al.</i> (1986) McCanny <i>et al.</i> (ms.)
canopy form	Givnish (1987) Shipley <i>et al.</i> (1990)
genomic form	Bennett (1987)
sensitivity to acid rain	Percy (1986)

<sup>1</sup> Only two species were 'screened', but these are included because it is an idea that merits further work

Screening for traits is a research strategy almost completely orthogonal to the traditional population approach (Harper, 1977, 1982) which emphasizes accumulating information on many aspects of one population (rows) rather than one aspect of many populations (columns). The recent literature would suggest that the latter is much less common than the former, but it may be argued that general predictive

relationships are more likely to emerge from systematic comparative studies (Peters, 1980; Rorison *et al.*, 1987; Keddy, 1989b).

In conclusion, the three steps in producing an ecological trait matrix are (1) to decide the functions which the plant must perform to survive in a community, (2) to measure the traits which measure these functions, and (3) to devise the screening technique(s) for those traits.

#### IV. Traits in Wetland Plants

The following studies illustrate the progress to date in applying the scheme in Figure 2 to the study of wetland plant communities. While the central objective remains predicting future states of these communities, there are important evolutionary and ecological sub-questions which can be asked along the way. I will therefore begin by illustrating the side branch labelled hypothesis testing. This is partly because this where we have completed most work to date, and partly because there are many important evolutionary questions which can be answered using such data.

##### A. Correlation of adult and juvenile traits

One of the early questions which can be posed in deciding upon traits to measure is whether juvenile and adult traits are strongly correlated. If they are, fewer traits need be measured. If they are not, then there can be different adult and juvenile strategies. There are models which predict that adult and juvenile traits are correlated (r-K) and those which predict they are uncorrelated (C-S-R). To test between these, 7 juvenile traits and 13 adult traits were measured on 25 species of wetland plants (Shipley, 1987; Shipley *et al.*, 1990). Using the test developed by Lefkovitch (1984), Shipley was able to show that the adult and juvenile traits are uncorrelated. Functional classifications must consider both juvenile and adult traits (Figure 3). In the case of wetland plants, the principal adult trait axis appears to be capacity of adult plant to occupy space and intercept light; this is consistent with other studies on plant competition (e.g., Givnish, 1982, 1987; Tilman, 1988; Keddy, 1989a,b; Keddy and Shipley, 1989). The major juvenile axis is traits associated with regeneration. This yields four functional types of species (Fig. 3), which can be differentiated on relatively few traits.

##### B. Traits in wetland plants

Figure 4 shows four different pairs of traits we have measured in wetland plant communities, and relationships among them.

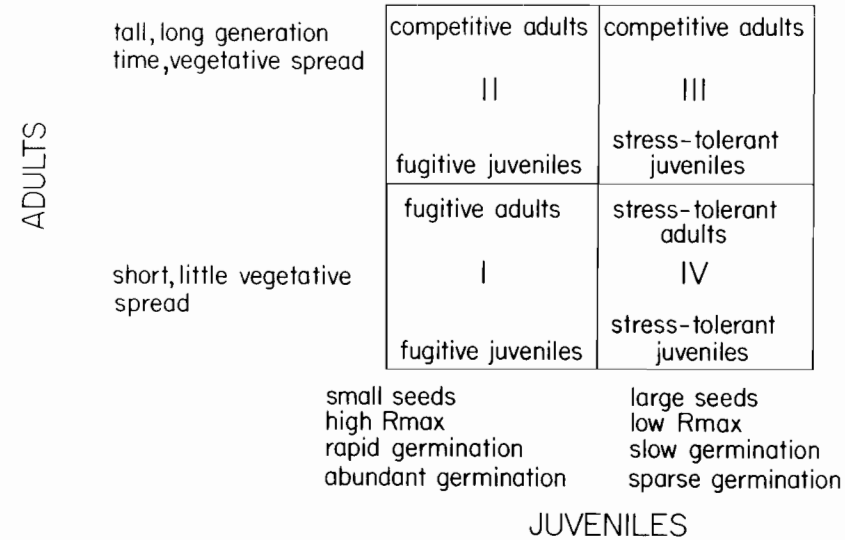


Fig. 3 Juvenile traits are uncorrelated with adult traits, so both must be screened for. In the case of wetland plants, the combination of adult traits associated with holding space (vertical axis) and juvenile traits associated with regeneration (horizontal axis) yield four basic functional groups of wetland plants (after Shipley, 1987; Shipley *et al.*, 1990).

