NOTICE

The quality of this microform is heavily dependent upon the quality of the original thesis submitted for microfilming. Every effort has been made to ensure the highest quality of reproduction possible.

If pages are missing, contact the university which granted the degree.

Some pages may have indistinct print especially if the original pages were typed with a poor typewriter ribbon or if the university sent us an inferior photocopy.

Previously copyrighted materials (journal articles, published tests, etc.) are not filmed.

Reproduction in full or in part of this microform is governed by the Canadian Copyright Act, R.S.C. 1970, c. C-30.

AVIS

La qualité de cette microforme dépend grandement de la qualité de la thèse soumise au microfilmage. Nous avons tout fait pour assurer une qualité supérieure de reproduction.

S'il manque des pages, veuillez communiquer avec l'université qui a conféré le grade.

La qualité d'impression de certaines pages peut laisser à désirer, surtout si les pages originales ont été dactylographiées à l'aide d'un ruban usé ou si l'université nous a fait parvenir une photocopie de qualité inférieure.

Les documents qui font déjà l'objet d'un droit d'auteur (articles de revue, tests publiés, etc.) ne sont pas microfilmés.

La reproduction, même partielle, de cette microforme est soumise à la Loi canadienne sur le droit d'auteur, SRC 1970, c. C-30.

Canada

Pattern and Mechanism in the

Emergent Macrophyte Communities Along the Ottawa River (Canada)

by

John William (Bill) Shipley

submitted in partial fulfillment of the requirements

for the degree of Doctor of Philosophy

University of Ottawa

Ottawa, Ontari

Canada

ISBN 0-315-46855-6

UNIVERSITÉ D'OTTAWA
UNIVERSITY OF OTTAWA

Abstract

This thesis examined the relationship between pattern and mechanism in the emergent macrophyte communities along the Ottawa River, Canada. This was done by (a) statistically analyzing the distribution of species' boundaries along a gradient of water depth; (b) performing a 15 month field experiment in which ramets of three species (Carex crinita, Acorus calamus and Typha angustifolia) were transplanted into four sites along the water depth gradient, both in the presence and in the absence of the natural vegetation of each site; and (c) describing the distribution of 25 morphological and physiological plant traits along environmental gradients found along the shores of the Ottawa River.

Chapter 1 considered the pattern of species' distributions along the water depth gradient from the perspective of the community-unit and individualistic concepts by reformulating these concepts as falsifiable hypotheses concerning the distribution of species boundaries. These boundaries were found to be clustered at certain height intervals, contradicting the individualistic concept, but upper and lower boundaries did not behave similarly along the gradient, contradicting the community-unit concept. It was concluded that these concepts require testing by manipulative field experiments, and a mechanistic hypothesis for the individualistic concept was introduced.

Chapter 2 reported the results of the field experiment and compared these results to three published models designed to explain community organization along environmental gradients.

Species' realized distributions were not equivalent to their potential distributions, all three species did not grow best at the same point on the gradient in the absence of competitors, and each species was least affected by competitors in that part of the gradient that it normally inhabited.

In chapter 3 this description of causes was further investigated by measuring 20 morphological and physiological traits of 25 species, describing the correlations between these traits, and relating these to environmental gradients. There were strong correlations between seven traits related to seeds and seedlings, as well as between 13 adult traits, but no association between these two sets of traits. The high intra-class correlations resulted in low-dimensional principle co-ordinate ordinations, which were interpreted as differing strategies to disturbance, competition and stress-tolerance.

Table of Contents

Acknowledgements

I would like to thank Paul Keddy, Len Lefkovitch and John Lambert, whose advice and guidance has greatly improved this research. Dwayne Moore, Irene Wisheu, Connie Gaudet, Scott Wilson and Robin Day are all my friends as well as fellow graduate students. Their ideas, criticisms and free beer have all been instrumental in the development of this thesis. Kim Lemky, Rodney Bennet, Charles Kettle and Dann McCann have put in many long hours of field work with unflagging enthusiasm. Without their help I could not possibly have finished my work.

Mme. Claire Gauthier graciously allowed me to do field work on her property. Jacques Helie drew all of the figures. George Bentchavtchavadze, and Paul Brunon produced all of the photographs. Nino Cavacciutti and Andre Richer helped in all matters related to construction. The National Sciences and Engineering Research Council of Canada, as well as the University of Ottawa, supported this work through their generous scholarships.

Finally, I wish to especially thank my wife, Lyne Labrecque, and my parents, Jim and Margaret, for their unquestioning love and support. My parents taught me early that learning has intrinsic value in its own right. This thesis is the result of their influence, and is dedicated to them.

General Introduction

Science is objective in so far as it concerns itself with repeatable, observable phenomena. On the other hand, in any scientific study, the researcher must choose a small subset of questions for investigation out of an almost unlimited pool of potential questions. Therefore, the task of deciding upon which questions to ask (and by extension, those that won't be asked) is much less objective. The inevitable biases which result from such a choice are often more insidious than biases in methodology because the criteria are usually implicit. Therefore, before entering into the biological details contained in this thesis I would like to explain <u>why</u> I have asked the questions posed in the thesis, and <u>why</u> I have tried to answer them in the way that I have. The themes upon which my research is based are described under the following headings.

1. Concepts and hypotheses

Ecology is rich in concepts. By "concept", I refer to general bodies of ideas often stated in the form of analogies. Concepts are necessary because they bring together disparate ideas and suggest new and interesting avenues for research. I believe though, that ecologists have been cursed by their good

fortune. We have a storehouse full to bursting with concepts (adaptation, the niche, the competitive exclusion principle, for example) but this wealth of concepts has not produced an equally large store of testable hypotheses - that is, statements specifying functional relationships between measurable variables.

One example is the debate concerning the nature of communities along environmental gradients, cast as a dichotomous choice between the community-unit concept and the individualistic concept (Whittaker 1962). This argument has existed for almost a century without a satisfactory resolution. In chapter one I extract mutually exclusive predictions from these two concepts. Throughout this thesis I have attempted to derive testable hypotheses from the various concepts related to community organization along environmental gradients by clearly defining the variables involved and the predicted functional relationships between them.

2. Pattern and mechanism, predictions and assumptions

This thesis is concerned with the relationship between pattern and mechanism, specifically, the pattern of distribution of emergent macrophytes in freshwater marshes and the mechanisms producing such patterns. This dialectic between pattern and mechanism is central to science, but it is important to recognize

the unidirectional relationship in the logical structure of pattern and mechanism. Consider the structure of a typical application of the hypothetico-deductive method in ecology. A series of assumptions is assembled into a mechanistic model of community organization, predicted patterns are derived as logical consequences of these assumptions, and then these predicted patterns are compared to those observed in the field. If the observed and predicted patterns disagree, then the underlying mechanistic model is rejected. This is justified. If the observed and predicted patterns are the same, then this is not sufficient to justify an inference that the underlying mechanistic model is correct. All that one is capable of concluding is that the underlying model is consistent with the observed pattern. If more that one mechanistic model can account for the same pattern, not much information has been gained by showing a concordance of observed and predicted patterns. That more than one model can predict the same pattern is a real possibility in ecology, where there are many forces potentially affecting the distribution of species. One example of this is studied in chapter two, where three different models generate exactly the same zonation pattern of the emergent macrophytes. In such situations, a more powerful analysis can be done by testing the assumptions of the models rather than their predicted patterns.

3. Description, explanation and prediction

At the risk of overgeneralizing, I categorize the different goals in science as (1) describing the system (2) explaining how the system works and (3) predicting the behaviour of the system under perturbations. Some authors (Peters 1982) have argued that only the third goal, that of prediction, is justified in ecology. I have approached my research by assuming that all three are valid goals but that each is incomplete in isolation.

Each chapter reflects one of these goals. Chapter one is primarily a description of the emergent macrophyte community. Chapter two is concerned with explaining the mechanisms generating the patterns observed in chapter one. Chapter three attempts to predict life history traits of plants, and therefore represents a compromise amongst the three primary goals.

4. Pluralism of methods

There is a tendency amongst ecologists to argue about the one "right" way to study ecology (Diamond and Case 1986). In contrast, I have assumed that one such "right" way does not exist; instead I have relied on three different methodologies: pattern description, manipulative field experiments and comparative ecology. I have done this because it is obvious (at

least to me) that each method had its own inherent strengths and weaknesses and so each in isolation can only produce a caricature of the system under study.

Multivariate ordinations can simultaneously take into account all species in the community, allowing one to quickly and objectively detect patterns from complicated data sets. The obvious weakness of this approach is that the underlying processes generating these patterns are veiled and cannot be convincingly exposed.

Manipulative field experiments allow one to better control variables and convincingly demonstrate mechanisms, but there are two main drawbacks to this approach (Diamond 1986). First, because they are labour intensive, only a small subset of the species in a community can be included in the experiment, making it difficult to extrapolate to more general situations. Second, field experiments cannot normally continue for long periods of time, yet it is possible that some important structuring agents act only periodically (MacArthur 1972), or on a time scale longer than that of the experiment. This is especially relevant in communities of long-lived perennial plants. Thus, the types of interactions that can be studied by field experiments are ones which are continuous and intense.

Comparative ecology represents a compromise between the

first two methods. The goal is to look for correlations between life-history characteristics and environmental gradients. Since the types of physiological and morphological traits used can be shown to affect the fitness of individuals possessing them, a link between pattern and mechanism is available. Thus, comparative ecology shares both the strengths and weaknesses of the first two methods.

This pluralism of methods is necessary because each method, by itself, gives a biased view of the system under study. Hopefully, I have obtained a more realistic understanding of emergent macrophyte communities by juxtaposing the biased "snapshot" that each method provides.

Finally, in assembling the evidence presented in this thesis, I became convinced that I actually understood the organization of plant communities in detail. Of course, this too, was due to an unconscious bias: I was preoccupied with what I had learned, and had overlooked all that I still do not know. I, and other ecologists, will have developed a solid understanding of natural communities when we can read the following quote (taken shamelessly out of context) and not fall silent:

> If you can look into the seeds...
> And say which grain will grow and which will not,
> Speak then to me.
>
> William Shakespeare

Chapter 1

The community-unit and individualistic concepts as falsifiable hypotheses

Introduction

The debate concerning the nature of community organization has continued sporadically for more than 70 years (see Whittaker 1962 for a review of the controversy). The Clementsian interpretation (Clements 1916), often called the "community-unit concept" (Whittaker 1975) was accepted by the majority of ecologists during the first part of this century. The work of a number of ecologists however (Cain 1947; Egler 1947; Mason 1947; McIntosh 1967; Whittaker 1951,1956,1967) quickly converted the majority of community ecologists (McIntosh 1975) to the "individualistic concept" of community organization based primarily on the ideas of Gleason (1926,1939). This transition to an individualistic viewpoint was due in part because, by using direct or indirect gradient analysis (Whittaker 1967), the observed pattern of species replacements along a gradient was stated to be inconsistent with the patterns predicted by Clements. This transition (Mirkin 1987 calls it a "paradigm change") occurred in Europe and the Soviet Union as well as in North America (Mirkin 1987).

Gradient analysis methods have improved the study of community organization by insisting on objective sampling. They still suffer from the problem of using subjective methods of analyzing the observed patterns by failing to use inferential

statistics to compare empirical data with proposed models.

In this chapter I use a direct gradient analysis (Whittaker 1967) of the emergent vegetation of a freshwater marsh to obtain data on the distribution of species' boundaries relative to a gradient-complex of water depth. After stating falsifiable hypotheses based on the predicted patterns of the individualistic and community-unit concepts, the observed pattern of boundaries along the gradient is compared to these hypotheses using an analysis of deviance (McCullagh and Nelder 1983).

Hypotheses for the patterns implied by the two concepts

The community-unit concept claims that when species' distributions are plotted along some gradient or gradient-complex whose rate of change is constant, there exist groups of species,i.e. "communities", which replace themselves along the chosen gradient (Whittaker 1975). Within each grouping most species have similar distributions and the end of one group coincides with the beginning of another (figure 1.1).

The individualistic concept states that "centers and boundaries of species' distributions are scattered along the environmental gradient" (Whittaker 1975). No distinct groups of

species are predicted to exist, therefore precluding the coincidence of one group with another.

Explicit hypotheses of these two concepts are formulated using the following terms. Define "upper boundary" as that point on the gradient where the distribution of a species (not a group) begins relative to an arbitrary direction on the gradient. Define "lower boundary" of a species as that point on the gradient where its distribution ends.

The individualistic hypothesis states that:

(i) the average number of boundaries (both upper and lower) in each interval of the gradient should be equal except for random variation about the mean;

(ii) the number of upper boundaries per interval of the gradient should be independent of the number of lower boundaries.

The community-unit hypothesis states that:

(i) there should be significantly more boundaries (both upper and lower) in some intervals of the gradient than in others, i.e. boundaries are clustered;

(ii) the number of upper and lower boundaries per interval. should increase and decrease together along the gradient.

The patterns predicted by these hypotheses are shown in figure 1.2. Note that the 2X2 table suggests at least two other possibilities for patterns along a gradient, as pointed out by Whittaker (1975).

Methods

The study site is near Breckenridge, Quebec, which is approximately 40 km. northeast of Ottawa, Ontario, Canada (figure 1.3). This marsh occurs on a very gently sloping shoreline. On the highest ground is a forest dominated by Acer saccharinum which is flooded during the high water period each spring. The study site itself consists of herbaceous emergent species (see figure 1.5); this portion of the marsh extends for approximately 200m although not all of this section of marsh was actually sampled. Beyond 200m from the edge of the tree canopy, floating leaved species such as Nuphar variagetum and Potomogeton spp. are found, giving way finally to submerged vegetation. To obtain a random sample of the emergent community a 200 m line was established running along the edge of the tree canopy and divided into 5 m segments. Thirteen of these segments were chosen using a random number table to be the locations of belt transects running down into the marsh. Each transect was therefore at least 5m distant from any other transect.

The water level on July 24 1984 was marked and will be called the "standard zero" water level; this corresponds to a Geodetic height (Water Survey of Canada) of 58.40 m based on water level records from the Brittania Bay, Ontario measuring station (number 02KF005) located in the same drainage basin.

Using a surveying level, each transect was divided into 5 cm height intervals based on the standard zero mark. Each transect was surveyed down to a height of -40 cm and up to, but not including, the edge of the tree canopy. Transects were not extended into the forested region to avoid the confounding affect of an animal runway. Because the edge of the tree canopy varied along the marsh, the upper limit of each transect corresponded to a height of from 30 cm to 15 cm above the standard zero mark. Thus, -40 cm refers to a point on the water depth gradient which is 40 cm below the standard zero water level.

Transects were censused in the order in which they had been randomly chosen and in each 5 cm height interval of all transects the presence or absence of all species was recorded. All species found in the section of the marsh actually surveyed were herbaceous emergent plants; no transects penetrated into the region of the marsh containing floating-leaved or submerged vegetation.

Voucher specimens for all species were collected and sent to the Biosystematics Research Centre of Agriculture Canada for verification and deposited in their herbarium (DAO). Nomenclature throughout the thesis follows Gleason and Cronquist (1963) unless otherwise indicated, except for the grasses, which are from Dore and McNeill (1980). Note that two species, Lysimachia terrestris and Lysimachia thursiflora, could not be

separated in their vegetative state and were therefore grouped together as Lysimachia spp.

In order to determine the location of boundaries it had to be assumed (Pielou 1977; Underwood 1978a,b; Keddy 1983) that a gap in the distribution of a species along the gradient did not represent a true disjunction. In reality, only species that were uncommon in the marsh showed such gaps and so it seems reasonable to accept such an assumption. If the highest height interval censused contained a species it follows that the upper boundary for that species could not be determined, nor can the lower boundary be found if the species was present in the lowest height interval censused. Finally, if a species had both its upper and lower boundary in the same height interval it was excluded from the analysis to avoid a bias in part (ii) of the two hypotheses.

The procedure described above yields a contingency table consisting of the number of upper and lower boundaries found in each relative height interval of each transect. These data were analyzed by an analysis of deviance (Karson 1982; McCullagh and Nelder 1983), using a generalized linear model assuming a multinomial distribution.

An analysis of deviance is analogous to an analysis of variance but is not restricted to assumptions of homogeneity of variance in the error structure of the model. To test for

significant systematic components of the data, one looks at the difference between the deviance of the data from a model not incorporating the factor of interest and the deviance of the data from a model in which the factor is included. The change in deviance, twice the negative log-likelihood ratio is asymptotically distributed as a Chi-Squared variate.

Part (i) of the two hypotheses can be evaluated by testing for a main effect of relative height along the gradient; if this effect exists then there are significantly more boundaries in some height intervals than in others. The interaction term between the type of boundary (upper or lower) and relative height is used to evaluate part (ii) of the two hypotheses. If this interaction term exists then the number of upper and lower boundaries per height interval does not increase and decrease together.

Since I collected data using relative height intervals, the actual distance of marsh included within an interval varied depending on the slope of the shore; for instance, in Breckenridge Marsh the height intervals had distances from a minimum of 0.8 m to a maximum of 19.1 m. If boundaries are randomly distributed along the relative height gradient but some intervals are correlated with longer distances, then a spurious clustering of boundaries would be found. To solve this problem the distance occupied by each height interval was included as a

covariate and its effects removed. Appendices 1.2 and 1.3 give the actual data sets for the boundary data and the length of height intervals, respectively.

The Genstat IV statistical package was used and the data were analyzed on the Agriculture Canada computer network.

Results

Both upper and lower boundaries were clustered ($p<0.001$; figure 1.4). The individualistic hypothesis was therefore rejected. As well, there was a significant interaction between the type of boundary (upper or lower) and the main effect of relative height on the gradient, indicating that the pattern of clustering with respect to upper boundaries differed from the pattern of clustering amongst lower boundaries along the gradient ($p<0.001$, table 1.1). In fact, there was no correlation between the number of upper and lower boundaries per relative height interval ($r=0.009$, $p>0.38$). I must therefore reject the community-unit hypothesis as well.

Although the covariate, the actual distance of marsh included in each interval, was significant (table 1.1), the effect was to increase the importance of clustering along the gradient since when the covariate was excluded from the analysis, the change of deviance due to relative height was decreased from 55.6 to 43.5. This was because some of the longest relative height intervals contained very few boundaries. In any case, the amount of variation explained by the covariate was small. It should also be noted that after including the effects of the covariate, the relative height term, and the interaction term, the residual deviance of the model became non-significant ($p>0.05$) indicating that all but random

variation has been accounted for by the model.

In order to better visualize these results, figure 1.5 shows the distribution of each species plotted against relative height in the marsh, averaged over the 13 transects. It can be seen that there exists one group of species (Lycopus uniflorus, Carex vulpinoidea, Potentilla anserina, Equisetum arvense, Aster simplex, Onoclea sensibilis, Plantago major, Carex crinita, Lysimachia nummularia) which all reach their lower distributional limits in the interval from 10 to 20 cm. Equally important is the absence of any species whose distribution begins at this part of the gradient. In the interval from -10 to -25 cm there occurs another group of species (Iris versicolor, Scirpus americanus, Spartina pectinata, Eleocharis erythropoda Studel, Carex vesicaria) who all reach their lower distributional limits but there also exists a group of species who simultaneously begin their distribution (Sparganium eurycarpum, Carex retrorsa, Dulichium arundinaceum, Rumex verticillatus, Polygonum hydropiperoides, Equisetum fluviatile, Scirpus fluviatilis, Penthorum sedoides, Typha augustifolia). It is this disconcordant pattern of upper and lower boundaries that causes the interaction term in table 1.1.

In order to compare these results with those of other studies, I have computed Underwood's (1978a) statistic. Using that test, lower boundaries are again found to be clustered

($p<0.01$) but upper boundaries appear to be randomly distributed ($0.1>p>0.05$). Note however, that Underwood's test can fail to detect non-random patterns (appendix 1.1), which explains the differences between the results of the two tests.

Discussion

In order to relate the results of this study to the debate concerning the individualistic and community-unit concepts it is necessary to consider the argument both from the perspective of pattern and from the perspective of the mechanism. In this section then, I will concentrate separately on three different, but related, questions. First, from the perspective of pattern, I will consider the results of this study in relation to previously published results. Second, I will discuss the acceptability of using predicted patterns to test hypotheses of mechanism. Finally, I will examine a hypothesis of the individualistic concept as a statement of the mechanisms controlling the distribution of species along a gradient.

1) Hypotheses of pattern

The debate concerning pattern has usually been structured as a dichotomous choice between the predicted patterns of the community-unit and individualistic concepts (Curtis 1955; Gleason 1926; McIntosh 1967; Whittaker 1951; but see Whittaker 1975 for an exception). Such a dichotomy is misleading however, because it implies that evidence contradicting one expected pattern can be interpreted as evidence supporting the other. Such

reasoning has been used to support the individualistic concept (Curtis 1955; Whittaker 1951, 1967). If we recognize that the two predicted patterns do not exhaust the number of possible patterns available (Whittaker 1975) then one can no longer rely on negative evidence to support either of the two usual concepts of community organization along a gradient.