Size and competitive ability

There is general agreement that competition is one of the major forces involved in the assembly of plant communities (Grime, 1979; Tilman, 1982, 1988; Keddy, 1989a). But there is consensus neither on what traits confer competitive ability, nor on how competition assembles communities. In Gaudet and Keddy (1988) we developed a bioassay for competitive ability and showed across 44 wetland plant species that it was predictable from above ground biomass. We attributed this to the importance of competition for light. Whether this relationship occurs in other plants and in other sets of environmental conditions can only be tested by using the bioassay design with other species in other environments.

Investment in plant defenses

Grazing is another factor known to be important in plant communities (Harper, 1977; Grime, 1979; Sheldon, 1987). There are good evolutionary reasons for expecting the chemical defenses in plants to be negatively correlated with relative growth rate (Coley *et al.*, 1985; Southwood *et al.*, 1986). In McCanny *et al.* (manuscript) we developed a simple bioassay for palatability of wetland plants to generalist herbivores. In this case, we used extracts from field-collected plant tissue

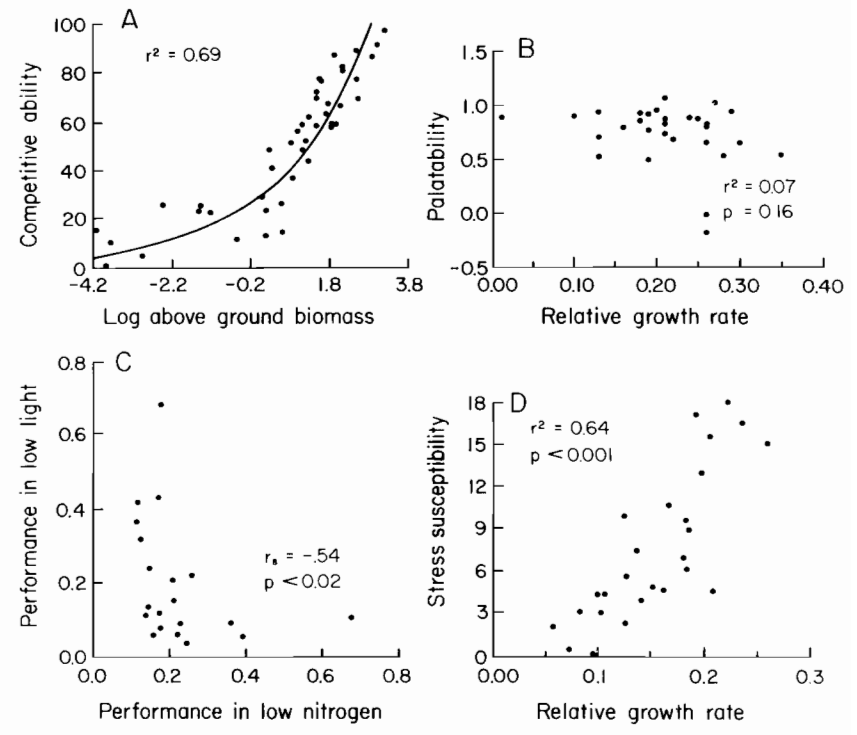


Fig. 4 Once ecological traits have been measured in large numbers of species, it is possible to look for relationships among them. These examples all come from wetland plants.  
 A. Competitive ability plotted against plant biomass (Gaudet and Keddy, 1988)  
 B. Palatability plotted against relative growth rate (McCanny *et al.*, manuscript)  
 C. Performance in low light plotted against performance in low nitrogen (Fricker, unpublished data)  
 D. Stress susceptibility plotted against relative growth rate (Shipley and Keddy, 1988).

in diet cubes fed to an herbivorous insect. We found no significant relationship between palatability and relative growth rate. There are other traits which may be associated with resistance to herbivory such as rate of resprouting, position of meristems, etc, so there are many opportunities for extending this work.