In this paper I have shown that the distributions of the species in Breckenridge Marsh are non-random, but do not correspond to the patterns predicted by the community-unit hypothesis. This demonstrates that the historical dichotomy is too limited, but might also be taken to suggest that Breckenridge Marsh is exceptional, since the results disagree with a large body of evidence apparently demonstrating individualistic communities (for example: McIntosh 1975; Whittaker 1962,1975). Although this may be true, there are two reasons to believe that such a conclusion should be questioned.

First, the only other study in which both direct-gradient analysis and inferential statistics was used (Keddy 1983) found boundary clustering in a lakeshore plant community. Three other studies have used inferential statistics to test boundary distributions, although the species ranges were not obtained using direct gradient analysis. Of these, Pielou and Routledge (1976) found clustering, Underwood (1978a,b) found a random distribution (but see appendix 1.1) and Dale (1984) found a

contiguity of upper and lower boundaries.

Second, the studies supporting the individualistic concept did not use inferential statistics to compare observed patterns with those predicted by the individualistic hypothesis and therefore may have failed to detect true non-random patterns. By subjectively scanning the distributions of many species along a gradient by eye, all but the most pronounced structure of such data would appear random, therefore biasing conclusions in favour of the individualistic concept.

Using pattern to deduce mechanism

In this chapter I study the pattern of species' ranges relative to an obvious environmental gradient, but make no attempt to interpret the results as a test of any causal hypotheses. In the context of this debate however, pattern has generally been used to prove or disprove proposed mechanisms of community organization (Clements 1919; Gleason 1926; Whittaker 1951,1975). Certain assumptions are combined to produce a model of community organization, predicted patterns are derived as logical consequences of the model, and then the observed patterns of natural communities are compared with those predicted by the model. If the observed and predicted patterns are different then the underlying mechanistic model is assumed to be wrong. If the

observed and predicted patterns are similar then the underlying mechanistic model is assumed to be correct (Whittaker 1951). The problem with such an approach is that, given the large number of abiotic, biotic, and interactive factors to choose from, there are so many degrees of freedom that many different causal mechanisms could all 'explain' the same empirical pattern.

Consider this demonstration of boundary clustering in Breckenridge Marsh. This can be made consistent with the individualistic hypothesis by assuming that there are one or more (unknown) abiotic factors which change rapidly at those points on the gradient where boundaries are clustered. There exists in Breckenridge Marsh, as in all natural communities, many abiotic factors which could possibly explain such a pattern: the degree of anoxia due to flooding or to ice cover, the degree of moisture stress when the water level falls, changes in any one of many mineral nutrients or ratios of nutrients, disturbance due to ice damage or wave action in the spring, and so on. If it is possible to find a correlation of boundary clustering with a rapid change in any one of the large number of abiotic factors to choose from, should this correlation be interpreted as agreement with the individualistic concept? If some other abiotic factor is shown to change rapidly in a section of the marsh where there are relatively few boundaries, should we then conclude that the individualistic concept is still correct but that the factor in question plays no causal role? By arguing in

such a way we render the individualistic concept unfalsifiable at the level of pattern analysis.

The problem is not solved by choosing strong environmental gradients such as the altitudinal gradient up mountainsides (Whittaker 1951, 1956) or the gradient of relative water depth in a lake (Keddy 1983) or in a marsh, in which many abiotic gradients are correlated to produce a gradient-complex. This is shown in figure 6.1 where the distributions of various species are plotted along a hypothetical gradient. The values of two abiotic factors, A and B, are also plotted. If one were to do two different direct-gradient analyses of this 'gradient', then relative to factor A the boundaries would be clustered but relative to factor B the boundaries are regularly spaced. These two different results are obtained even though the two factors are positively correlated. Thus, the problem remains: the individualistic hypothesis is unfalsifiable when using pattern to deduce mechanism.

Hypotheses of mechanism

Whereas hypotheses regarding pattern can be tested using inferential statistics, hypotheses regarding mechanisms must be tested with experiments.

Levins and Lewontin (1982) and Simberloff (1982b) restate the

assumed mechanisms producing individualistic communities in an experimentally testable form. In Simberloff's words: "species are individually distributed according to their interactions with their physical surroundings and ... only upon falsification of this hypothesis ought one to move on to more complex (physical environment X other-species interaction) ones". Such a hypothesis has the advantage of not only being falsifiable but, contrary to Simberloff (1982 a,b), has actually been falsified in many field experiments. These experiments test the assumed mechanisms and not the predicted patterns which may arise as logical consequences from the mechanisms.

Sharitz and McCormick (1973) have demonstrated that the distribution of Sedum smallii on granite outcrops in the southeastern United States is controlled by a complex interaction of abiotic factors and competition with Minuartia uniflora. One boundary of Sedum smallii on these outcrops is determined by moisture stress and shallowness of the soil. The other end of its distribution is controlled through competitive exclusion from Minuartia uniflora. Studies on the rocky intertidal zone (Connell 1972; Paine 1984; Lubchenco 1980) have also demonstrated the importance of both biotic factors as well as interactions between biotic and abiotic factors in determining the structure of such communities. Grace and Whetzel (1981) give evidence that the distribution of Typha augustifolia is partly determined by competition with Typha latifolia in the

ponds which they studied. Silander and Antonovics (1982), in a series of removal experiments, showed that the distributions of most of the plant species in a coastal plant community were profoundly affected by the types of neighbors that were removed. Snow and Vince (1984) and Vince and Snow (1984) used transplant experiments in an Alaskan salt marsh to demonstrate the interaction of biotic and abiotic factors in determining the structure of that community. Other papers reaching similar conclusions were reviewed by Connell (1983) and Schoener (1983). Finally, Turkington and Aarssen (1984 and references therein) present evidence that biotic interactions can produce coevolutionary differences between local genotypes, depending on the types of species which each interacts with, therefore biotic interactions may affect community structure on an evolutionary time scale as well.

There is therefore a large body of evidence which falsifies the causal assumptions of the individualistic concept and demonstrates integrated, that is causally dependent, responses of species within a community.

Hypotheses of pattern should be tested using inferential statistics. Hypotheses of mechanism should be tested by experimental manipulations, making sure not to equate correlation with causation (Levins and Lewontin 1982). The way out of the community-unit vs. individualistic community debate is to deny

the dichotomy and to consider multiple working hypotheses of community structure.

Table 1.1: Analysis of deviance of the boundary distributions in Breckenridge Marsh, Quebec, Canada. The 'residual deviance' column gives the goodness-of-fit of each model to the observed distribution. The 'change of deviance' column tests the significance of each term in improving the goodness-of-fit in each successive model. **: $p<0.001$; probability values greater than 0.05 are not concidered significant and are not indicated by asterisks.

Terms	d.f.	Residual deviance	d.f.	Change of deviance
Constant	297	433.4	-	-
Interval length (covariate)	296	420.5	1	12.8**
Height interval	283	365.0	13	55.6**
Boundary type	282	364.0	1	1.0
Height interval X Boundary type	269	293.7	13	70.3**

Figure captions

figure 1.1: Predicted distributions of species along an environmental gradient, according to the two concepts. Above:the community-unit concept; below:the individualistic concept (after Whittaker 1975).

figure 1.2: The number of community patterns which could be obtained from species whose boundaries are either (a) randomly distributed or clustered and whose upper and lower boundaries are either (b) coincident or independent. Note that the two historical community concepts do not exhaust the possibilities shown.

figure 1.3: Breckenridge Marsh, latitude 45° 48' 00'', longitude 45° 57' 30''. The study site is located within the square. The city of Ottawa is located approximately 40 km to the southeast.

figure 1.4: The mean number of species boundaries in each 5 cm. height interval plotted against relative height. Within each rectangle the mean number of upper boundaries (hatched) and lower boundaries (clear) are shown.

figure 1.5: The distribution of all plant species occurring in at least two transects, relative to the height gradient. These distributions are determined by calculating the average position of each species' upper and lower boundaries over the thirteen transects.

figure 1.6: (a) the field distributions of nine species is plotted in a hypothetical gradient along with the values of two correlated abiotic factors. (b) The distribution of species' boundaries obtained from direct-gradient analyses of this marsh relative to the two abiotic factors.

figure 1.1

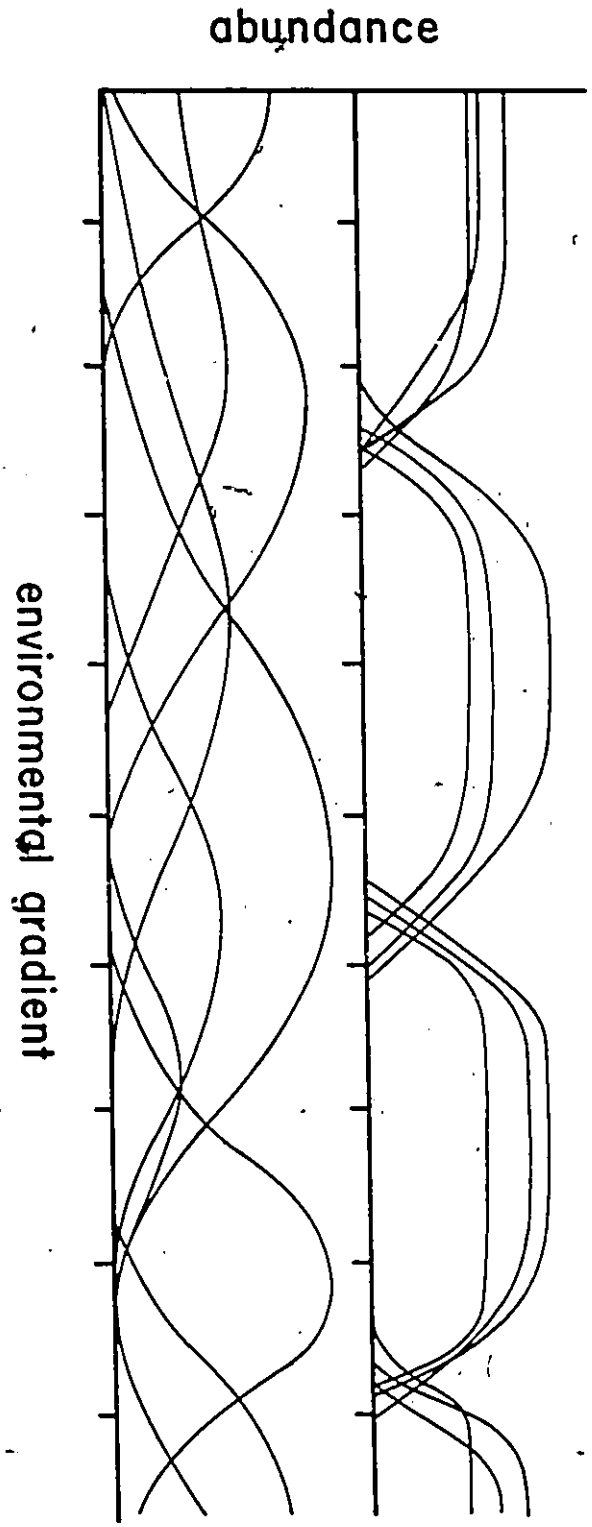


figure 1.2

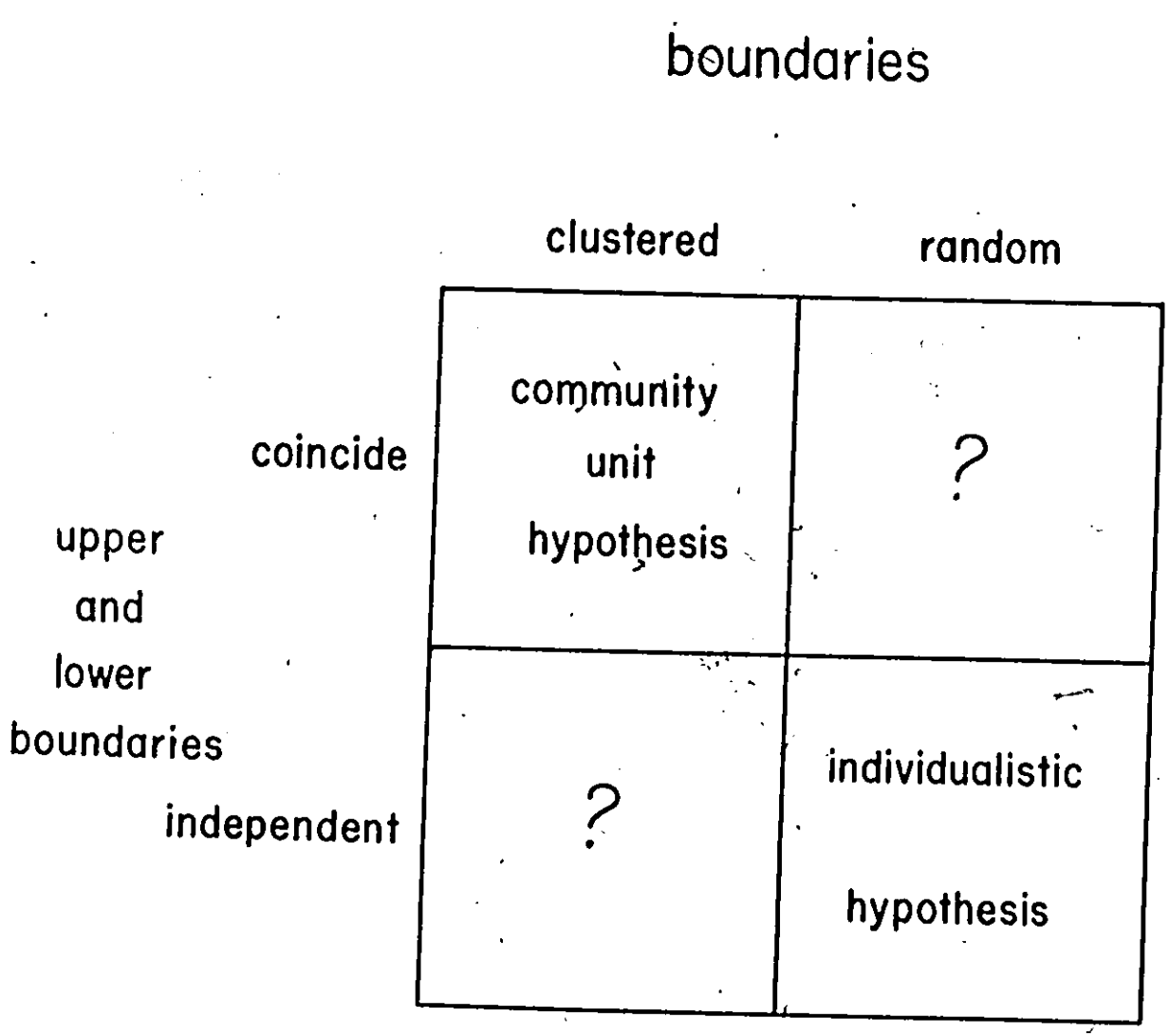

boundaries
clustered
random
coincide
upper and lower boundaries
independent
community unit hypothesis
?
?
individualistic hypothesis

figure 1.3

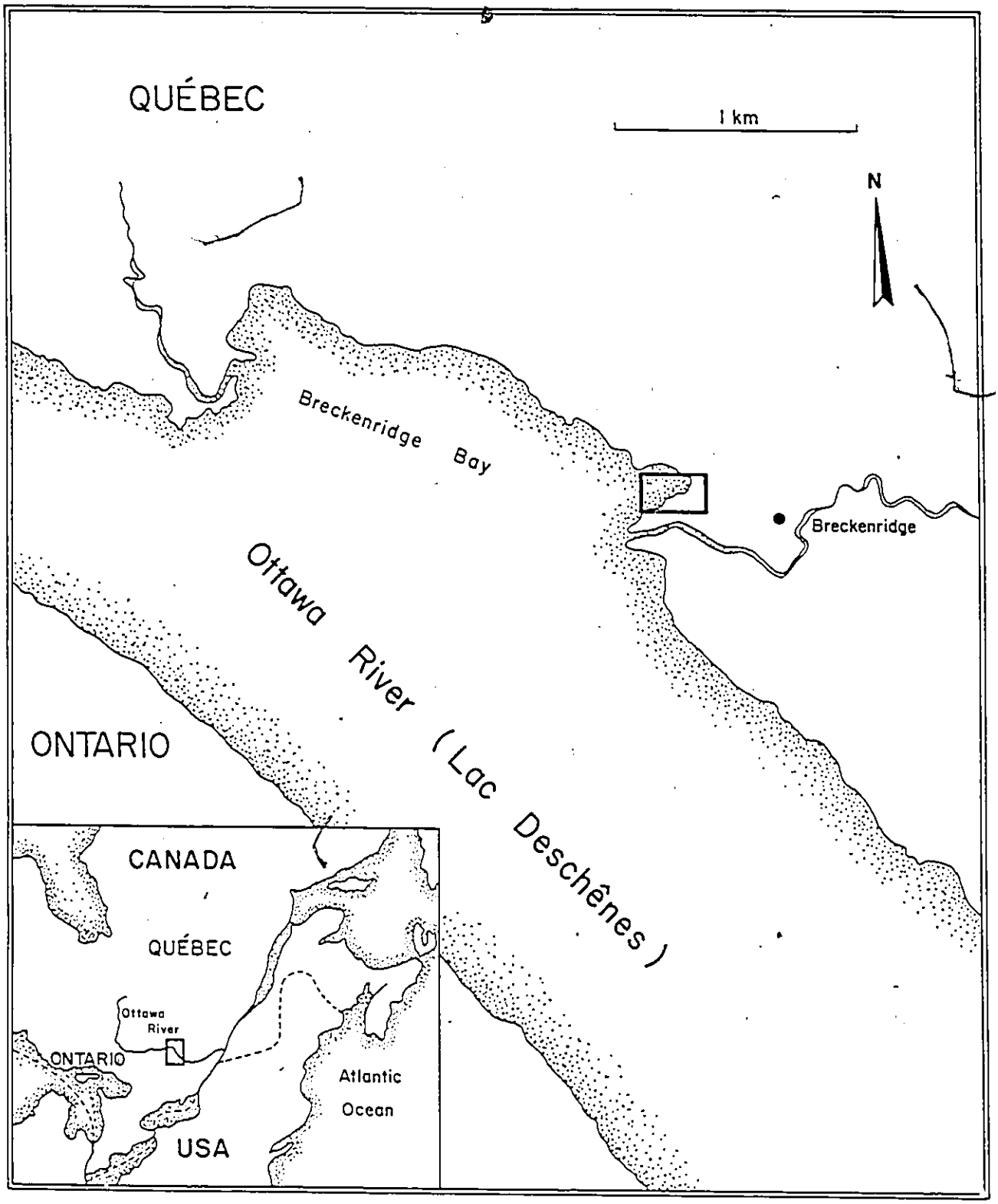

QUÉBEC
1 km
N
Breckenridge Bay
Breckenridge
Ottawa River (Lac Deschênes)
ONTARIO
CANADA
QUÉBEC
Ottawa River
ONTARIO
Atlantic Ocean
USA