Trade-offs in competitive ability

In studies of plant competitive ability, Tilman (1982) has argued that there should be a negative relationship between above and below ground competitive ability. Fricker (unpublished data) has tested for this relationship in 20 wetland plant species by screening for their ability to grow under low nutrient and light regimes. We found a significant negative correlation in these traits. Apparently traits which

confer the ability to tolerate low light levels are negatively correlated with those which confer ability to tolerate low nutrient levels.

#### Stress tolerance and relative growth rate

Shiple and Keddy (1989) screened 28 wetland plant species for ability to tolerate low nutrient conditions. They found that those species which grew fastest under high nutrient levels (e.g. *Lythrum salicaria*, *Leersia oryzoides*, *Scirpus acutus*) were those species most sensitive to reductions in nutrient supply. Species with slower growth rates (e.g. *Triadenum fraseri*, *Scirpus americanus*, *Juncus filiformis*, *Iris versicolor*) were more stress-tolerant; that is, their growth rates were proportionally less-depressed by low nutrient levels.

These four examples illustrate the possibility for testing general hypotheses about the evolution of plant traits using trait matrices constructed from screening. While the ultimate goal may be to predict how species possessing these traits will respond to different environments (e.g. increased grazing, decreased fertility, etc.), in the short term they provide valuable information on the co-evolution of plant traits. In the long run, only a subset of such traits will probably need to be measured in order to make ecological predictions.

## V. Functional Groups in Wetland Vegetation

To construct functional groups we need systematically collected data on the traits of many species in a specific vegetation type.

Boutin and Keddy (manuscript) have recently finished a functional groups classification based upon a matrix of 43 species by 27 traits. The species were selected to represent wetland habitats and functional groups from across eastern North America. Species included rare or endangered taxa from infertile lakeshores (*Coreopsis rosea*, *Panicum longifolium*), annuals typical of mud flats (*Bidens cernua*, *Cyperus aristatus*), large perennials (*Phalaris arundinacea*, *Typha glauca*), reeds from river banks (*Scirpus acutus*, *Eleocharis calva*), and a wide array of other species which represented other life forms and habitats. They were grown in a large outdoor experiment. Additional traits were measured in the field and in more controlled conditions.

Classification revealed three major groups (Figure 5). The first separation was between perennials and ruderals. Ruderals (sensu Grime, 1977) were species with the capacity to behave as annuals, which included facultative annuals (perennials with nearly 100 percent flowering the first year). They also had proportionally less biomass allocated to below ground structures. The perennials then split into two groups based largely upon traits associated with ability to hold space: a group of large space-holding species with clonal spread, and a group of species without vig-