figure 1.4

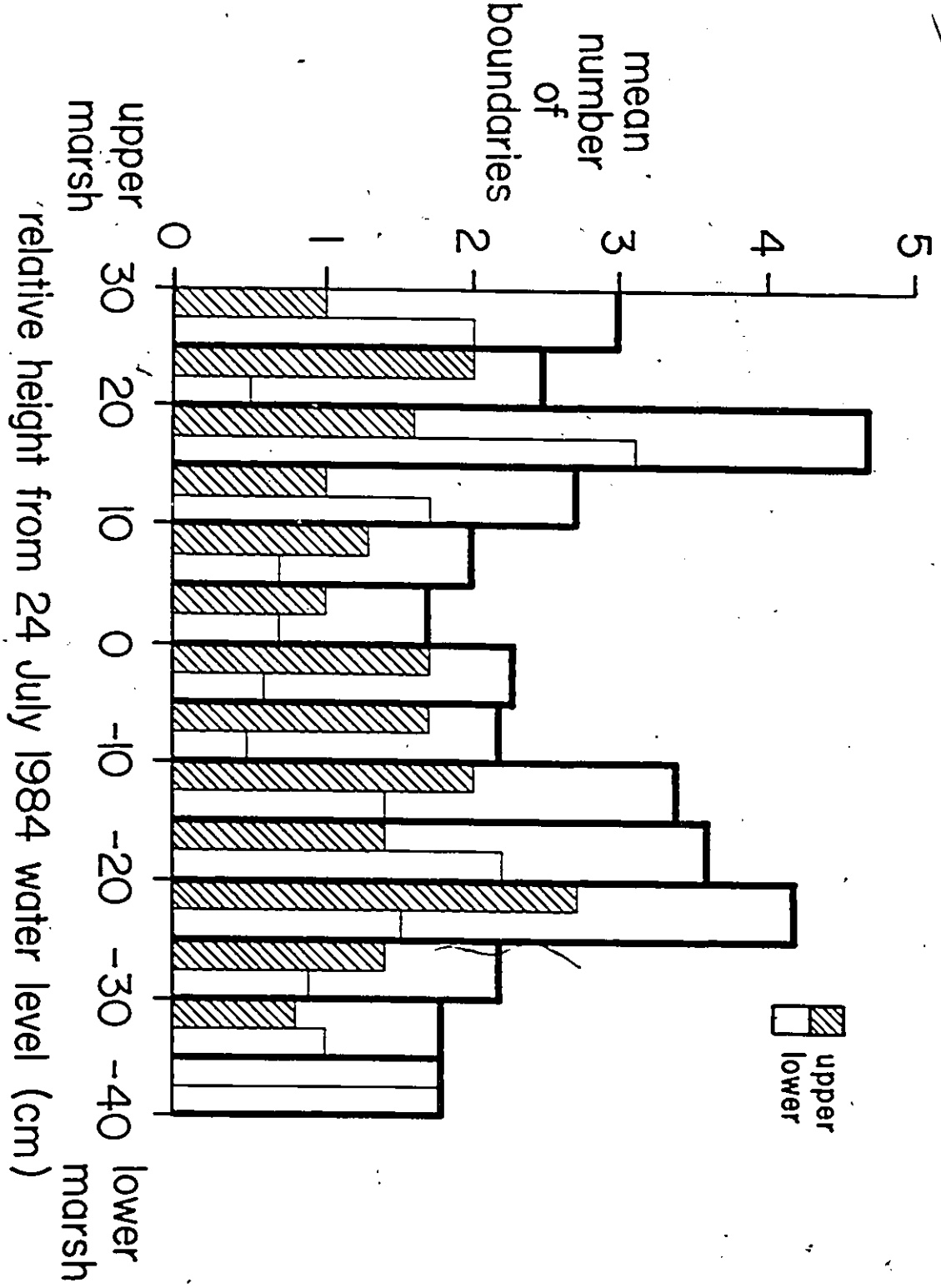
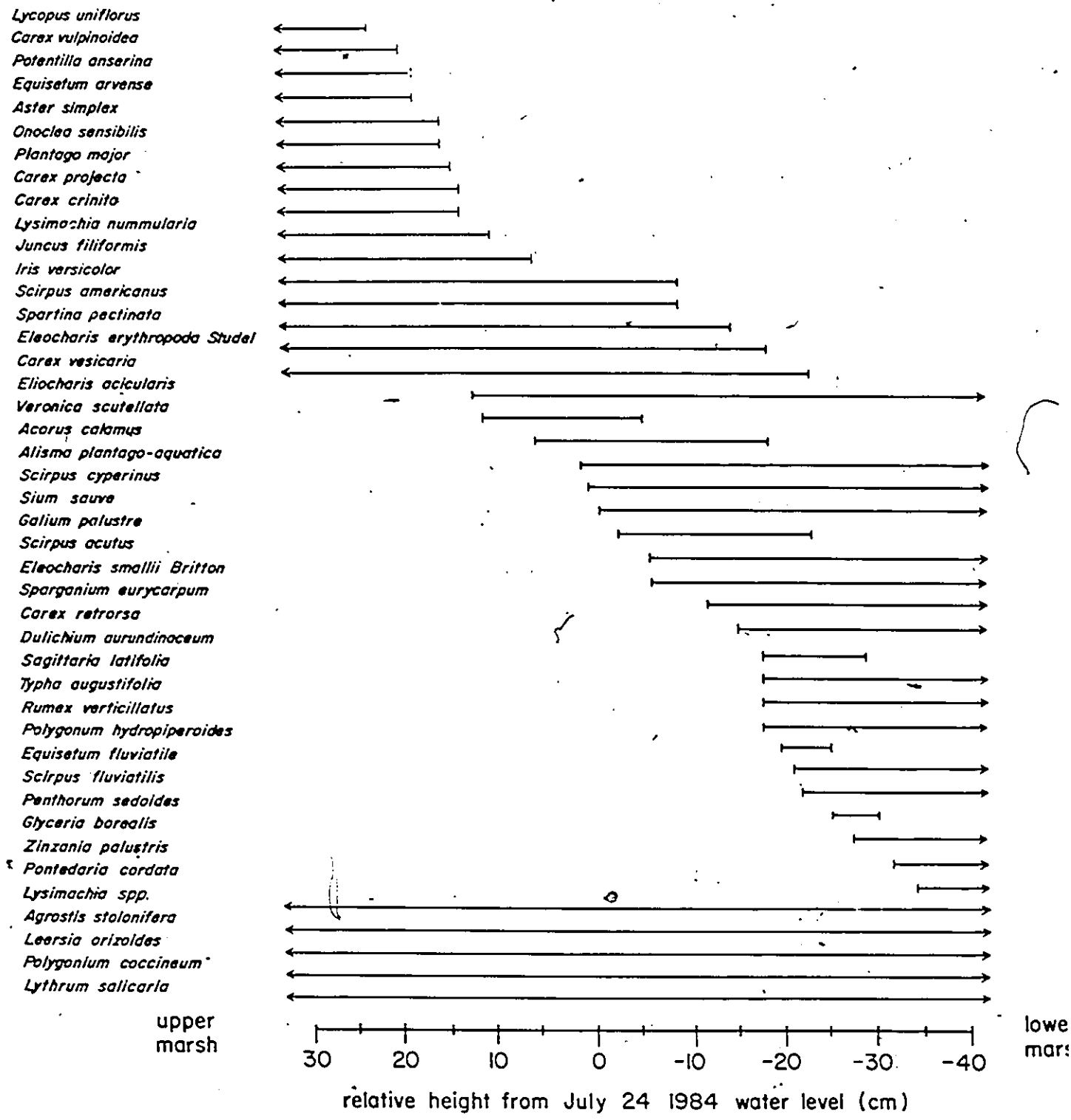
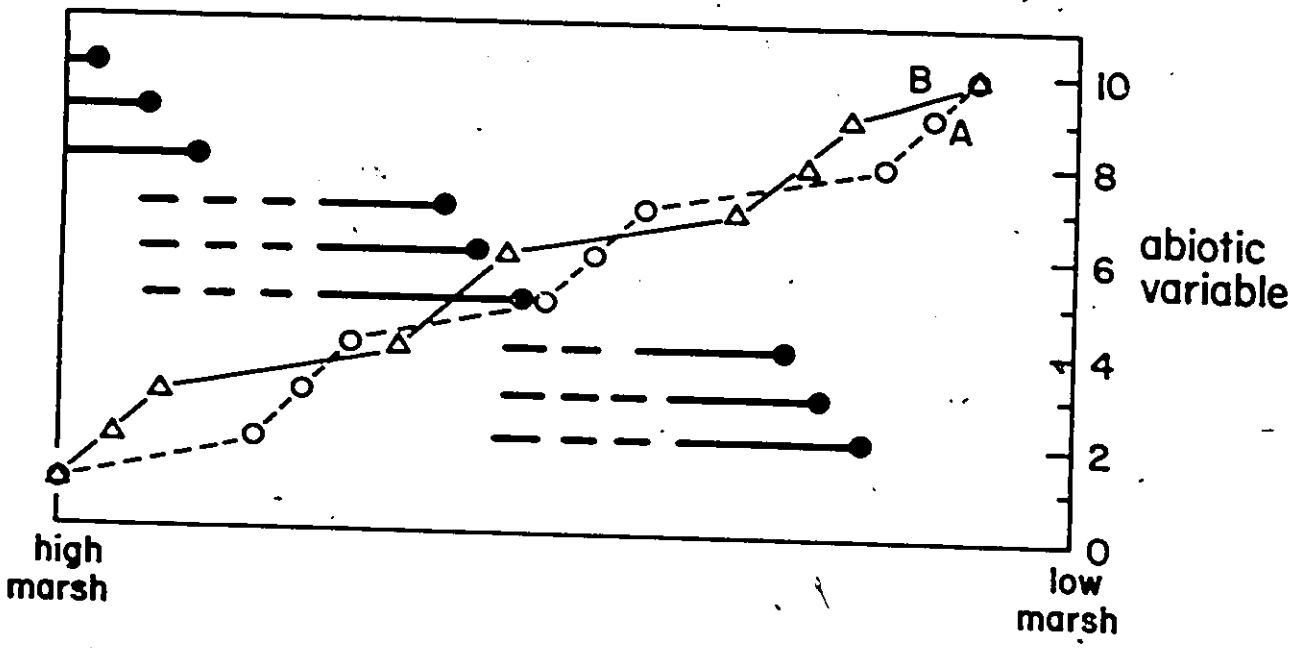

mean number of boundaries
0
1
2
3
4
5
upper marsh
30
20
10
0
-10
-20
-30
-40
lower marsh
relative height from 24 July 1984 water level (cm)
upper
lower

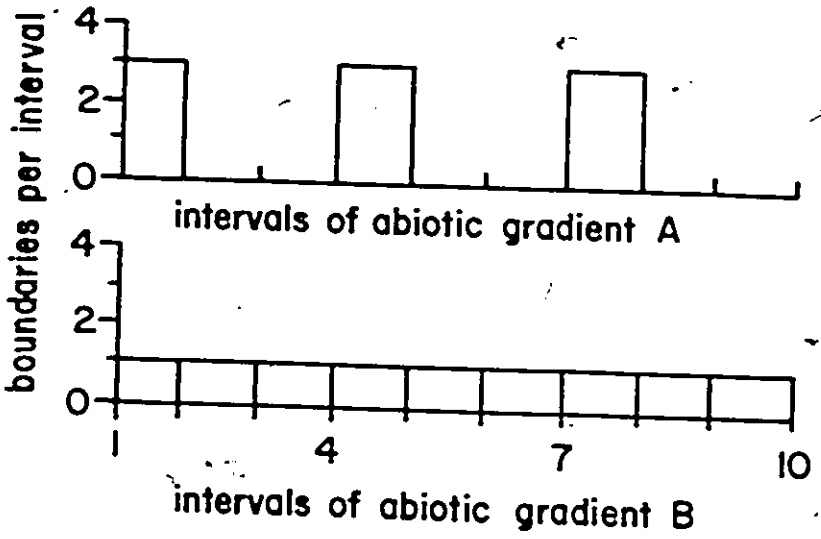
figure 1.5


Lycopus uniflorus
Carex vulpinoidea
Potentilla anserina
Equisetum arvense
Aster simplex
Onoclea sensibilis
Plantago major
Carex projecta
Carex crinita
Lysimachia nummularia
Juncus filiformis
Iris versicolor
Scirpus americanus
Spartina pectinata
Eleocharis erythropoda Studel
Carex vesicaria
Eliocharis acicularis
Veronica scutellata
Acorus calamus
Alisma plantago-aquatica
Scirpus cyperinus
Sium sauve
Galium palustre
Scirpus acutus
Eleocharis smallii Britton
Sparganium eurycarpum
Carex retrorsa
Dulichium arundinaceum
Sagittaria latifolia
Typha augustifolia
Rumex verticillatus
Polygonum hydropiperoides
Equisetum fluviatile
Scirpus fluviatilis
Penthorum sedoides
Glyceria borealis
Zizania palustris
Pontederia cordata
Lysimachia spp.
Agrostis stolonifera
Leersia orizoides
Polygonium coccineum
Lythrum salicaria
upper marsh
lowe
mars
30
20
10
0
-10
-20
-30
-40
relative height from July 24 1984 water level (cm)

a.


B
A
10
8
6
4
2
0
abiotic variable
high marsh
low marsh

b.


boundaries per interval
4
2
0
intervals of abiotic gradient A
4
2
0
1
4
7
10
intervals of abiotic gradient B

Chapter two

A test of hypotheses concerning community organization along an environmental gradient

Introduction

Mechanisms producing (or not producing) structure in ecological communities have frequently been inferred from observed species' distributions (MacArthur 1972, Pielou and Routledge 1976, Diamond 1975,1979, Simberloff 1978, Connor and Simberloff 1978,1979, Grant and Abbott 1980, Wright and Biehl 1982, Silvertown 1983, Keddy 1983). An underlying mechanistic model is often hypothesized, predicted patterns are derived, and then the observed pattern of species' distributions is compared to the predicted pattern. With this method it is possible to reject models whose predicted patterns are inconsistent with those observed in real communities, but what can be concluded if very different models produce identical patterns? In such situations no amount of debate concerning inferences from patterns can resolve the issue. Only experimental manipulations designed to test the validity of the premises of the models will suffice. I will illustrate this problem, and its resolution, by examining plant distributions along an environmental gradient, where three different models yield identical predictions.

Zoned plant communities are found in many systems, including the rocky intertidal zone (Connell 1972, Underwood 1978a,b, Lubchenco 1980, Paine 1984), salt marshes (Pielou and Routledge 1976, Snow and Vince 1984), mountainsides (Whittaker 1956,

Terborgh 1971) and freshwater wetlands (Buttery and Lambert 1965, Nicholson and Aroyo 1975, Grace and Wetzel 1981, Keddy 1982,1985, Wilson and Keddy 1986a,b). Rabinowitz (1978) has summarized the three very different mechanisms which can produce such distributions (figure 1.2) and these are described below.

The first model assumes that the differential distribution of species along an environmental gradient is determined solely by the individual tolerances of each species to the changing physical conditions of the gradient, as well as stochastic factors relating to dispersal. Abele et al. (1984) claim that this mechanism is of general occurrence, and Simberloff (1982a,b) suggests that this model should be assumed correct until explicitly falsified. Of course, this model is not new; it is simply a mechanistic reformulation of Gleason's (1926, 1939) individualistic concept of plant communities (Chapter 1, Shipley and Keddy 1987). A critical assumption of this model is the equivalence of realized (field) distributions and potential distributions. A potential distribution is the distribution that a species would have along an environmental gradient when the effects of neighbors have been removed.

The second and third models each assume a role for both biotic and abiotic factors in determining the differential distributions of species along an environmental gradient. They differ in the way these two classes of factors interact. The

second model assumes that zonation patterns result because there is a trade-off between the ability to tolerate stressful (sensu Grime 1979) conditions and the ability to be a competitive dominant. Thus, dominants occupy the least stressful part of the gradient and competitive subordinates are excluded to the more stressful parts of the gradient. Note that according to this model, species' potential distributions are necessarily inclusive (sensu Colwell and Fuentes 1975) and species' ranks on a competitive hierarchy do not change along the gradient, a point stressed by Grime (1977).

The third model is reminiscent of MacArthur's "limiting similarity" concept (MacArthur 1972) and has been proposed to account for wetland plant distributions by Hutchinson (1975, p. 497). Species have widely overlapping potential distributions but with different maxima, and zonation occurs because species' ranking on a competitive hierarchy changes along the gradient. Each species is the competitive dominant at some point along the gradient and excludes all others in that region.

These three models cannot be tested by comparing observed and predicted patterns, since they predict the same patterns. On the other hand, these models make various, and often mutually exclusive assumptions. These assumptions will be tested in this study, using transplant experiments of three species of emergent macrophytes (Carex crinita, Acorus calamus and Typha

angustifolia) having contiguous distributions along a water depth gradient in a zoned freshwater marsh plant community. Specifically I ask:

1) can species expand their range along the water-depth gradient in the absence of interspecific competition?

2) are the potential distributions of these species along the water depth gradient inclusive?

3) does the ranking of species in a competitive hierarchy vary along the water depth gradient?

Methods

1. Description of the marsh

The field site is a freshwater marsh located near Breckenridge, Quebec, Canada, along the Ottawa River (45° 48' 00" N, 45° 57' 30" W). This is the same marsh as described in chapter 1. The distribution of all emergent macrophytes along the water depth gradient between the average yearly maximum and minimum water levels can be found in figure 1.4 of Chapter 1. The study site is located in a sheltered bay and has fertile, organic soil.

Figure 2.2 shows the average monthly water levels in this marsh over the last twenty years as well as one standard derivation, based on the records at a monitoring station (number 02KF005) located within the same drainage basin; the standard zero mark is equivalent to a geodetic height of 56.40 m (Water Survey of Canada). Also shown are the water levels during the experiment, from July 1985 to September 1986. As can be seen, water levels were above average over most of the experiment, but not abnormally high.

The boundaries of the species distributions along the water depth gradient are not randomly located. Rather, there are three

groups of species distributions (Chapter 1, Shipley and Keddy 1987). The first group all stop at around the average May 20 water level (see figure 2.2). Carex crinita is one of the dominant species in this group. A second, smaller, group of species have distributions straddling the water depth gradient, with upper limits at around the average June 1 water level and lower limits at around the average June 20 water level. Some of the species in this group are rare in the marsh and so their placement in this group may be due to the vagaries of sampling, but Acorus calamus is abundant in this part of the marsh. The third group of species begin their distribution at around the average July 20 water level and Typha angustifolia is the dominant in this part of the marsh.

2. Transplant experiment

Four locations were chosen along the water depth gradient. The first site was established within the realized distribution of Carex crinita, the second site within the realized distribution of A. calamus, the third within the realized distribution of T. angustifolia, and the fourth site beyond the realized distributions of all three test species. This last site was dominated by Sparganium eurycarpum and was at the average yearly low water level. Therefore, each site was in progressively deeper portions of the marsh and was inundated for progressively longer periods of the growing season.

Within each site, thirty quadrats were established (20x40 cm). Each quadrat was separated from the next by 50 cm, was divided into two (20x20cm) subplots and was surrounded by a plastic barrier sunk 10 cm into the soil to prevent rhizomes from growing into or out of the subplot. One of the two subplots was randomly chosen and all above-ground biomass was removed (removal treatment). The thirty quadrats in the site were divided into ten blocks of three quadrats each. Within each block each of the three test species was randomly assigned to one of the quadrats. One ramet of the chosen species was planted in the centre of each subplot. This was therefore a three factor experiment: (1) species, (2) site and (3) treatment, i.e. removal of neighbors. The actual layout of this experiment, as well as the dry weight per ramet and relevant covariates, are given in appendix 2.1.

Ramets of the three test species were collected from within the same local region of the marsh from July 7 to July 9 1985. The ramets of each species were chosen to be approximately the same size and the rhizome of each was cut to a standard length. Roots were not immediately washed of soil, instead the ramets were placed in standing water for up to six days, after which most soil had fallen off naturally without damaging the fine roots. Before planting, 15 ramets of each species were randomly chosen to determine the initial biomass per ramet of each

species. These initial biomass values were obtained after drying the ramets at 60°C to a constant weight. Plastic tags were placed around the rhizome of each ramet so that they could be identified at the end of the experiment.

Ramets were planted from July 9 to July 12 1985 following a randomized planting schedule to avoid the confounding effects of planting time. During the first two weeks following planting, the transplants were shaded and misted to prevent transplant shock; only six out of 240 plants died during this period. Any plants showing obvious signs of transplant shock during the first month following transplanting was replaced. No further ramets were replaced after August 12 1985. All quadrats were monitored and weeded regularly during the experiment and their condition noted, including evidence of herbivory, which was due almost exclusively to muskrats. The experiment ran from July 1985 until September 1986; the test plants therefore experienced the natural conditions of all four seasons.

Competitive ability includes both the ability to reduce the growth of neighbors and the ability to resist the depression of one's own growth due to the presence of neighbors. In this study, only the second effect could be measured. Thus, the competitive ability of species i at site j ($D_{i,j}$) was measured as

$$D_{i,j}=(C_{i,j}-U_{i,j})/C_{i,j}$$

where C_{ij} (cleared) is the average biomass of species i in the subplot cleared of neighbors and U_{ij} (uncleared) is the average biomass of species i in the subplots not cleared of neighbors and therefore containing the natural vegetation of site j. A value of zero implies that the presence of neighbors had no measurable affect on the growth of the test species at that site. The final biomass of the ramets was again obtained after drying them at 60°C to a constant weight.

Results

No test plants survived at site 4 over the course of the experiment, except for two lone individuals of T. angustifolia. Therefore, site 4 was not included in the analysis of variance. ANOVA of the remaining data (table 2.2) revealed that all three species were similarly affected by the presence of neighbors. Competitive depression decreased the growth of the test plants in all three sites. On the other hand, the responses of each species to competitive depression changed with position on the water-depth gradient. This is shown by the significant three-way interaction term in the ANOVA, indicating that ranks in the competitive hierarchy varied according to gradient position. Figure 2.3 illustrates this by plotting the competitive depression of each species at each site.

Since the rhizomes of the test ramets had been tagged before planting and all quadrats were regularly monitored, I were able to classify all deaths as due to (1) herbivory by muskrats, (2) unknown disturbance events during the winter or early spring, most likely caused by wave or ice action, or (3) deaths not due to disturbance (i.e. plant still present and intact,but dead). The relative contributions of these three classes of factors are shown in figure 2.4. Deaths not due to disturbance could be attributed to abiotic effects since the proportion of deaths in

cleared and uncleared plots were approximately equal.

C. crinita was excluded from sites 3 and 4 primarily because of an inability to tolerate the abiotic conditions of the site (figure 2.4). In site 4 none of the twenty test plants survived to the end of the experiment and almost all (85%) of the deaths were due to abiotic effects. In site 3 there was a small reduction in growth due to competition (figure 2.5) for those plants that had not died, but this reduction was small compared to the large percentage of deaths (50%) due to abiotic conditions and to disturbance events (20%). On the other hand, C. crinita was capable of growing in site 2. Only one of the twenty test plants died and surviving ramets increased their biomass beyond their initial level in the absence of surrounding vegetation (figure 2.5). Thus, C. crinita appears to be excluded from site 2 because of competitive depression.

Ramets of A. calamus were excluded from site 4 by the actions of muskrats. Since only one ramet remained uneaten by the end of the experiment it is unknown whether this species could survive in site four in the absence of herbivory. Ramets of A. calamus were also eaten in site 3, although to a lesser degree (35%). Of those plants that survived, competition severely reduced the growth of ramets planted within uncleared plots (figure 2.5). In the plots cleared of surrounding vegetation, ramets were able to maintain their initial reserve

of biomass but did not increase in size. Presumably populations of A. calamus in site 3 would be vulnerable to both herbivory and competition and therefore would not persist for long. In site 1 A. calamus could grow quite well in the absence of competitors, but was depressed in their presence. Thus, it is presumably excluded from site 1 by competition.

T. angustifolia was excluded from site 4 due to disturbance events. The majority of these events (70%) occurred during the winter and early spring when monitoring was impossible. It is possible that these plants were eaten during this time but it seems much more likely that they were uprooted by wave and ice action, since the above-ground parts of the plants had been frozen in the ice during the winter. The very loose mucky soil at this site would have made secure rooting very difficult and many uprooted ramets of Sparganium eurycarpum were found at this site in the spring. Despite the severe mortality at site 4, two ramets of T. angustifolia survived, and in fact grew extremely well. In site 1, T. angustifolia maintained, but did not increase its initial biomass reserve when grown in the absence of competitors. In their presence, biomass decreased. Therefore, it seems unlikely that T. angustifolia could maintain a population at this site even in the absence of competition. In site 2 T. angustifolia had an increase in the average biomass of ramets when grown in the absence of surrounding vegetation, but was depressed when in the presence

of competitors. I. angustifolia appears to be excluded from site 2 due to competition.

Discussion

The first model, that of equivalence between realized and potential distributions, must be rejected. Although physical factors did eliminate all three species from the fourth site, the presence of neighbors had obvious effects in general, both on the growth of the plants and on the expansion of the potential ranges of the three test species along the water depth gradient. There are a few published field experiments showing no apparent effect of neighbors on the distribution of non-motile species in zoned communities (Buckley 1982) but most field experiments have found competitive effects to be present (Clements et al. 1929, Connell 1972, Sharitz and McCormick 1972, Colwell and Fuentes 1975 and references therein, Grace and Wetzel 1981, Silander and Antonovics 1982, Paine 1984, Wilson and Keddy 1986a,b, Gurevitch 1986).

In spite of this, a number of descriptive studies of zoned communities (Gleason 1926, 1939, Walker and Wehrhahn 1971) as well as physiological autecological studies (Kozlowski 1984 and references therein) accept the first model of community organization. In fact, Spence (1982), in his major review of freshwater plant zonation, lists a large number of abiotic factors but does not discuss biotic interactions among vascular plants at all. Hutchinson's (1975) book on aquatic botany is

devoted mostly to abiotic factors as well, despite the author's many contributions to the concept of competition. He does mention the probable existence of competitive interactions in his book (for instance, on pages 118, 497) but does not go into any more detail, presumably because of a lack of published papers investigating the existence of such interactions.

This curious contradiction between experimental field studies and descriptive or autecological physiological studies may be due to a failure to distinguish correlation from causation. When analyzing patterns, if species distributions can be shown to be correlated with various physical factors, one should conclude that model one cannot be rejected, not that it should be accepted. This distinction has important ramifications for the current debate concerning "null" models in ecology (Simberloff 1978, Connor and Simberloff 1978,1979, Diamond 1979, Wright and Biehl 1982, Roughgarden 1983, Gilpin and Diamond 1984, Colwell and Winkler 1984). Since often more than one model can predict the same pattern, as in this study, analyses of pattern alone can provide little if any evidence in support of any conclusions.

I do not claim that the first model is never correct since it may reasonably apply in those systems where the effects of neighbors are minimal, for instance in highly disturbed or very stressful habitats (Grime 1979). Another system which might be a likely candidate for model 1, though not in the context of

plant communities, is one in which the organisms are highly motile and transient, at least seasonally, such as the bird communities studied by Weins (1984). However, as stressed above, strong evidence for this can only come from experimental manipulations of either the species or the gradient.

The second model must also be rejected. However, I failed to reject the third model. The potential distributions of the three species were not inclusive and the species ranks on a competitive hierarchy changed along the gradient. Competitive dominants did not occupy the least stressful parts of the gradient because "competitive dominance" varied with gradient position. Competitive subordinates were not excluded to the most stressful parts of the gradient because "stress" was experienced differently by the three species. These two results have important implications for Grime's (1979) model. If each species experiences the gradient differently, then one cannot speak of stress as an attribute of a community. If competitive ability, in this case the ability to resist competitive depression, depends on where along the gradient the interactions are occurring, it is difficult to speak of " competitor" as an invariant attribute of a species.

There are, however, a number of systems in which this second model has been shown to operate. In the rocky intertidal zone (Connell 1972) the lower parts of the water depth gradient are

less stressful for most of the species studied, and it is this part of the gradient in which biotic interactions are most important. Grime (1979) has compiled a large body of evidence suggesting that this model operates along moisture and soil fertility gradients in terrestrial grasslands. Wilson and Keddy (1985) have shown that stress was experienced similarly by a group of twelve wetland species growing along a exposure gradient. As well, Colwell and Fuentes (1975) have documented a number of examples in which this model applies. Finally, Grace and Wetzel (1981) have shown that in their artificial ponds containing T. latifolia and T. angustifolia, the potential distribution of the former species was included within the potential distribution of the latter. T. latifolia was capable of competitively excluding T. angustifolia from the higher shoreline, causing its realized distribution to be truncated. Zonation in that system was apparently consistent with model 2. Interestingly, T. angustifolia was also competitively excluded from the higher shore in our study as well.

This apparent disagreement between my results and those cited above can be reconciled by considering the types of gradients involved. Those gradients whose communities are arranged according to model 2 appear to be ones consisting of increasing quantities of some essential resource (sensu Tilman 1982) or condition. It seems quite reasonable to expect most plant species to respond similarly to a gradient of nutrient or

soil water concentration, as described by Grime (1979), over the range of concentrations normally encountered in those communities. On gradients consisting of non-resources or of substitutable resources (sensu Tilman 1982) there is no reason to expect a shared response. On gradients of this type different morphological adaptations, such as bill size in birds to eat different sizes (qualities) of seeds, or different physiological adaptations, such as the ability to tolerate soil anoxia in wetland plants, may result in distinct responses by each species to the same gradient. These differential adaptations may also affect competitive ability. For instance, C. crinita did not begin growth until the soil was uncovered by receding water, after which it grew well in the cleared subplots even in the deeper sites, while both A. calamus and T. angustifolia could grow while still submerged. As a result, C. crinita was more severely affected by competitive depression in the deeper sites because by the time the water level had fallen sufficiently, the natural vegetation of the site had already established a canopy.

The three models discussed in this paper may be mutually exclusive for a particular gradient, but different types of gradients may possess communities constructed according to different mechanisms. In emergent wetlands, for example, there exist two different types of gradients, one of water depth and one of exposure, and there may therefore be two different mechanisms operating (figure 2.6). The exposure gradient is

perpendicular to the water-depth gradient and involves correlated changes is disturbance (sensu Grime 1979) and soil fertility. One end of this exposure gradient consists of nutrient-poor, sandy beaches which are exposed to the full force of incoming waves. The other end of this exposure gradient consists of sheltered, nutrient-rich bays (Keddy 1982, 1983). At a constant water depth and moving along the exposure gradient, model 2 may apply (Wilson and Keddy 1985, 1986a,b). At a constant level of exposure and moving along the water depth gradient, as done in this study, model 3 apparently applies. Finally, model 1 may apply along the water depth gradient at the most exposed shores, where a combination of low soil fertility and extreme exposure to wave and ice action prevents an extensive vegetation cover from forming.

Whether this pluralistic model is correct cannot be resolved by inferences from pattern. Experimental tests of the assumptions will provide the best method for examining the hypothesized relationships between patterns and the mechanisms which generate them.

Table 1.2. Summary of the analysis of variance. Subplots that were disturbed, and all of site 4, have been removed from the analysis. Ramet biomass values, the response variable, are log-transformed.

Source	D.F.	SS	MS	Significance
species (Sp)	2	43.13		
treatment (T)	1	9.62	9.62	0.002
site (S)	2	54.33	27.25	<0.001
T × S	2	0.67	0.33	0.72
Sp × T	2	2.17	1.09	0.34
Sp × S	4	31.97	7.99	0.001
Sp × T × S	4	13.04	3.27	<0.01

Figure captions

Figure 2.1. Realized distributions of three species along an environmental gradient are shown at left. The three panels on the right depict models 1,2 and 3, respectively. Realized distributions are shown with solid lines, the potential distributions are shown with broken lines.

Figure 2.2. The thick, solid line shows the average monthly water levels in Breckenridge Bay over the last twenty years. The thin, solid lines give one standard deviation above and below the monthly averages. The broken line shows the actual monthly water levels during the experiment. The four stippled regions mark the position of the four experimental sites relative to the water-depth gradient. The months are shown along the bottom and those enclosed in the box represent the growing season.

Figure 2.3. The percent reduction in growth in the presence of surrounding vegetation for each of the three test species (C. crinita, A. calamus and T. angustifolia respectively) is shown in each block of three histograms. The three sites are shown along the bottom. Cross-hatched histograms indicate the species that normally occurs in each site.

Figure 2.4. The percent mortality due to herbivory (H), abiotic disturbance (AD) and abiotic conditions (AC) respectively are shown in each block of three histograms. Each block represents one of the four experimental sites.

Figure 2.5. Average final ramet biomass of the three test species in the four sites. Bars represent 95% confidence intervals. The stippled region gives the 95% confidence intervals for the initial ramet biomass values. Data are log transformed.

Figure 2.6. Hypothesized relationship between the two environmental gradients found on shorelines and the three models of zonation. The cross-hatched area marks the position of the study site.

figure 2.1

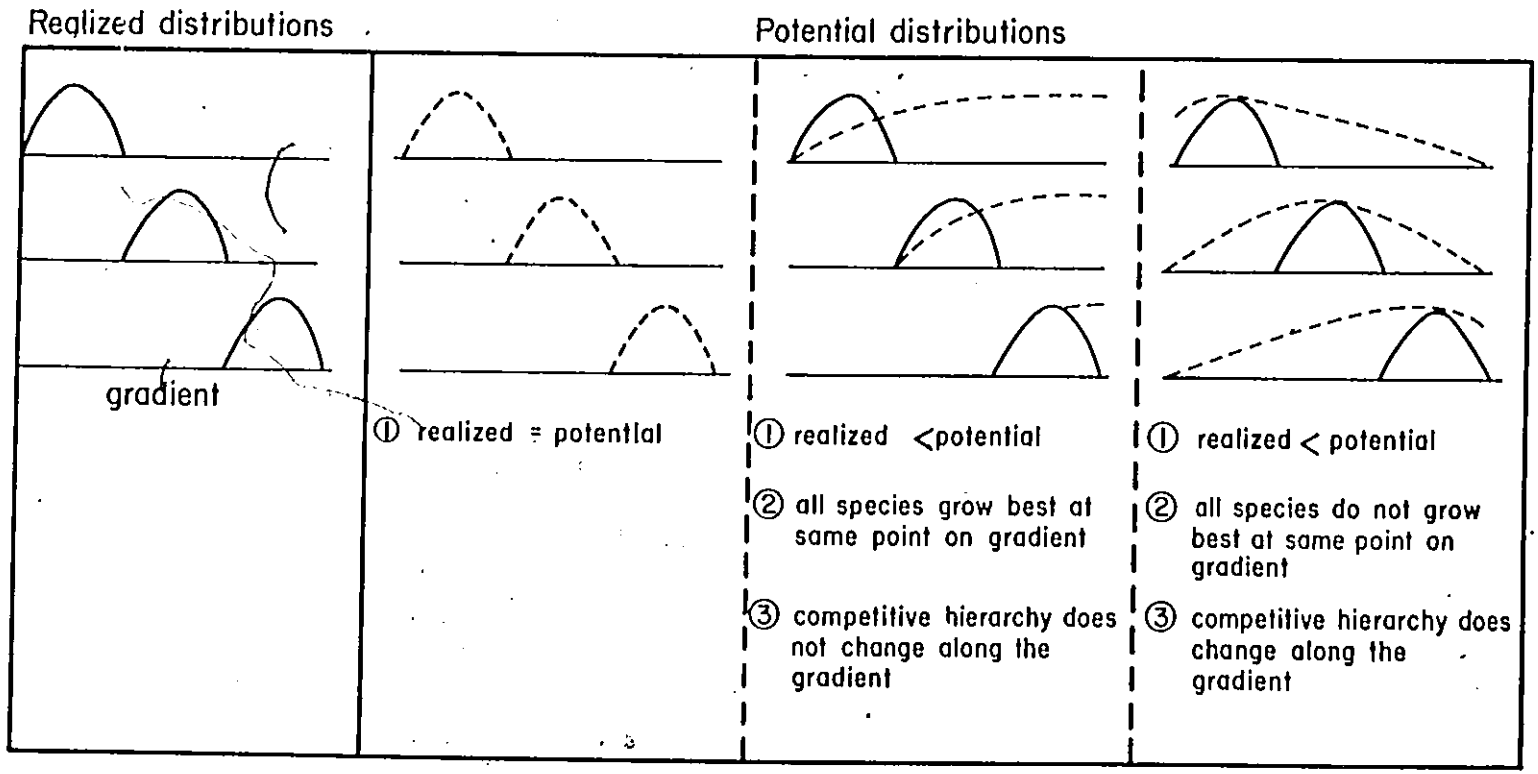

Realized distributions
Potential distributions
gradient
① realized = potential
① realized < potential
② all species grow best at same point on gradient
③ competitive hierarchy does not change along the gradient
① realized < potential
② all species do not grow best at same point on gradient
③ competitive hierarchy does change along the gradient

figure 2.2

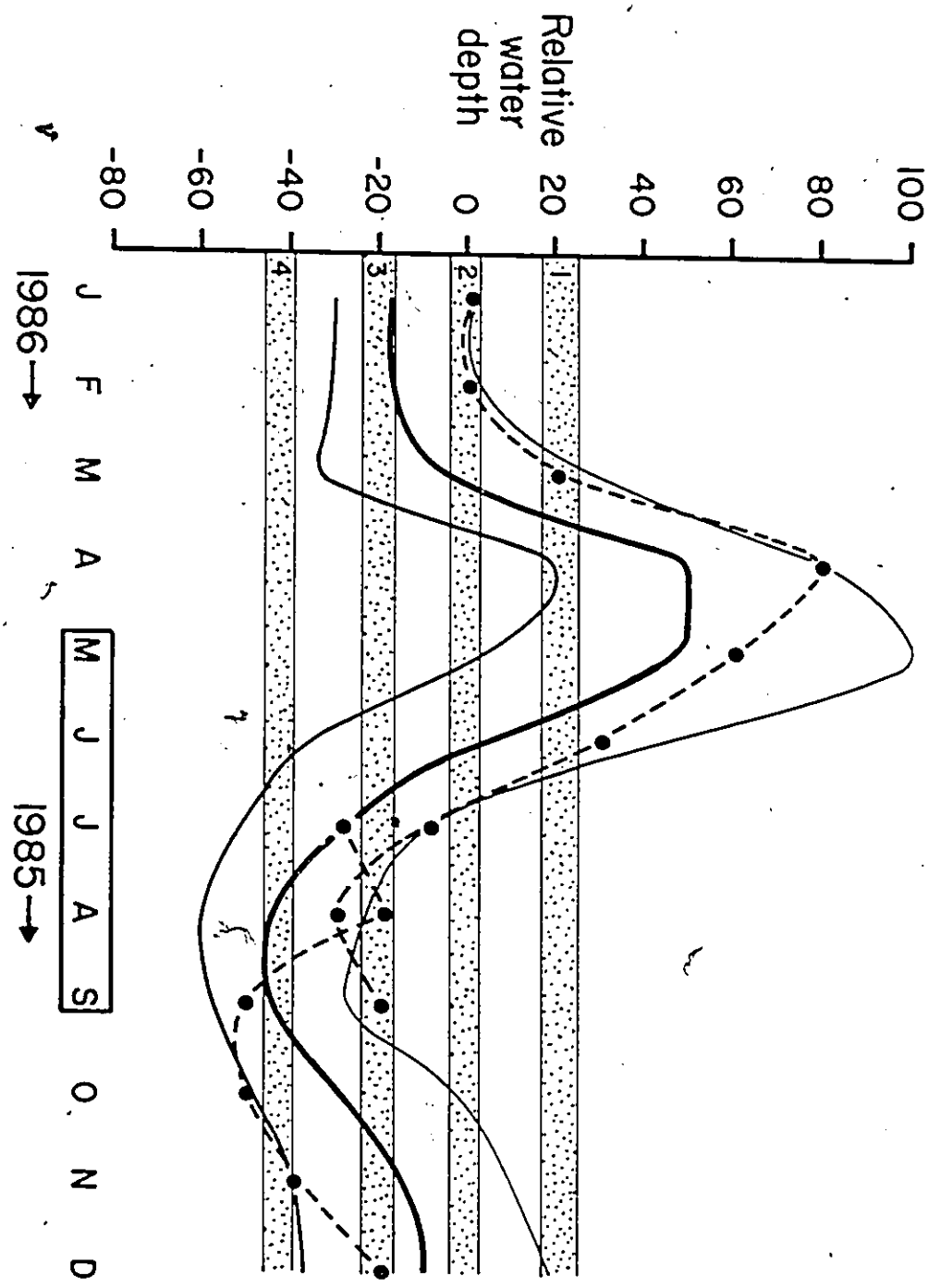
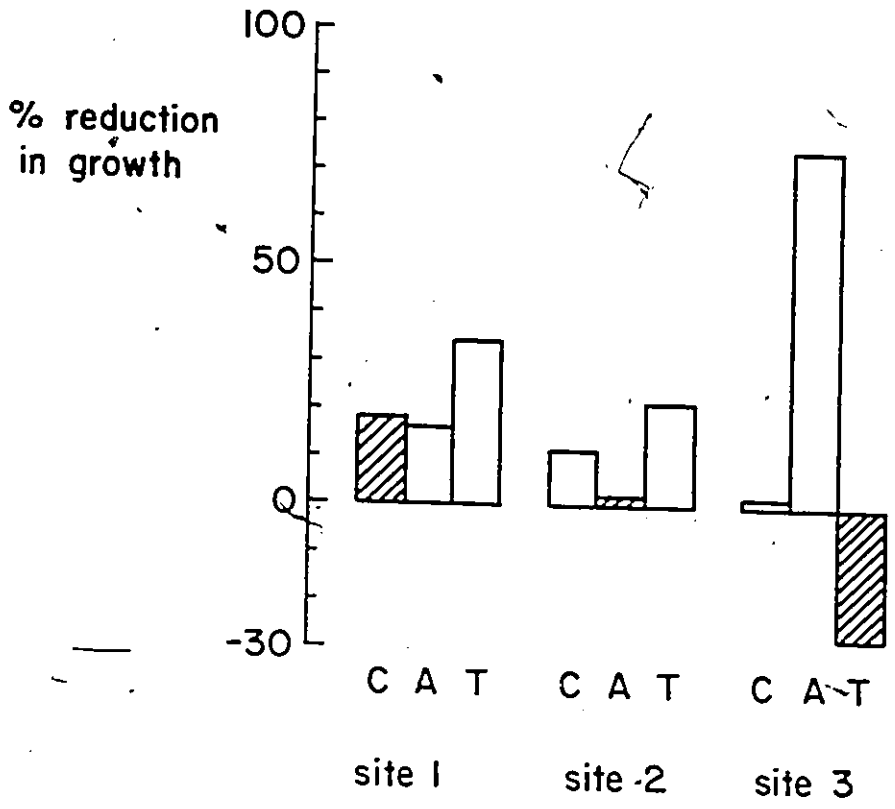