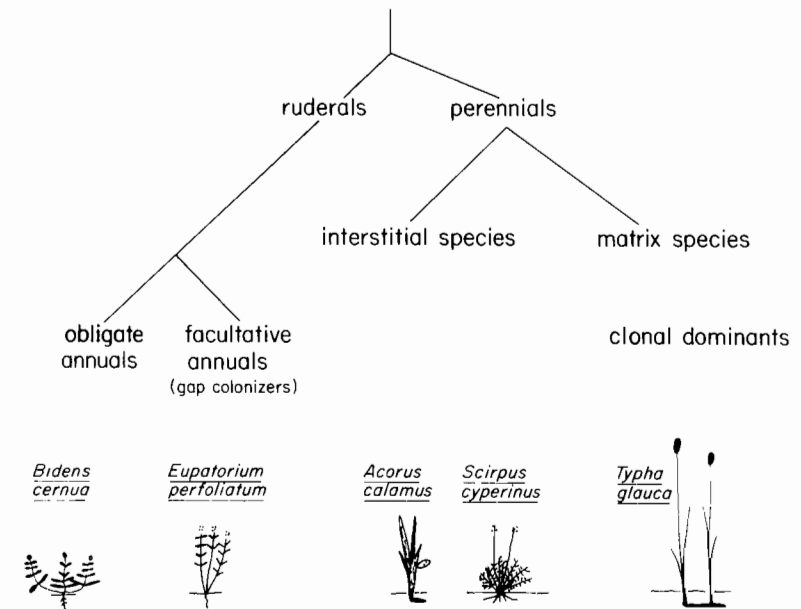


Fig. 5 A preliminary classification of guilds in wetland plants based upon clustering of a matrix of 27 traits measured upon 43 wetland plant species from across eastern North America. They are arranged along an axis of increasing ability to hold space (after Boutin and Keddy ms).

orous clonal spread and with shallow rhizomes. This group apparently occupies gaps in the large clonal species. Grubb (1986) has termed these two groups 'matrix' and 'interstitial species'. Let us explore these four groups without at the moment concerning ourselves with the other subgroups of interstitial or matrix species. It is noteworthy that these functional groups all appear to fall along a continuum of life histories adjusted to different light regimes. This is consistent with the growing body of literature showing that standing crop gradients can predict species richness and life form in plant communities (Grime, 1973, 1979; Al-Mufti *et al.*, 1977; Moore *et al.*, 1989; Wisheu and Keddy, 1989).

### A. Obligate annuals

Obligate annuals (e.g. *Bidens cernua*, *Cyperus aristatus*, *Eleocharis obtusa*, *Echinochloa weigandii*) lived for only one growing season, and for this reason shared many other traits such as low rates of shoot extension, high rates of tiller production, and high rates of biomass production. These species emerge en masse from buried seeds after the adult vegetation has been killed (van der Valk and Davis, 1978; van der Valk, 1981; Keddy and Reznicek, 1982, 1986).

### B. Facultative annuals

Facultative annuals (e.g., *Lythrum salicaria*, *Verbena hastata*, *Mimulus ringens*, *Eupatorium perfoliatum*) all flowered at the end of the first year and therefore could, if necessary, function as annuals. They normally overwinter and send up several slender stalks from the base of the previous year's shoot. The seeds are borne at the very top of a tall stalk, presumably assisting with locating new gaps. Other traits included the highest rates of extension of the main shoot, and lowest rates of tiller production. Although these species can be found on mud flats, they also regenerate in smaller gaps and along animal trails. This group of species could also be called 'gap colonizers' (Day *et al.*, 1989) and similar functional groups have been described in prairie vegetation (Platt and Weiss, 1977, 1985).

### C. Interstitial species

The interstitial species (e.g. *Carex crinita*, *Scirpus cyperinus*, *Asclepias incarnata*, *Iris versicolor*, *Alisma plantago-aquatica*) were the most heterogeneous group of species. However, almost all lacked the ability for clonal spread, and had shallow root systems compared with the following group of matrix species. They also tended to have compact arrangements of foliage, suggesting that they hold small areas of space against invasion from neighbours.

### D. Matrix species

Matrix species (e.g. *Phalaris arundinacea*, *Typha glauca*, *Scirpus americanus*) were the tallest group with the most deeply buried rhizomes and extensive clonal spread. They dominate fertile, undisturbed environments (Day *et al.*, 1989).

## VI. Guilds and Prediction

Two possible approaches to prediction are 'assembly rules' and 'response rules' (Keddy, 1989a,b). Let us consider them in turn.