Relative water depth
100
80
60
40
20
0
-20
-40
-60
-80
1
2
3
4
J F M A M J J A S O N D
1986
1985

figure 2.3



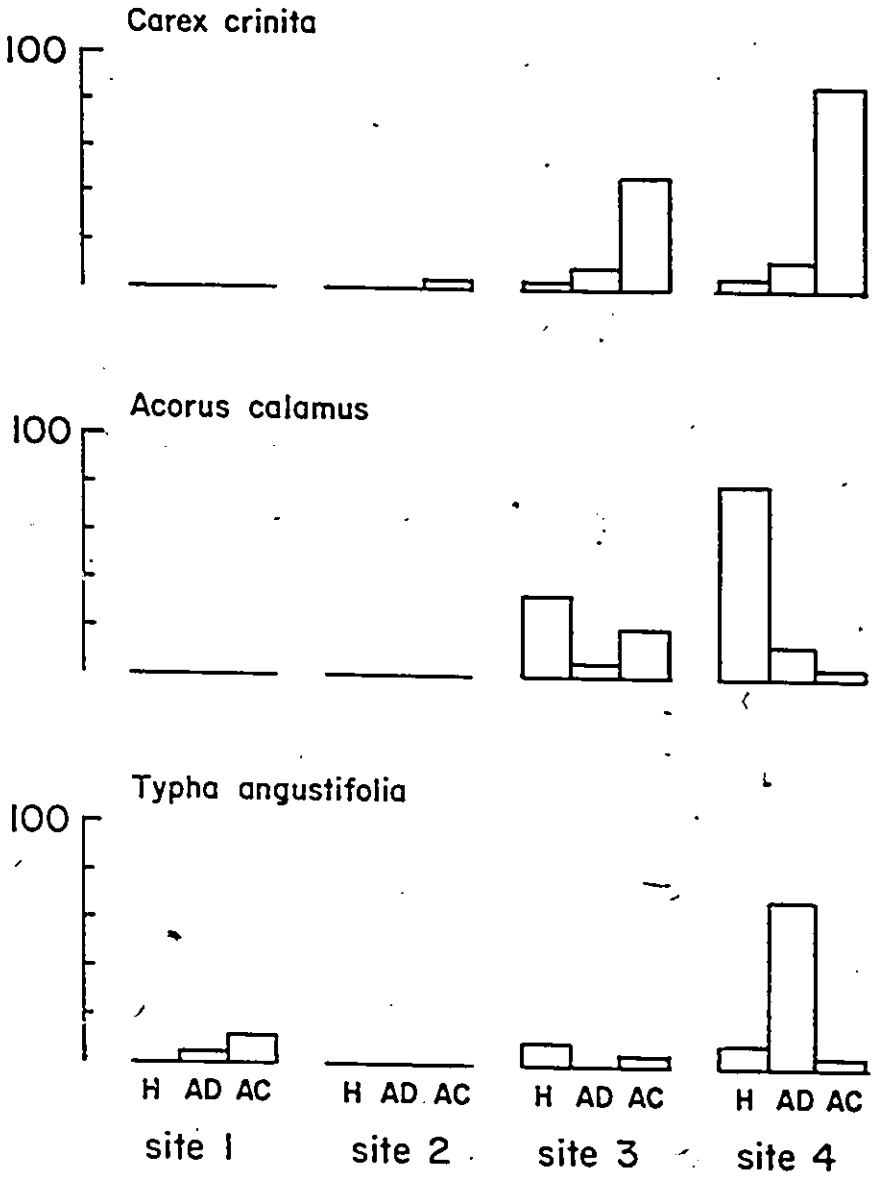

Carex crinita
100
Acorus calamus
100
Typha angustifolia
100
H AD AC
H AD AC
H AD AC
H AD AC
site 1
site 2
site 3
site 4

figure 2.5

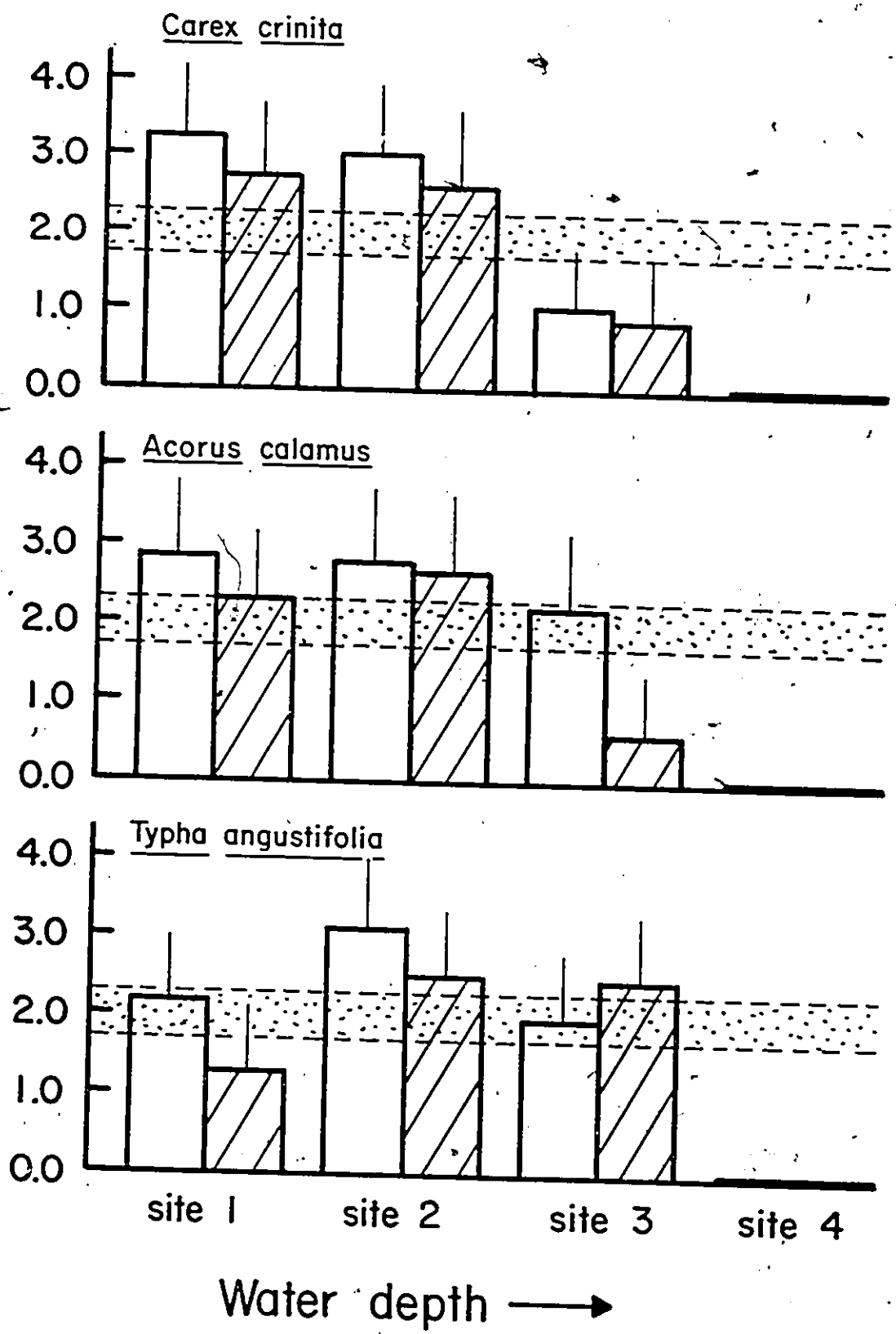
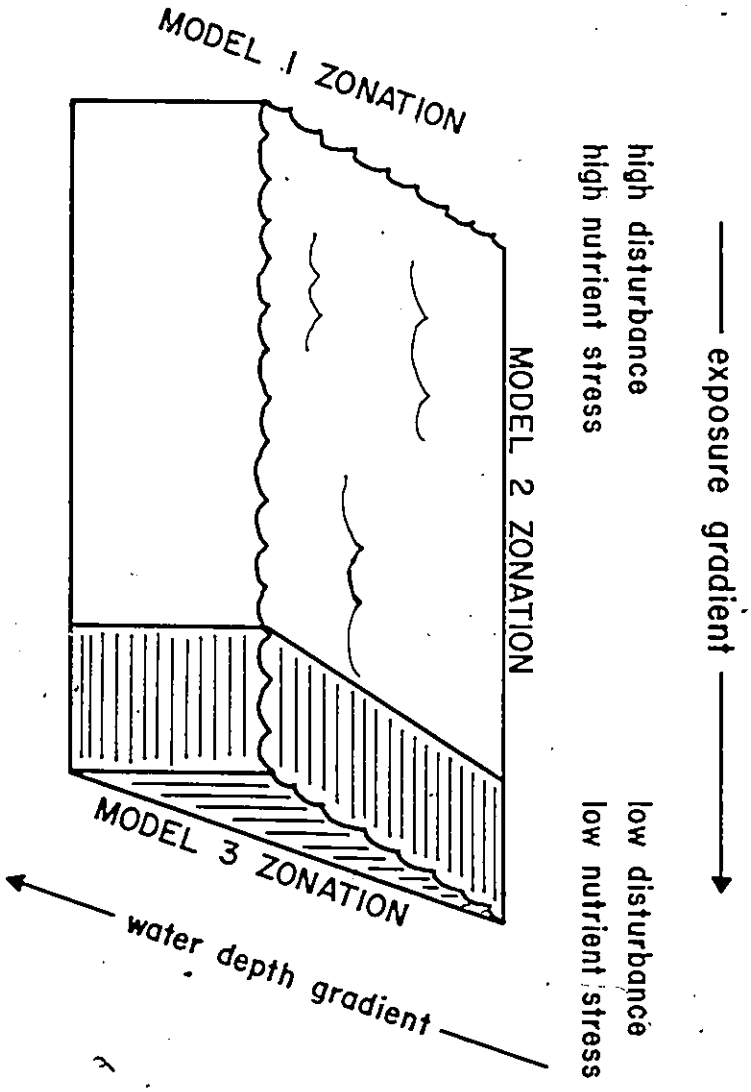

Carex crinita
4.0
3.0
2.0
1.0
0.0
Acorus calamus
4.0
3.0
2.0
1.0
0.0
Typha angustifolia
4.0
3.0
2.0
1.0
0.0
site 1
site 2
site 3
site 4
Water depth

figure 2.6


MODEL 1 ZONATION
MODEL 2 ZONATION
MODEL 3 ZONATION
water depth gradient
high disturbance
high nutrient stress
exposure gradient
low disturbance
low nutrient stress

Chapter Three

Plant strategies of emergent macrophytes

Introduction

Plant communities change along environmental gradients. The species found at consecutive points along a gradient change, as shown in chapter one. The mechanisms controlling community structure change, as shown in chapter two. The types of morphologies and physiologies of the plants found along a gradient also change, and this leads naturally to the concept of ecological strategies. In this third chapter I will propose an operational definition of a strategy and use this definition to (1) demonstrate an uncoupling of juvenile and adult traits in emergent macrophytes, (2) propose the existence of two plant strategies: regeneration and establishment, (3) show that Grime's (1979) classification of plant strategies is consistent with these results but that earlier models of ecological strategies are not, and (4) interpret these strategies in the context of the exposure gradient described in Chapter 2.

Definition of a strategy

Ecologists have often used the term "strategy" intuitively to convey the idea of a solution to some ecological or evolutionary problem (eg. Stearns 1976, Pianka 1978, Smith 1982, van Hulst 1987a,b). Colinvaux (1986) for instance, defines a

strategy as "any pattern of life history or behaviour of an organism, or all members of a population, that is adapted to gaining fitness by the efficient collection or use of resources". This definition suggests that a strategy involves physiological, morphological or (for animals) behavioral attributes which have some functional relationship to environmental conditions.

Grime (1977, 1979) has also given a definition of a strategy: "groupings of similar or analogous genetic characteristics which recur widely amongst species or populations and cause them to exhibit similarities in ecology". Though quite different from Colinvaux's definition, Grime too implied that a strategy must have a predictable relationship to the environment. He went on to introduce two new aspects of a strategy not found in Colinvaux's definition. First, a strategy must involve a suite of correlated characteristics, and therefore emphasises the entire organism, rather than a reductionistic treatment of traits in isolation. Second, he emphasised that there will be a convergence of traits in similar environments even though the actual species comprising the various communities may differ. This definition of a strategy is similar to Stearn's (1976) definition of a "tactic".

In this chapter I define a strategy as a correlated set of traits, possessed by an assemblage of species, which is

functionally related to some combination of environmental variables. This definition explicitly hypothesizes a predictable relationship between a set of predictor (environmental) variables and a set of response variables (the plant traits).

The emergent zone of rivers and lakes is an excellent system in which to evaluate this definition of a strategy. There are two obvious environmental gradients, water-depth and exposure. Equally important, there is a wide range of morphologies found among the emergent macrophytes. Above-ground ramet biomass varies from 0.02 g to 20.53 g in the set of 25 species examined in this study. Seed weights in these 25 species range from 1×10^{-5} g to 5.2×10^{-1} g; this covers the entire range of seed sizes found in herbaceous species (Harper and White 1970). Morphologies vary from leafless, photosynthetic stems (e.g. Scirpus acutus) to grass-like forms (e.g. Carex crinita) to branching forbs (e.g. Penthorum sedoides). Since this variation is found amongst taxonomically unrelated species, any predictable relationship between morphologies or physiologies and the exposure gradient is considered to be evidence for the existence of differing plant strategies, as defined above.

Methods

Average values for 20 morphological and physiological traits (appendix 3.6) were determined for each of 25 species (Appendix 3.1). Seven of these traits are properties of seeds or seedlings and are therefore juvenile traits. The remaining thirteen traits are properties of adult plants. One trait, maximum relative growth rate, R_{max}, was ambiguous. It was measured on seedlings aged between 10 and 30 days, but Grime (1979), who also measured seedling R_{max}, discusses it in the context of adult plants. Furthermore, Hunt (pers. comm.), who collaborated with Grime in their study of R_{max} (Grime and Hunt 1975), has shown that seedling R_{max} is correlated with R_{max} of adult ramets. In the test of association between juvenile and adult traits, described below, I have therefore included R_{max} in both the adult and juvenile data sets.

Seed collection and storage

Seeds of the 25 species were collected during September 1985. Most were collected in Breckenridge marsh, but those of Dulichium aurundinaceum and Scirpus americanus were collected in Luskville marsh, five kilometers upstream. All seeds were kept in porous nylon bags and stored in 75% saturated sand at 4°C from October 1985 until the various experiments began. This storage treatment has been shown to satisfactorily maintain viability and subsequent germination in a wide variety of wetland plant species

(Moore 1985).

Seed weight

All appendages were removed from the seeds before weighing. Fifty seeds of each species were randomly chosen, except those that were obviously inviable, dried to a constant weight at 60°C, and weighed individually to within ten micrograms. A few species had seeds too light to accurately weigh; for these species (Appendix 3.5) samples of fifty seeds each were measured and then transformed to average individual weights. For all statistical analyses average seed weights were transformed to the negative of their natural logarithms to produce linearity with the other variables.

Germination trials

1. Growth chamber

Seeds were removed from cold storage and counted into each of 176 (2 treatments X 4 replicates X 22 species) 5 cm petri-dishes, in lots of 25 seeds per dish. Each petri-dish had two Whatman #1 filter papers which were saturated with 4 ml of distilled water. Temperature was held constant at 20°C. Petri-dishes were randomly arranged in the growth chamber. The "light" treatment involved a regime of 14 hours light followed by 10 hours of darkness. In the "dark" treatment, seeds were removed from cold storage in the dark, counted using a dim neutral green

light to avoid disturbing the phytochrome system of the seeds, and then covered with aluminum foil. The experiment began on June 19 1986 and terminated on July 5 1986.

2. Greenhouse

This experiment was similar to the "light" treatment described above except that the petri-dishes were placed in a greenhouse which experienced natural fluctuations in temperature (from 10°C to 30°C) and light conditions. There was no "dark" treatment since this experiment was meant to more closely simulate conditions experienced in vegetation gaps on the shoreline. The experiment began on April 1 1986 and finished on April 14 1986.

Appendices 3.3, 3.4 gives the actual data from the two germination experiments done in the light. Data from the dark treatment are given in appendix 3.6, since only the final number of germinating seeds were determined.

Germination traits

1. Average time to germination

The average time to germination was calculated as a weighted mean according the formula

$$r=\Sigma_i(p_i \times i)$$

where p_i is the proportion of all seeds capable of germination

during the experiment which germinated on the i^{th} day of the experiment. Therefore, a small value for r means that almost all seeds capable of germination during the experiment did so rapidly.

2. Germination percentage

Germination percentage was simply the proportion of all seeds which had germinated during the experiment.

Maximum relative growth rate (R_{max})

For 23 species (Appendix 3.6) the relative growth rate of seedlings from day 10 to day 30 was measured. Each seedling grew in an individual container with 500 cm of soil. This quantity of soil was shown by Grime and Hunt (1975) to be sufficient to allow even large seedlings such as sunflowers to grow unhindered for up to four weeks. The rooting medium was a 2:1 mixture of fertile potting soil and vermiculite, augmented with 50 ml of RX-15 commercial (15-30-15) fertilizer before the experiment began. Soil analyses were done on the rooting medium by the Ontario Ministry of Agriculture and Food and the results are shown in table 3.1. Since these values are higher than those found naturally along the Ottawa River (Day et al. 1987) we can safely assume that the plants were less nutrient stressed (sensu Grime 1979) than under natural conditions. Whether the resulting relative growth rates were maximal in any absolute sense is

unknown but they are likely maximal relative to the field gradient and so we can differentiate between the innate abilities of different species to attain a high R_{max} (Grime and Hunt 1975). Relative growth rate (g/g week) for each species was calculated according to the formula (Fisher 1920)

$$R_{max} = 7(\ln(b_{30})-\ln(b_{10}))/(30-10)$$

where b_{30} is the average dry weight per seedling at the 30th day.

Species were planted in a complete randomized design. The experiment contained twenty blocks. Each block consisted of 23 pots, one for each of the 23 species. The position of each species within each block was randomized. Appendix 3.2 gives the dry weight biomass of each plant. Seeds of a particular species were placed in the appropriate pot and the first seedling to emerge was marked and its date of emergence noted. Unless this seedling died soon after emergence, it was used and all other seedlings emerging later were removed.

Of the twenty blocks, ten were randomly chosen for the first harvest, independently for each species. The individual of each species within each of the ten chosen blocks was then harvested ten days after it had emerged, dried to a constant weight at 60°C, and weighed to within 10 micrograms. The same procedure was followed with the remaining ten blocks and the individuals in

these pots were harvested thirty days after emergence.

Adult traits

The rest of the traits listed in Appendix 3.5 were measured in the field during late August and early September 1986. At this time, all species had begun flowering and were at their maximal seasonal height. All reported adult traits are averages over five randomly chosen individuals per species. These individuals were chosen by pacing out a random number of steps using a rnadom number table, and then taking the closest ramet. Since these traits were measured in the field they should not be interpreted as genotypic potentials.

The shortest and longest distance between successive shoots on a rhizome or stolon was used to measure the degree of clumping of a genet. Canopy diameter was the widest diameter of the canopy of a single ramet. The weight of mineral nutrients in a known dry weight of tissue was determined by ashing the tissue at 600°C for four hours, and was measured to within 10 micrograms. The weight of carbon was calculated by subtracting the ash weight from the dry weight. The ratio of carbon weight to the weight of total inorganic minerals was included because stress tolerant species are hypothesized to have larger nutrient concentrations per gram of tissue than fast growing species; when grown in fertile conditions (Chapin 1980).

Association between juvenile and adult traits

The null hypothesis of no association between a species' juvenile and adult traits was tested using Lefkovitch's non-parametric test of association (1984, 1985) based on dissimilarities calculated from the Gower (1971) general coefficient of similarity. This was used of necessity because the dichotomous and unordered multistate nature of some of the traits prevented the use of more conventional techniques such as canonical correlations. Lefkovitch's test moreover, has the advantage that it tests for an association but does not require that the association take any special functional form, unlike canonical correlations, and so makes fewer assumptions about the data.

Predictable variation of traits along an environmental gradient

Whittaker (1967) classifies gradient analysis into two basic types: direct and indirect gradient analysis. An example of direct gradient analysis is found in chapter one. Indirect gradient analysis however, is the most common type and most of the multivariate ordination methods used by ecologists produces indirect gradients. With such ordination methods, the resulting axes approximate the observed similarities of the species in the community (if the ordination is successful), which then permits

a search for environmental gradients which are correlated with the ordination axes; thus, the environmental gradient is indirect.