### A. Assembly rules

In the case of assembly rules, we can ask which subset of the species pool for a region will be found in a specified environment (Diamond, 1975; Keddy, 1989a). If we know the species pool for any particular system, we can picture a series of sieves which progressively eliminate species or guilds until only a specific subset are left (Figure 6). If an entire trait matrix is available for a flora, then such sieve

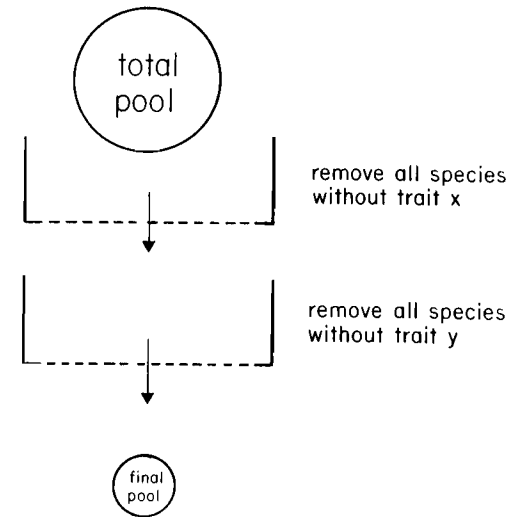


Fig. 6 By starting with the total species pool for an area and then subtracting species lacking the traits to tolerate the local environment, one is left with the pool of species which will comprise the local vegetation.

models could be based upon actual measured traits for each species. But a far more efficient approach is to develop guild classifications based upon the minimum number of traits necessary and then consider which guilds are filtered out by the environment. The remaining functional groups will form the vegetation. Box (1981) has developed such a model to predict world vegetation types. The model starts with the total pool of plant life forms, and then progressively subtracts those which cannot tolerate the local climate. A second step is to examine dominance relations (competitive interactions) among life forms, with position in dominance hierarchy determined largely by size. This is an example of assembly rules for plant communities at the largest scale; a similar approach should be possible at local scales.

### B. Response rules (transformation rules)

In the case of response rules we wish to predict how a specified perturbation will convert one vegetation type (that is, one vector of species abundances) to another (Lewontin, 1974; Keddy, 1989a). Again, this would be a complex process if attempted on a species by species basis, but it is greatly simplified by using guilds. Figure 7 illustrates one approach to response rules. Here the 43 species we studied (which represent the range of variation found in hundreds of other wetland plant species), can be reduced to a column vector of only 4 guilds. We can then explore how changes in different sets of environmental factors will transform the abun-



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Fig. 7 One method of using guilds to make ecological predictions. In this case, the 43 wetland plant species can be represented by a vector of only four guilds, greatly simplifying the process of predicting future states of the system.

dances of these guilds through time. For example, any factor which increases productivity or decreases disturbance will reduce light availability and reduce regeneration opportunities; we would then predict a gradual shift away from annuals and facultative annuals to clonal dominants. That is, the matrix A would have negative coefficients for all but element  $a_4$ . Conversely, if the wetland were subjected to fluctuating water levels, grazing, or recreational development, we would expect a shift towards the ruderal and gap colonizer end of the continuum, in which case only  $a_1$  and  $a_2$  would have positive coefficients. If the disturbances created only small gaps -- say due to increased population sizes of a small mammal, then only the interstitial species and facultative annuals would be predicted to increase. The process of estimating these coefficients and predicting future states has been briefly addressed in Keddy *et al.* (1989) but much remains to be done. Van der Valk (1981) has illustrated one approach to response rules for prairie pothole vegetation; in this case he recognized 12 life history types and showed how knowledge of their traits (e.g. germination requirements) and changes in the environment (e.g. flooding) could predict future vegetation states. Once guilds are recognized, and key environmental factors determined, this approach could presumably be used in most other vegetation types.

The potential for using functional classifications and trait matrices in predictive ecology has barely been explored. They may offer both a new avenue of work for biosystematists, and a research path that will maximize our rates of progress in achieving predictive community ecology.

### C. Questions remaining

Since we are in the early phase of classifying plants into functional groups, and in developing predictive models based upon them, there are many opportunities for research. Unanswered questions would include:

- (1) What are the best traits for measuring the functional roles of plants in vegetation?
- (2) What are the minimum number of traits we need to measure to produce accurate and useful classifications of functional groups?
- (3) What are the most efficient methods for screening for the above traits?
- (4) How many functional groups are necessary for particular levels of accuracy of prediction?
- (5) Across how many vegetation types can one extrapolate with a particular model? Is it possible to develop one or two simple models that could be distributed and used around the world?

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