In order to determine the positions of the species along environmental gradients, the indirect gradients obtained by Day et al (1987) were used. They did a multivariate study using detrended correspondence analysis (DCA) (Hill and Gauch 1980) of the emergent wetland communities including the same section of the Ottawa River in which my study site was located. The DCA scores of each species on the first three axes (listed in appendix 3.7) represented their position along the gradients in that section of the Ottawa River. Day et al. (1987) interpret their indirect gradients as combinations of stress, disturbance and water depth.

There were thirteen species in common between my data set of plant traits and the data set of Day et al. (1987). These thirteen species were subsequently used to test the null hypothesis that there is no relationship between plant traits and environmental gradients. I first performed a series of univariate step-wise multiple regressions of each quantitative plant trait on the DCA scores to identify a subset of traits which were most useful in predicting gradient position; note that, since the predictor variables were means and therefore had error associated with them, the use of ordinary regression can be

misleading. I then tested the significance of the canonical correlation between the matrix of trait values (chosen by the step-wise regressions) for the thirteen species, measured by me, and the matrix of DCA scores for the same thirteen species, given by Day et al. (1987).

Relationships between plant traits

Principal Coordinates Analysis (Gower 1966) using Gower's similarity coefficient was employed to identify the major axes of covariation in the matrices of juvenile and adult traits. The squared length of a particular eigenvalue of the dissimilarity matrices is analogous to an eigenvalue in principal components analysis, and can be interpreted in the same way.

Results

1. Uncoupling of juvenile and adult traits

Table 3.2 lists the Pearson correlation coefficients between all of the quantitative traits measured. There was no association between juvenile and adult traits for the twenty five species examined (X^2=2.10, 1 d.f.,$p>0.1$) using Lefkovitch's test. This means that, given the juvenile trait values for any species, this information is of no use in predicting the traits possessed by adults of the species.

2. Correlation with environmental gradients

The univariate step-wise multiple regressions identified three traits which best predicted position on the indirect gradients: the rate of germination in the light with fluctuating temperatures, maximum relative growth rate, and above ground ramet biomass. There were other traits which were correlated with the DCA scores and with each other (tables 3.2 and 3.3) but they had lower predictive ability and were therefore not selected by the step-wise regressions. Species' scores on the first DCA axis was not predictable from these three traits, but scores on the second and third axes were highly predictable with adjusted R^2 values of 0.94 and 0.85 between the three plant

traits and the scores on axes two and three, respectively. There were two significant canonical correlations between the three plant traits and the scores on the three DCA axes. The largest canonical correlation was 0.96 and the second was 0.94.

The null hypothesis that there is no relationship between the types of traits that a species possesses and its position on an environmental gradient can be confidently rejected.

Juvenile traits

Figure 3.1 shows the first two axes of the principal coordinate analysis based on the juvenile traits. Table 3.3 gives the Pearson correlations between the juvenile traits and these first two axes. The first axis identifies the major trend for species with small seeds to germinate rapidly and abundantly, and to have high seedling R_{max}; this accounts for 35% of the total squared length. The second axis represents a subordinate trend of species having above average seedling R_{max} but below average quantities of seeds germinating under constant temperatures for a given rate of germination and accounts for a further 16% of the total squared length. There is also some indication that the ability to germinate in the dark is important in defining this second axis. Thus 50% of the total squared length was accounted for by these first two axes. The

third axis (not shown) identified the ability of species to germinate in the dark, but accounts for only 8% of the total squared length.

Adult traits

Figure 3.2 shows the first and third axes of the principal coordinate analysis based on the adult features. Table 3.3 gives the Pearson correlations between the species scores on the first three axes and those traits which were continuous; no measure of association could be calculated for the dichotomous or unordered multistate variables. The first axis identified the major trend amongst the adult traits and was related to the ability to occupy space. This first axis accounted for 25% of the total squared length. Species that weighted heavily on this axis were those with ramets that were massive (i.e. those which produced large quantities of biomass), had a wide canopy diameter, thick rhizomes and thick leaves. The second axis identified a component of size independent of biomass and species that scored heavily on this axis were tall. This second axis accounted for a further 20% of the total squared length. The third axis, which accounted for a further 13% of the total squared length, identified those species that were both short and light, had thin rhizomes or none at all, roots close to the surface of the soil and thin leaves.

Discussion

I have defined an adaptive trait as one which varies predictably with an environmental gradient. Presumably such traits vary predictably because possession of them by a plant increases the probability that the plant will successfully establish itself at that point on the gradient. A number of experimental studies have shown this to be true, at least for seed size (Grubb 1975, Fenner 1978, 1985, Rabinowitz 1978, Gross 1985), relative growth rate (Grime and Hunt 1975, Fenner 1978, Gross 1984, McConnaughay and Bazzaz 1987), height (Smith 1982, Newman 1983, Mitchley and Grubb 1986, Weiner 1986, Weiner and Thomas 1986) and vegetative spread (Grime 1979). This experimental evidence can be used to interpret the strategies identified in this chapter.

Comparison of life history models

Most models of life history strategies implicitly assume that juvenile and adult adaptive traits are closely associated with each other. Consider the concept of r-K selection, for example. If the types of juvenile traits that a species possesses are known (for example, large numbers of very small, widely dispersed seeds) then the types of adult features that the species should possess can be inferred (short generation time,

small stature, poor competitive ability) as well as the relative position of the species along the r-K continuum (Pianka 1978). The same implicit assumption concerning the association between juvenile and adult traits can be found in other models of life history strategies such as the "bet-hedging" model (Murphy 1968, Shaffer 1974). Amongst the 25 species examined in this study there was no evidence of an association between juvenile and adult traits. Grime's (1979) C-S-R model explicitly states an uncoupling of juvenile and adult traits and therefore coincides better with the observed covariation in plant traits.

Regeneration strategies

Competition is comprised of two distinct abilities (chapter 2): the ability to suppress other individuals and the ability to resist suppression by others. These two abilities need not be closely associated. Seedlings are not likely to suppress the growth of established vegetation. There are therefore two ways that a juvenile plant can increase the probability that it will survive to adulthood in the presence of established vegetation; either it avoids suppression by escaping in time or space, or it resists suppression due to details of its physiology (Fenner 1985).

These two different ways of avoiding suppression are reflected in the juvenile traits used in this study (figure 1.3, table 2.3). At one end of figure 1.3 is a juvenile strategy consisting of large, slow germinating seeds and seedlings having a slow R_{max} and at the other end is a juvenile strategy consisting of small, rapidly germinating seeds and seedlings having rapid R_{max}.

Although not explicitly measured, I observed a negative correlation between seed size and the number of seeds produced per ramet; species with small seeds produced far more seeds per ramet than did those with large seeds. This is in agreement with the correlation described by Salisbury (1942), by Harper and White (1970) and by Fenner (1985).

There is some evidence that these traits affect the ability of a seedling to establish in a closed canopy. Gross (1985) found that, in the absence of established vegetation, small seeded species had a higher relative growth rate and quickly occupied space. In the presence of established vegetation, the large seeded species had the more rapid relative growth rate because they were less severely suppressed. Similar conclusions were drawn by Fenner (1978) and by McConnaughay and Bazzaz (1987).

Plants with large numbers of very small seeds are generally

better able to disperse to new locations (Harper and Lowell 1970, Fenner 1985), are better able to enter the seed bed (Fenner 1985) and are subsequently dormant until they encounter high light intensities and fluctuating temperatures. We can therefore interpret the juvenile traits as a continuum of strategies from "fugitive" juveniles, that require major gaps in the vegetation to establish, to "tolerant" juveniles, that can establish in the smaller gaps of a less disturbed canopy. Thus, the juvenile strategies are reminiscent of the r-K continuum.

Strategies of established plants

While the regeneration strategy was presumably involved with the range of responses to different kinds of gaps in the canopy, the strategies of established plants are apparently involved principally with the ability to occupy space. Thus, the one adult trait selected by the step-wise regressions was ramet biomass. This is best shown by ignoring the second axis, which is mostly height independent of other traits associated with space occupancy, and plotting the first and third axes of the PCO of adult traits (figure 3.2, table 3.2). The reason for ignoring the second axis will be explained below. Apart from those species with a leafless morphology (numbers 8,9,12,19 and 20 in figure 3.2), the species fall approximately into a strait line. The species on the upper left are small plants with little or no capacity for aggressive vegetative spread (with the

exception of Agrostis stolonifera) and which are not massive. Interestingly, some of these species are also facultative annuals (Agrostis stolonifera, Juncus filiformus, Lycopus uniflorus, Lythrum salicaria, Penthorum sedoides, Plantago major). At the lower right of figure 3.2 are the more massive species capable of aggressive vegetative spread (Typha angustifolia, Sparganium eurycarpum, Acorus calamus).

It may at first appear surprising that height was not one of the important traits or this first axis since height is definitely of adaptive advantage in thick vegetation (Mitchle, and Grubb 1986, Weiner 1986, Weiner and Thomas 1986) where light attenuation through the canopy decreases exponentially (Smith 1982, Fitter and Hay 1983). This is presumably because in shoreline vegetation height has another, and conflicting, adaptive function.

In order to survive, emergent plants must get above the water surface. Failure to do this for an extended period of time results in the death of emergent plants (Harris and Marshall 1963, Hutchinson 1975, van der Valk 1981, Lieffers and Shay 1981). Some plants however, (Scirpus americanus, Scirpus acutus, Eleocharis smallii) are found in deeper water but in relatively infertile soil (Day et al. 1987, Hutchinson 1975) and have, as predicted by Grime (1979), low R_{max} values. These plants have leafless, hollow, photosynthetic stems. This

morphology maximizes height while minimizing biomass allocation, a necessary consequence of low R_{max} associated with stress tolerance (Niklas 1986). The second axis of the adult PCO was primarily one of height, and it is for this reason that the second axis was not used to interpret the strategies of established plants along the exposure gradient.

In general, both the regenerative and establishment strategies are in agreement with the r-K selection categorization when considered in isolation, yet there is no association between juvenile traits and adult traits. Thus the r-K selection model breaks down when both juvenile and adult traits are considered together: species having r-selected traits as adults may have either r-selected or K-selected traits as juveniles. An excellent example of this is Typha angustifolia. As an adult it is tall, massive, has thick, rapidly growing rhizomes and is a long lived perennial. As a juvenile its features are those of a fugitive species since it produces very large numbers of very small seeds are generally better able to disperse to new locations (Harper and Lowell 1970, Fenner 1985), are better able to enter the seed bed (Fenner 1985)small seeds showing rapid germination in the light with fluctuating temperatures, and whose seedlings have the highest R_{max} values of the 23 species studied.

This uncoupling of juvenile and adult traits, and the

resulting contradiction with r-K selection, can be explained by considering two different properties of disturbance (density independent mortality): frequency and size (Miller 1982). The frequency of disturbance is the rate at which new gaps are formed in the vegetation and the size of a disturbance is the amount of bare ground exposed after an individual disturbance event. Consider areas having fertile soil, and therefore having low nutrient stress, but differing in the frequency and size of disturbance events. In areas having both intense and frequent disturbances, there will be sparse vegetation cover most of the time. Competitive pressures will be low (Wilson and Keddy 1986a,b) and because of the frequent and intense density-independent mortality, the probability of survival of long-lived perennials will also be low. Thus, the typical r-selected strategy will be favoured (Pianka 1978, Roughgarden 1979), both for juvenile and adult traits, In areas in which disturbance is neither intense nor frequent, typical K-selected traits will be favoured, both for juveniles and adults. On the other hand, in areas with intense, but infrequent, disturbances, there will be a thick vegetation cover most of the time, interrupted by occasional episodes in which intense density-independent mortality destroys most of the adult vegetation. This occurs in emergent plant communities when, for example, unusually high or low water levels kill off most of the established emergent plants. In such conditions r-selected adult traits would not be favoured because of the intense competitive pressures which

exist most of the time, yet K-selected juvenile traits would not be favoured either because of an inability to repopulate after the disturbances. Species with K-selected adult traits but with r-selected juvenile traits would be best adapted to these environments. These conclusions are mirrored in Chesson's (1981, 1982) theoretical studies of the "storage effect", relevant to populations with overlapping generations and variable juvenile recruitment.

These hypothesized relationships between juvenile/adult traits and the size/frequency of gap formation await empirical tests.

Using the correlations identified by Day et al. (1987) between the DCA axes and indices of soil fertility and disturbance, and the correlations between plant traits and the DCA axes (table 3.3), it is possible to relate the morphologies and physiologies of the plants to the environments in which they normally occur. Low on the first two DCA axes and high on the third DCA axis one finds the least fertile, most disturbed sites. This environment contains species with large seeds, low R_{max} and small, light, leafless adults. These traits correspond to Grime's (1979) description of a stress-tolerator. Higher on the first two axes and lower on the third axis one finds the more fertile, less disturbed environments and also those species that possess typical competitor (sensu Grime 1979) traits.

The morphologies and physiologies of this assemblage of 25 taxonomically diverse species vary along the indirect gradients of Day et al. (1987). This variation is both predictable, as shown by the high canonical correlations, and also interpretable in the context of the experimental studies cited above, thus providing a link between pattern, explanation and mechanism.

If the concept of an ecological strategy is to be useful, then we must be able to (1) objectively derive a "strategy" from measurable quantities and (2) demonstrate predictable variation of a strategy with some combination of independent environmental variables. This chapter shows that this is both theoretically possible and also operationally feasible.

Table 3.1. Quantities (ppm) of three macronutrients and soil pH in a fertile marsh in Luskville, Quebec, dominated by Typha angustifolia, and the rooting medium for the R_{max} experiment.

Soil provenance	Phosphorus	Potassium	Magnesium	Soil pH
Luskville	5	107	254	5.8
R_{max}	82	372	700	6.3

Table 3.2. Pearson correlation coefficients between all quantitative traits measured; values of 0.5 or higher are underlined. See appendix 3.5 for details of trait name abbreviations.

✿	rlf	rlc	plf	plc	pdc	R_{max}	cn	rt	sd	ld	rd	b	h	d	lt	lw
w	-.7	-.6	.5	.2	-.2	.7	.1	-.1	-.2	-.3	-.2	-.1	-.1	-.1	-.4	.0
rlf		.5	-.7	-.6	-.1	-.5	-.3	-.1	.2	.4	.0	-.2	-.2	-.1	.1	.3
rlc			-.4	-.6	-.2	-.4	-.3	-.1	.2	.2	.3	-.1	-.1	-.2	.5	-.3
plf				.3	-.2	.5	.2	-.1	-.2	-.3	-.2	-.1	-.2	.1	-.2	-.3
plc					.3	.1	.6	.0	-.3	-.2	-.1	.1	.2	.3	-.3	-.4
pdc						-.3	.8	.1	-.1	.0	-.1	.2	.5	.2	-.2	-.1
R_{max}							.1	.2	.2	.3	-.1	.4	.0	.0	.2	-.1
cn								-.1	-.2	-.1	-.3	.1	.3	.3	-.3	-.5
rt									.3	.6	.5	.6	.4	.4	.3	.4
sd										.6	.0	.3	-.1	.2	.5	.7
ld											.3	.5	.2	.0	.6	.5
rd												.5	.5	.1	.6	-.1
b													.8	.5	.8	-.1
h														.4	.5	-.3
d															.3	-.2
lt																-.1

Table 3.3. Pearson correlations between all quantitive traits and the first three DCA axes, the first two PCO axes based on juvenile traits, and the first three PCO axes based on adult traits. Values of 0.5 or larger are underlined. See appendix 3.e for details of the trait name abbreviations.

	Vegetation data			Juvenile PCO		Adult PCO		
	DCA1	DCA2	DCA3	PCO1	PCO2	PCO1	PCO2	PCO3
w	.5	.0	-.2	.7	.4			
rlf	-.3	.6	.8	-.9	.2			
rlc	-.4	.1	.3	-.7	.1			
plf	.1	-.4	-.7	.9	-.2			
plc	.1	-.5	-.7	.7	-.7			
pdc	-.1	-.5	-.2	.0	-.4			
rgr	.5	.5	-.4	.6	.7			
cn	.2	-.5	-.6			.2	.3	.3
rt	.2	.1	-.5			.4	.1	-.5
sd	.1	.4	.2			.4	-.2	-.1
ld	-.1	.4	.0			.1	.1	-.5
rd	.3	.3	.0			-.1	.4	-.7
b	.3	.3	-.6			.5	.3	-.7
h	.2	-.1	-.6			.3	.7	-.5
d	.3	.2	-.5			.8	.1	-.1
lt	-.2	.4	-.2			-.7	-.1	-.7
lw	-.1	.3	.8			.1	-.3	-.1

Figure captions

Figure 3.1. Relationships among twenty five wetland species based on seven measured juvenile traits (axes 1 and 2 of the Principal Coordinate Analysis). To see how the traits load on these axes, see table 3.3. Species names are listed in Appendix 3.1.

Figure 3.2. Relationships among twenty five wetland species based on thirteen measured adult traits (axes 1 and 3 of the Principal Coordinate Analysis). To see how the traits load on these axes, see table 3.3. Species names are listed in Appendix 3.1.

figure 3.1

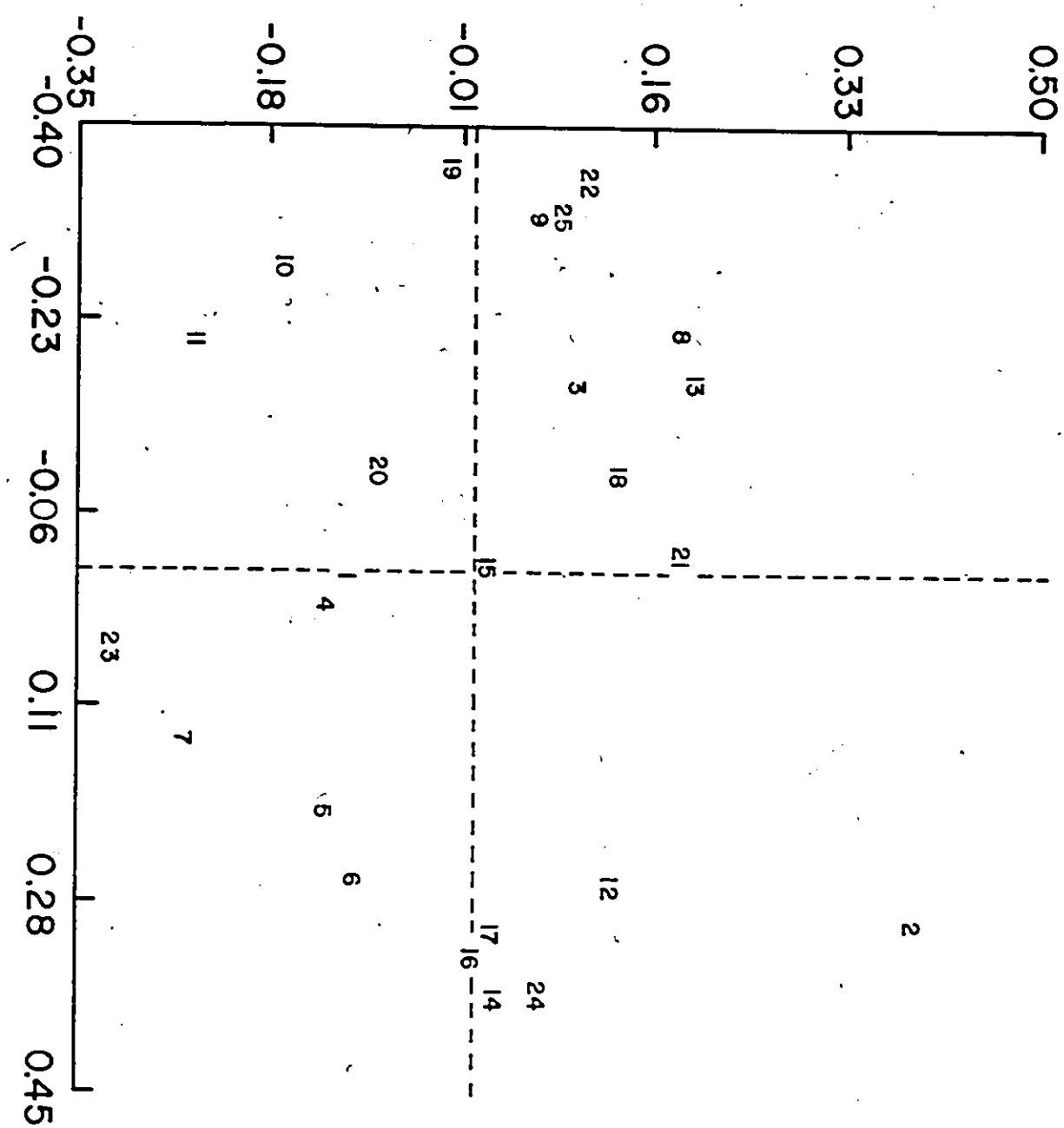
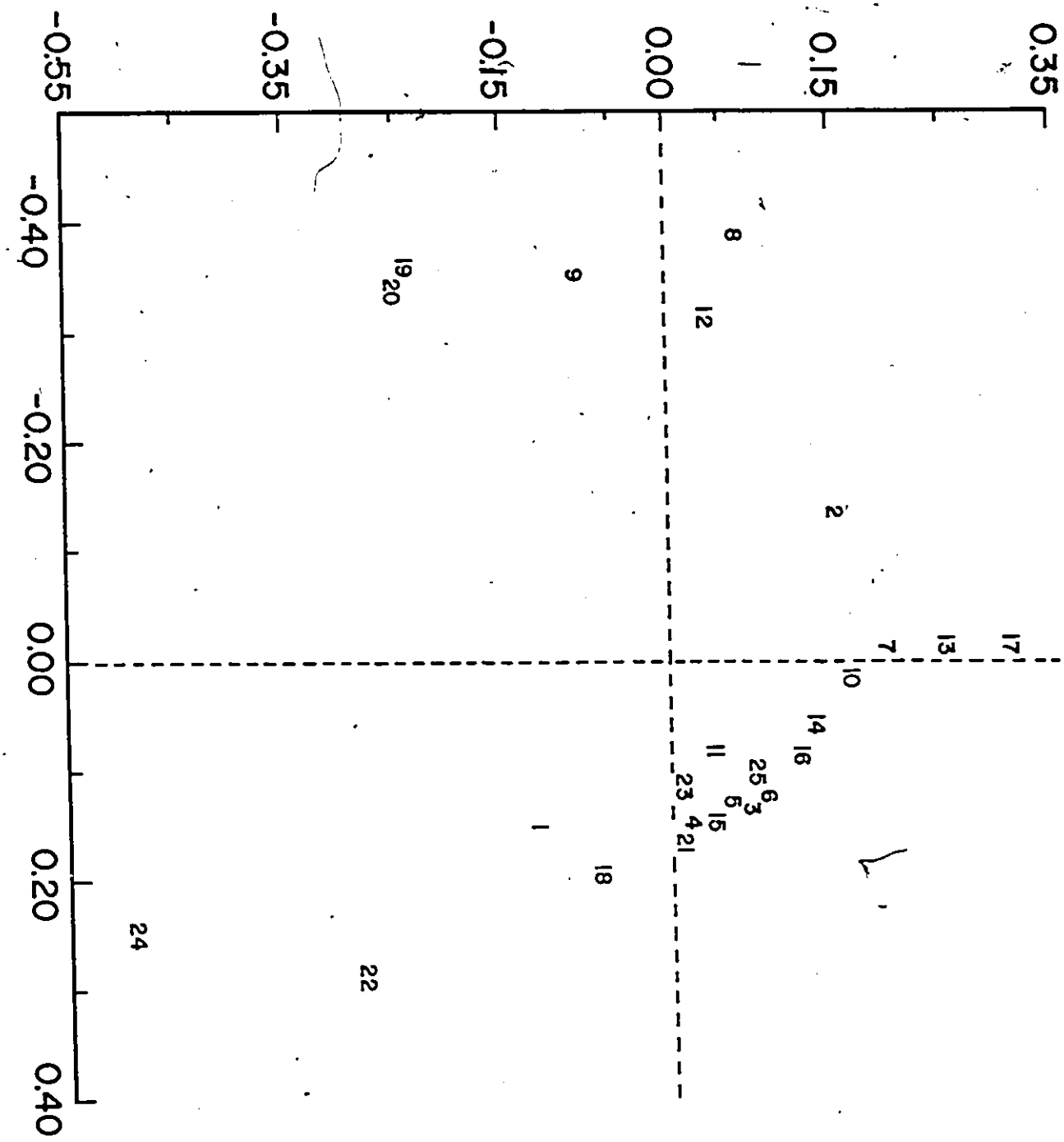

-0.35
-0.40
-0.23
-0.06
0.11
0.28
0.45
-0.18
-0.01
0.16
0.33
0.50
19
22
25
9
10
11
8
13
3
18
20
21
15
4
23
7
5
6
12
2
17
16
14
24

figure 3.2


-0.55
-0.35
-0.15
0.00
0.15
0.35
-0.40
-0.20
0.00
0.20
0.40
8
19
20
9
12
2
7
13
17
10
14
18
11
25
6
3
23
4
6
15
21
1
18
24
22

General Conclusions

In this final section I will draw together the results of the first three chapters and suggest where they might lead.

It appears that the patterns of species distributions on shorelines are not random, but do not necessarily agree with either the community-unit or the individualistic concepts. In fact, the difficulties of adequately testing these ideas suggest that they have outlived their usefulness; it seems better to concentrate on the types of mechanistic models introduced in chapter 2.

These mechanistic models are more productive, not only because they are easier to test, but also because it seems possible to relate different models to different environments, as done in figure 2.6. This is important because, if the relationships are general, one can predict mechanisms from knowledge of environments.

Knowing the underlying mechanisms operating at a site is necessary but not sufficient to tell us which species to expect under given conditions. In model 2 of figure 2.6 for instance, we must not only know that the best competitors occupy the least stressful part of the gradient, but also which species these might be. The results of chapter 3 suggest that we can also predict the morphological and physiological traits of species based on environmental variables. Thus, it may eventually be possible, given information of the physical environment, to say (1) the mechanisms controlling species distributions, and (2) the

types of species which will occur in that environment.

Appendix 1.1

Clustering statistics of Pielou and Underwood

The purpose of this appendix is to twofold: (1) to point out some undesirable properties of the tests developed by Pielou (1977) and by Underwood (1978a,b) and (2) to justify why I have expressed reservations in Chapter 1 for accepting Underwood's (1978a,b) detection of a random distribution of boundaries.

Before describing the tests in detail, it is useful to describe the problem to be solved. Imagine that a belt transect is established along an environmental gradient, as done in Chapter 1, and divided into a series of cells. The cells can be contiguous quadrats, as used by Pielou and Routledge (1976), or environmental intervals, as done in Chapter 1 and in Kedd (1982). If there are a total of k cells and a total of N boundaries then there will be an observed vector of occupancy values $(n_1, n_2, \ldots, n_k)$. There are three different possibilities concerning how the boundaries will be distributed amongst the cells: they can be unusually clustered in a few cells and unusually sparse in other cells, they can be independently distributed amongst cells and therefore producing a random pattern, or they can be spaced regularly amongst cells.

The purpose of the tests of Pielou (1977) and of Underwood (1978a) is to distinguish between clustered, random and regular

patterns. In order to do this, it is necessary to define a measure of "clustering". In order to detect clustering, both Pielou (1977) and Underwood (1978a,b) derive the probability of obtaining U, where U is defined as the number of cells containing at least one boundary; the probability distributions differ because each author assumes a different randomization procedure (Pielou 1979). In both tests boundaries are clustered if the U value is unusually small and boundaries are regularly spaced if the U value is unusually large.

Thus, these two tests classify cells into one of two states: having no boundaries or at least one. In so doing, they reduce the information available and therefore reduce their power to detect nonrandom patterns. Consider a transect with, say, seven boundaries placed into seven cells according to some discrete random process. One possible arrangement is: (5,1,1,0,0,0,0). Another possible arrangement is: (3,2,2,0,0,0,0). Although the first arrangement is intuitively more clustered and is much less likely to occur under the null hypothesis of random placement (table 1.1.1), U equals three in both instances and so neither Pielou's nor Underwood's test would detect any difference. Furthermore, neither pattern is significant at the 0.05 significance level using the U definition, yet the probability of obtaining a pattern at least as clustered as (5,1,1,0,0) is only 0.009. It is for this reason that I expressed some reservations in Chapter 1 about accepting Underwood's (1978a,b) conclusion

that boundaries in his study were randomly placed.

Table 1.1.1. Maxwell-Boltzmann distribution for all possible configurations of occupancy vectors when seven boundaries are randomly assigned to seven cells. p is the probability of obtaining a particular occupancy vector. ΣP is the probability of obtaining an occupancy vector at least as clustered as the one shown. ΣP(U) is the probability of obtaining at least as small a U value as the one shown. Adapted from Table 1 of Feller (1968).

Occupancy	p	ΣP	U	ΣP(U)
7000000	0.000008	0.000008	1	0.000008
6100000	0.000357	0.000365	2	
5200000	0.001071	0.001436	2	
4300000	0.001785	0.003221	2	0.003221
5110000	0.005355	0.008576	3	
4210000	0.026775	0.035351	3	
3310000	0.017850	0.053201	3	
3220000	0.026775	0.079976	3	0.079976
4111000	0.035699	0.115675	4	
3211000	0.214197	0.329872	4	
2221000	0.107098	0.436970	4	0.436976
3111100	0.107098	0.544068	5	
2211100	0.321295	0.865363	5	0.865363
2111110	0.128518	0.993881	6	0.993881
1111111	0.006120	1.000000	7	1.000000

Appendix 1.2

Number of upper (u) and lower (l) boundaries per relative height interval for each of the thirteen transects.

Height interval	Transect																									
	1		2		3		4		5		6		7		8		9		10		11		12		13	
	u	l	u	l	u	l	u	l	u	l	u	l	u	l	u	l	u	l	u	l	u	l	u	l	u	l
30/25	1	2																								
25/20	2	1	1	0	2	1					3	0														
20/15	1	3	2	1	0	2	0	4	5	5	0	2	3	5												
15/10	0	0	0	2	0	0	0	1	1	3	5	3	0	0	1	4	2	2								
10/5	1	0	1	1	3	1	1	0	1	1	0	1	1	0	2	1	0	1	3	2	1	0				
5/0	2	2	1	0	2	2	1	0	0	0	0	0	1	0	0	1	2	0	1	1	1	0	1	3	1	0
0/-5	1	2	1	3	3	0	3	0	2	0	0	1	0	0	2	1	1	0	2	1	2	0	3	0	2	0
-5/-10	1	0	3	1	0	0	3	1	0	0	1	0	1	0	2	0	0	0	0	0	3	2	6	2	2	0
-10/-15	1	1	0	2	1	1	2	1	4	2	3	2	4	0	1	2	1	1	2	0	2	3	2	1	3	2
-15/-20	1	0	2	0	0	2	1	2	1	4	3	3	1	2	2	2	1	0	1	4	1	3	2	2	2	5
-20/-25	4	1	1	0	2	1	4	0	5	2	3	1	3	4	0	1	5	4	4	0	1	1	1	3	2	2
-25/-30	2	2	2	0	2	0	0	0	0	1	1	0	0	4	3	0	3	1	2	3	2	0	0	0	1	1
-30/-35	1	2	1	1	1	1	0	3	0	2	0	0	1	1	2	0	0	0	2	1	1	1	2	0	0	1
-35/-40	0	2	0	2	0	3	0	2	0	1	0	2	0	5	0	3	0	1	0	0	0	0	0	1	0	2

Appendix 1.3

Lengths in metres of each height interval of each transect. This is the covariate in the analysis of deviance done in Chapter 1.

Height interval	Transect												
	1	2	3	4	5	6	7	8	9	10	11	12	13
30/25	3.6												
25/20	6.0	2.0	4.8			4.4							
20/15	3.8	2.2	4.8	4.8	5.7	2.0	4.5						
15/10	3.1	4.2	2.2	5.6	4.2	7.1	2.2	4.4	3.8				
10/5	5.2	6.7	2.2	2.4	3.7	3.7	3.2	2.2	1.0	3.1	2.7		
5/0	3.1	4.6	6.1	0.8	2.3	3.3	3.3	2.8	3.5	3.0	1.4	4.2	3.7
0/-5	6.8	6.0	5.8	4.5	2.2	2.5	4.6	3.4	5.5	4.5	4.8	5.3	4.5
-5/-10	5.9	7.5	7.2	6.2	4.5	3.0	6.0	5.8	5.9	6.4	18.5	14.6	9.7
-10/-15	4.1	5.2	6.7	15.0	12.8	13.9	9.0	11.6	6.9	10.6	9.4	5.1	5.1
-15/-20	1.7	5.7	7.2	4.4	11.2	9.5	5.6	8.1	9.2	13.2	4.9	10.2	16.6
-20/-25	4.2	7.9	5.3	10.1	13.7	8.2	10.2	8.1	12.2	8.8	9.6	10.1	11.5
-25/-30	6.8	10.7	8.6	10.0	2.9	4.5	8.2	18.9	12.0	14.0	12.7	7.3	6.8
-30/-35	4.7	8.2	13.8	13.1	10.7	17.5	17.4	8.5	8.0	15.0	9.9	17.1	19.1
-35/-40	10.2	8.3	7.7	8.8	5.4	7.3	14.6	18.8	17.7	8.3	14.4	11.7	9.4

Appendix 2.1

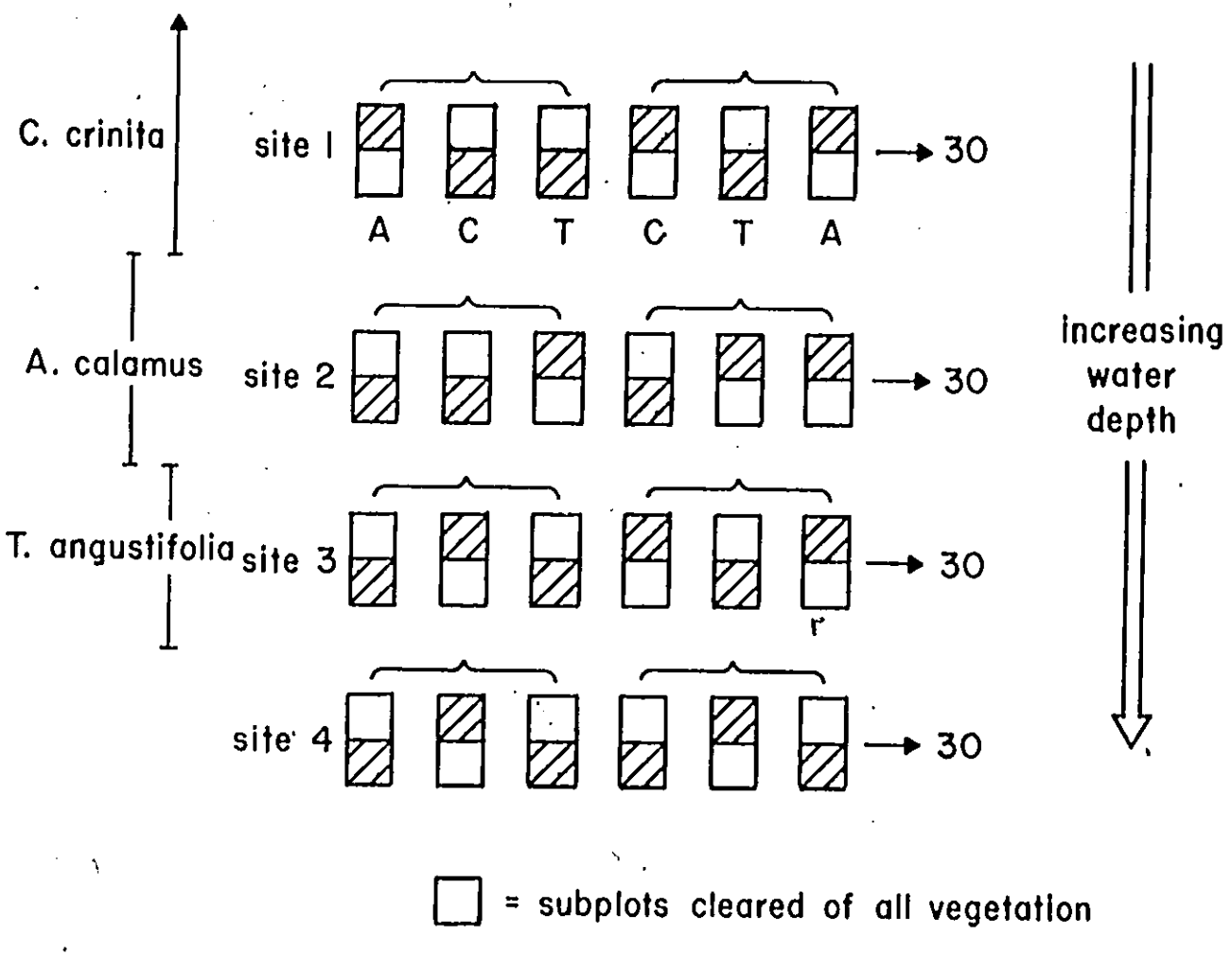
Dry weight biomass values (g) of Acorus calamus (A), Carex crinita (C), and Typha angustifolia (T), in the transplant experiment of chapter 2, both for cleared (C) and uncleared (U) plots, in all but the fourth site (since no ramets survived in this site). Also shown are two covariates: disturbance (N=none, G=grazed but not killed, E=completely eaten by muskrats) and the amount of surrounding biomass in the uncleared plots. Dashes represent missing values. The accompanying figure shows the physical layout of the experiment.

Species	Site	Replicate	Treatment	Biomass	Disturbance	Uncleared
A	1	1	C	16.05	N	
A	1	1	U	10.92	N	19.09
A	1	2	C	21.29	N	
A	1	2	U	1.66	N	29.87
A	1	3	C	14.92	N	
A	1	3	U	4.68	N	28.98
A	1	4	C	18.92	N	
A	1	4	U	13.59	N	40.14
A	1	5	C	23.62	N	
A	1	5	U	-	N	-
A	1	6	C	11.64	N	
A	1	6	U	6.85	N	15.77
A	1	7	C	4.73	N	
A	1	7	U	8.52	N	14.64
A	1	8	C	10.22	N	
A	1	8	U	10.63	N	6.41
A	1	9	C	9.18	N	
A	1	9	U	7.76	N	11.10
A	1	10	C	9.99	N	
A	1	10	U	12.40	N	7.71
A	2	1	C	6.49	N	
A	2	1	U	7.05	N	9.58
A	2	2	C	23.91	N	
A	2	2	U	15.50	N	15.23
A	2	3	C	20.02	N	
A	2	3	U	18.39	N	17.06
A	2	4	C	10.87	N	

A	2	4	U	9.85	N	13.04
A	2	5	C	17.51	N	
A	2	5	U	7.85	N	20.31
A	2	6	C	5.89	N	
A	2	6	U	10.37	N	11.71
A	2	7	C	11.51	N	
A	2	7	U	0.00	E	1.49
A	2	8	C	8.43	N	
A	2	8	U	14.00	N	23.69
A	2	9	C	12.95	N	
A	2	9	U	14.70	N	1.70
A	2	10	C	16.73	N	
A	2	10	U	7.78	N	14.86
A	3	1	C	19.29	N	
A	3	1	U	0.0	N	1.41
A	3	2	C	-	G	
A	3	2	U	5.06	N	10.61
A	3	3	C	6.10	N	
A	3	3	U	0.0	N	15.16
A	3	4	C	7.71	N	
A	3	4	U	0.0	N	49.34
A	3	5	C	0.0	E	
A	3	5	U	2.74	N	31.95
A	3	6	C	0.0	N	
A	3	6	U	1.26	N	0.17
A	3	7	C	4.01	N	
A	3	7	U	0.0	N	28.75
A	3	8	C	0.0	E	
A	3	8	U	0.0	E	-
A	3	9	C	0.0	E	
A	3	9	U	0.0	E	26.02
A	3	10	C	0.0	E	
A	3	10	U	0.0	E	45.15
C	1	1	C	39.09	N	
C	1	1	U	22.66	N	30.08
C	1	2	C	26.29	N	
C	1	2	U	13.05	N	23.90
C	1	3	C	34.12	G	
C	1	3	U	11.30	G	25.52
C	1	4	C	76.54	N	
C	1	4	U	4.14	N	2.46
C	1	5	C	20.65	G	
C	1	5	U	15.09	G	12.13
C	1	6	C	15.63	G	
C	1	6	U	12.91	G	27.43
C	1	7	C	14.85	N	
C	1	7	U	28.31	N	14.39
C	1	8	C	16.84	N	
C	1	8	U	5.17	N	12.29
C	1	9	C	14.31	N	
C	1	9	U	8.41	N	21.81
C	1	10	C	7.52	N	

C	1	10	U	11.97	N	28.52
C	2	1	C	6.00	N	
C	2	1	U	12.85	N	24.39
C	2	2	C	29.72	N	
C	2	2	U	5.88	N	9.33
C	2	3	C	10.65	N	
C	2	3	U	13.21	N	18.47
C	2	4	C	21.49	N	
C	2	4	U	0.0	E	12.29
C	2	5	C	27.22	N	
C	2	5	U	15.20	N	16.72
C	2	6	C	13.62	N	
C	2	6	U	10.67	N	23.49
C	2	7	C	12.48	N	
C	2	7	U	1.74	G	15.0
C	2	8	C	20.93	N	
C	2	8	U	17.96	N	12.55
C	2	9	C	20.75	N	
C	2	9	U	10.40	N	18.12
C	2	10	C	17.58	N	
C	2	10	U	6.04	N	31.04
C	3	1	C	0.0	N	
C	3	1	U	0.0	N	24.75
C	3	2	C	27.19	N	
C	3	2	U	0.0	N	36.80
C	3	3	C	0.0	N	
C	3	3	U	0.0	N	20.95
C	3	4	C	0.0	N	
C	3	4	U	12.15	N	9.61
C	3	5	C	0.0	N	
C	3	5	U	28.11	N	11.38
C	3	6	C	0.0	E	
C	3	6	U	22.90	N	0.50
C	3	7	C	0.0	N	
C	3	7	U	0.0	N	19.33
C	3	8	C	29.64	N	
C	3	8	U	0.0	N	33.46
C	3	9	C	15.78	N	
C	3	9	U	0.0	E	54.19
C	3	10	C	0.0	E	
C	3	10	U	0.0	E	26.15
T	1	1	C	9.89	N	
T	1	1	U	30.35	N	16.69
T	1	2	C	41.72	N	
T	1	2	U	22.49	N	27.74
T	1	3	C	27.98	N	
T	1	3	U	31.55	N	17.46
T	1	4	C	32.04	N	
T	1	4	U	22.43	N	20.45
T	1	5	C	6.01	N	
T	1	5	U	20.03	N	25.53
T	1	6	C	11.86	N	

T	1	6	U	0.0	E	20.96
T	1	7	C	13.29	N	
T	1	7	U	8.18	N	14.76
T	1	8	C	9.28	N	
T	1	8	U	16.91	N	31.90
T	1	9	C	30.60	N	
T	1	9	U	0.0	N	20.95
T	1	10	C	37.80	N	
T	1	10	U	0.0	N	15,55
T	2	1	C	52.52	N	
T	2	1	U	33.12	N	21.57
T	2	2	C	49.14	N	
T	2	2	U	24.72	N	7.13
T	2	3	C	35.05	N	
T	2	3	U	22.67	N	9.83
T	2	4	C	41.91	N	
T	2	4	U	42.62	N	11.65
T	2	5	C	87.73	N	
T	2	5	U	10.91	N	21.24
T	2	6	C	39.13	N	
T	2	6	U	50.68	N	17.05
T	2	7	C	57.85	N	
T	2	7	U	57.86	N	11.95
T	2	8	C	61.24	N	
T	2	8	U	25.64	N	8.93
T	2	9	C	52.08	N	
T	2	9	U	29.45	N	25.25
T	2	10	C	52.69	N	
T	2	10	U	13.23	N	21.62
T	3	1	C	66.90	N	
T	3	1	U	47.30	N	27.07
T	3	2	C	39.64	N	
T	3	2	U	8.74	N	28.93
T	3	3	C	0.0	N	
T	3	3	U	24.98	N	37.59
T	3	4	C	6.57	N	
T	3	4	U	60.17	N	11.75
T	3	5	C	23.48	N	
T	3	5	U	41.11	N	-
T	3	6	C	53.89	N	
T	3	6	U	26.28	N	66.62
T	3	7	C	9.27	N	
T	3	7	U	16.51	N	27.77
T	3	8	C	0.0	E	
T	3	8	U	31.01	N	13.61
T	3	9	C	13.45	N	
T	3	9	U	16.45	N	13.90
T	3	10	C	0.0	E	
T	3	10	U	0.0	E	-


C. crinita
A. calamus
T. angustifolia
site 1
site 2
site 3
site 4
A C T C T A
30
30
30
30
increasing water depth
= subplots cleared of all vegetation
= subplots containing natural vegetation of the site

Appendix 3:1

Species used in chapter three as well as their reference numbers.

Species	number
Acorus calamus	1
Agrostis stolonifera	2
Alisma plantago-aquatica	3
Carex crinita	4
Carex projecta	5
Carex vulpinoidea	6
Dulichium arundinaceum	7
Eleocharis erythropoda	8
Eleocharis smallii	9
Elymus virginicus	10
Iris versicolor	11
Juncus filiformus	12
Lycopus uniflorus	13
Lythrum salicaria	14
Phalaris aurundinacea	15
Plantago major	16
Penthorum sedoides	17
Sagittaria latifolia	18
Scirpus americanus	19
Scirpus acutus	20
Scirpus cyperinus	21
Sparganium eurycarpum	22
Spartina pectinata	23
Typha angustifolia	24
Rumex verticillatus	25

Appendix 3.2

Dry weight biomass values (g) for all species (names listed in appendix 3.1) in the R_{max} experiment of chapter 3. Dashes represent missing values. Each value represents a different individual.

Species	Biomass at day 10	Biomass at day 30
1	0.00038	0.00163
	0.00023	0.00049
	0.00075	0.00157
	0.00024	0.00454
	0.00014	0.01072
	0.00011	0.00607
	0.00026	0.00929
	0.00032	0.00785
	-	0.02430
2	0.00025	0.01163
	0.00009	0.01994
	-	0.00669
	0.00028	0.03594
	0.00029	0.01348
	0.00040	-
	0.00009	-
3	0.00006	0.00038
	0.00021	-
	-	0.00459
	-	0.00343
4	0.00069	0.00856
	0.00103	0.01397
	0.00083	0.01852
	0.00062	0.01233
	0.00075	0.01246
	0.00071	0.01136
	0.00053	0.01587
	0.00086	0.00900
	-	0.02240
	0.00036	0.01258
5	0.00090	0.00471
	0.00086	0.01063
	0.00065	0.01677
	0.00046	0.01274
	0.00030	0.01443
	-	0.01412
	0.00022	0.01339
	0.00068	0.00981
	0.00038	0.00508
	0.00035	-

6	0.00090	0.01172
	0.00030	0.01010
	0.00032	0.00611
	0.00047	0.02367
	0.00061	0.01919
	0.00053	0.01016
	0.00049	0.01265
	0.00050	0.02535
	0.00046	0.00913
	-	0.01290
	-	0.01581
7	0.00041	0.00915
	0.00069	0.00634
	0.00059	0.00150
	0.00065	0.00962
	0.00042	0.01261
	0.00045	0.01013
	0.00064	0.00271
	0.00065	-
	0.00101	-
	0.00035	-
	-	-
	0.00185	0.02567
	0.00038	0.00558
10	0.00234	0.00655
	0.00096	0.03015
	0.00290	0.01247
	0.00134	0.02882
	0.00107	0.01152
	-	0.00614
	-	0.00396
11	0.00490	0.02739
	0.00059	-
	0.00136	0.00173
	0.00010	0.02976
	0.00232	0.01592
	0.00077	0.01063
	-	0.01740
	-	0.00725
	-	0.00853
12	0.00006	0.00374
	0.00007	0.00342
	0.00003	0.00477
	0.00011	0.00161
	0.00009	0.00238
	0.00004	0.00204
	-	0.00537
	0.00023	0.00672
	0.00008	0.00309
	-	0.00367
13	0.00143	0.04713
	0.00071	0.04194

	0.00197	0.01122
	0.00082	0.02664
	0.00180	0.04570
	0.00093	0.07049
	0.00060	0.06265
	0.00139	0.06580
	0.00669	0.08199
	0.00130	0.06173
14	0.00132	0.04392
	0.00121	0.06771
	0.00086	0.09358
	0.00128	0.17856
	-	0.05565
	0.00344	0.14133
	0.00148	0.04966
	0.00092	0.01354
	0.00124	0.05176
	0.00097	-
	0.00048	-
15	0.00065	0.04114
	0.00135	0.17183
	0.00279	0.08336
	0.00341	0.06013
	0.00370	0.04395
	0.00339	0.02236
	0.00109	0.05228
	0.00322	0.04512
	0.00327	0.03688
16	0.00098	0.05117
	0.00100	0.05700
	0.00124	0.14117
	0.00442	0.17667
	0.00328	0.05258
	0.00385	0.00477
	0.00253	0.09380
	0.00289	0.04824
	0.00329	0.02345
	0.00200	0.13214
	0.00552	-
17	0.00007	0.00202
	0.00033	0.00112
	-	0.00075
	0.00021	0.00279
	0.00009	0.00876
	0.00001	0.00031
	-	0.01904
	0.00015	-
18	0.00042	0.01902
	0.00067	0.02955
	0.00059	0.07385
	0.00074	0.01235
	0.00091	0.01712

	0.00087	0.00981
	0.00173	0.02441
	-	0.04422
	-	0.01526
	-	0.02520
19	0.00019	0.00053
	0.00103	0.00211
	0.00010	0.01489
	0.00018	-
	0.00173	0.01056
	-	0.01056
	-	0.00054
20	-	-
21	0.00012	0.01516
	0.00019	0.00325
	0.00011	0.00347
	0.00042	0.00266
22	0.00246	0.12245
	0.00157	0.06239
	0.00121	-
	0.00080	-
	0.00224	-
	0.00597	-
	0.00230	0.08333
	0.00137	0.01832
	-	0.02494
	-	0.05385
23	0.00103	0.02021
	-	0.02823
	0.00266	0.00378
	0.00212	0.02731
	0.00134	0.01707
	0.00104	0.02528
	0.00191	0.02859
	0.00397	0.01578
	-	0.01516
	-	0.00243
24	0.00008	0.02382
	0.00010	0.00608
	0.00011	0.01836
	0.00001	0.01187
	0.00015	0.01432
	0.00016	0.00671
	0.00008	0.02277
	-	0.01245
	0.00019	0.00524
	0.00033	0.01584
25	0.00266	0.09540
	0.00848	0.17774
	0.01057	0.17816
	0.00766	0.07318
	0.00715	0.07051

0.00673	0.26102
-	0.14866
-	0.10100
-	0.15417
-	0.19692

Appendix 3.3

Number of seeds germinating during each day in germination experiment 1 of Chapter 3. Values not measured are shown by dashes. Species names are given in appendix 3.1.

Species	Day							
	2	4	6	8	10	12	14	16
1	0	0	0	3	24	0	1	16
2	–	–	–	–	–	–	–	–
3	1	23	1	0	0	0	0	1
4	0	0	0	0	9	30	19	1
5	0	0	71	10	0	1	0	1
6	0	0	39	55	0	0	1	0
7	0	0	14	47	6	1	0	1
8	0	0	0	0	1	1	0	0
9	0	0	0	0	0	0	0	0
10	1	1	18	13	0	6	4	4
11	0	0	1	14	16	8	2	1
12	0	0	13	10	5	6	0	1
13	0	0	0	3	3	0	0	0
14	16	53	8	2	1	1	0	1
15	–	–	–	–	–	–	–	–
16	–	–	–	–	–	–	–	–
17	0	11	25	7	8	0	0	1
18	0	0	3	1	2	1	3	0
19	0	0	0	0	1	0	0	0
20	0	0	0	3	19	9	2	1
21	0	0	0	1	0	0	0	0
22	0	0	0	0	0	0	0	0
23	0	33	28	31	1	0	1	0
24	0	35	45	8	5	0	0	0
25	0	0	0	0	1	1	0	0

Appendix 3.4

Number of seeds germinating during each day in germination experiment 3 of CHapter 3. Values not measured are shown by dashes. Species names are given in appendix 3.1.

Species	Day															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1	0	0	0	0	0	0	36	24	7	4	0	0	0	0	0	0
2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
3	0	19	15	9	3	0	1	2	2	0	0	0	0	0	0	0
4	0	0	0	0	0	0	3	19	15	9	17	5	0	0	0	0
5	0	0	0	0	0	20	27	12	4	0	0	0	0	0	0	0
6	0	0	0	0	0	8	75	1	1	1	0	0	0	0	0	0
7	0	0	0	0	0	11	26	11	15	8	0	0	0	0	0	0
8	0	0	0	0	0	0	0	0	0	1	0	0	6	0	1	0
8	0	0	0	0	0	0	0	1	1	1	0	0	1	0	5	0
9	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
11	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
12	0	0	0	0	58	13	4	9	9	0	0	0	0	0	0	0
13	0	0	0	0	0	0	0	0	1	0	0	0	0	0	10	0
14	0	0	10	21	31	0	2	0	0	0	0	0	0	0	0	0
15	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
16	0	1	36	30	3	2	1	0	1	0	0	6	0	18	0	0
17	0	0	0	91	0	0	0	0	0	0	0	0	0	0	0	0
18	0	0	0	1	1	3	3	2	0	0	0	0	9	0	1	0
19	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
20	0	0	0	0	0	1	1	3	0	0	15	0	0	0	0	0
21	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
23	0	0	0	0	2	13	7	4	1	0	0	2	0	1	0	0
24	54	9	5	1	1	0	0	1	0	0	0	0	0	0	0	0
25	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix 3.5

Traits measured and their abbreviations. (1)

Trait	Abbreviation
negative $\log_e$ of seed weight(g)	w
average time to germination in the light under fluctuating temperatures (10°C to 30°C) (days)	rlf
average time to germination in the light under constant temperatures (20°C) (days)	rlc
percent germination in the light under fluctuating temperatures (20°C)	plf
percent germination in the light under constant temperatures (10°C to 30°C)	plc
percent germination in the dark under constant temperatures (20°C)	pdc
maximum relative growth rate of seedlings aged 10 to 30 days (g/g week)	R_{max}
ratio of carbon to total mineral nutrients in seedling tissues	cn
thickness of rhizomes or stolons (where present) (mm)	rt
shortest distance between successive shoots on a rhizome or stolon (where present) (cm)	sd
longest distance between successive shoots on a rhizome or stolon (where present) (cm)	ld

Appendix 3.5 continued

depth from soil surface to rhizome, stolon or roots (cm)	rd
dry weight of above ground biomass of a single ramet (g)	b
maximum height above ground of photosynthetic tissues of a single ramet (cm)	h
maximum diameter of the canopy of a single ramet (cm)	d
maximum leaf thickness (mm)	lt
maximum leaf width (cm)	lw
presence of rhizomes or stolons	vp
canopy type: i) leafy - monolayer (1) - multilayer (2) - graminoid (3) ii) leafless - single stem (4) - tussock of stems (5)	ct
growth form - creeping (1) - upright (2) - rosette (3)	gf

(1) The following species had seeds too light to accurately weigh individually; instead, five samples of fifty seeds each were weighed and then transformed to average individual weights: Agrostis stolonifera, Juncus filiformus, Lythrum salicaria, Penthorum sedoides, Scirpus cyperinus, and Typha angustifolia.

Appendix 3.6

Average trait values for all measured traits discussed in chapter 3. Also given are the standard errors of the measured R_{max} values. Species names are given in appendix 3.1 and trait names in appendix 3.5. One exception is seed weight, symbolized in this table as sw, which gives the actual average seed weights and standard deviations, not their natural logarithms.

Species	sw	rlf	rlc	plf	plc	pdc	vp
1	0.00091±(0.00017)	7.7	10.4	71	28	0	yes
2	0.00005	–	–	–	–	–	yes
3	0.00033±(0.00013)	16.0	3.9	0	25	0	no
4	0.00063±(0.00001)	11.2	10.5	68	58	0	yes
5	0.00019±(0.00004)	8.0	6.4	63	81	0	yes
6	0.00020±(0.00004)	7.7	7.2	78	93	0	yes
7	0.00053±(0.00011)	6.6	9.8	71	82	0	yes
8	0.00031±(0.00005)	12.9	10.3	16	4	0	yes
9	0.00145±(0.00018)	12.8	16.0	9	2	0	yes
10	0.00307±(0.00063)	16.0	8.7	0	57	6	yes
11	0.01364±(0.00529)	7.5	10.5	2	40	7	yes
12	0.00002	5.3	6.6	93	23	0	yes
13	0.00017±(0.00007)	14.5	10.3	16	7	0	no
14	0.00005	4.4	4.2	64	80	13	no
15	0.00031±(0.00011)	–	–	–	–	–	yes
16	0.00016±(0.00007)	6.1	–	98	–	–	no
17	0.00001	4.0	6.7	91	54	0	no
18	0.00029±(0.00010)	9.8	10.0	20.0	10.0	3	yes
19	0.00263±(0.00045)	13.0	15.0	1	2	0	yes
20	0.00161±(0.00033)	11.3	12.1	48	38	0	yes
21	0.00001	5.5	8.1	2	1	0	yes
22	0.05204±(0.01418)	7.2	6.1	30	0	0	yes
23	0.00161±(0.00038)	7.2	6.1	30	90	47	yes
24	0.00004	3.3	5.6	66	85	0	yes
25	0.00249±(0.00034)	16.0	11.0	0	2	18	yes

rt	sd	ld	rd	b	h	d
5.1	2.0	6.0	1.5	4.7	77.6	30.8
0.2	2.0	4.0	0.5	0.1	14.2	10.0-
-	-	-	2.0	2.9	27.6	23.0
5.0	0.5	2.0	2.5	0.9	57.2	84.8
3.2	0.5	1.0	2.5	0.4	55.0	33.4
3.7	0.5	1.0	2.5	0.4	46.6	35.0
3.0	3.0	5.0	5.0	0.8	48.0	20.0.
0.7	0.1	4.0	0.5	0.1	36.0	0.1
1.2	1.0	10.0	3.0	0.4	72.2	0.3
3.4	-	-	2.0	0.9	73.2	32.8
7.6	5.0	5.0	2.2	1.7	57.2	24.8
0.3	0.3	5.0	1.0	0.1	52.0	0.1
-	7.0	25.0	1.3	0.3	37.0	12.8
-	-	-	2.5	5.5	85.0	15.4
2.0	0.8	6.0	6.0	4.5	120.0	50.7
-	-	-	1	0.1	12.0	16.6
-	13.0	4.5	0.5	0.6	25.0	-
7.1	25.0	25.0	5.0	3.2	51.4	37.6
4.0	2.0	5.0	13.0	0.4	76.4	0.3
3.4	1.0	30.0	7.5	1.8	72.2	0.3
5.6	1.0	1.0	5.0	7.9	153.2	39.8
4.7	21.0	27.0	-	13.7	100.4	47.0
2.9	1.0	11.0	3.0	7.8	161.8	42.0
14.0	4.0	25.0	10.0	20.5	167.2	49.2
13.1	2.0	-	5.0	5.73	71.8	33.0

R_{max}	cn	ct	gf	lt	lw
1.00±(0.12)	7.43	3	2	1.2	1.0
1.52±(0.13)	13.35	1	1	0.1	0.3
1.05±(0.25)	2.00	3	3	0.3	6.1
1.04±(0.05)	-	3	2	0.3	0.7
1.07±(0.08)	10.39	3	2	0.2	0.5
1.17±(0.06)	8.53	3	2	0.1	0.3
0.89±(0.08)	6.94	2	2	0.1	0.5
-	4.79	5	2	-	-
0.92±(0.32)	5.06	4	2	-	-
0.74±(0.13)	8.15	2	2	0.1	0.9
0.76±(0.17)	8.28	3	2	0.4	1.8
1.30±(0.09)	-	5	2	-	-
1.18±(0.12)	6.86	2	2	0.2	1.8
1.42±(0.10)	7.96	2	2	0.2	1.4
1.12±(0.10)	7.91	2	2	0.1	1.4
1.16±(0.10)	5.09	3	2	0.2	2.7
1.25±(0.22)	-	2	2	0.1	2.0
1.21±(0.10)	6.74	3	3	0.4	3.5
0.76±(0.25)	2.08	4	2	-	-
-	-	4	2	-	-
1.18±(1.18)	6.33	2	2	0.7	0.9
1.16±(0.13)	5.83	3	2	3.6	1.0
0.77±(0.09)	16.62	2	2	-	1.2
1.63±(0.10)	6.89	3	3	1.8	0.7
1.05±(0.07)	9.84	2	2	0.2	1.9

Appendix 3.7

DCA values for 16 species (names given in appendix 3.1) from Day *et al.* (1987).

Species	Axis 1	Axis 2	Axis 3
1	382	68	53
2	-	-	-
3	332	364	433
4	-	-	-
5	-	-	-
6	-	-	-
7	302	41	142
8	421	338	317
9	157	160	263
10	-	-	-
11	-	-	-
12	298	137	206
13	344	354	365
14	413	238	107
15	444	353	132
16	-	-	-
17	-	-	-
18	429	241	277
19	452	264	455
20	46	240	229
21	-	-	-
22	234	485	243
23	264	-32	148
24	567	295	-1
25	-	-	-

References

Abele, L.G., D.S. Simberloff, D.R. Strong and A.B. Thistle. 1984. Preface. In: D.R. Strong Jr., D.S. Simberloff, L.G. Abele and A.B. Thistle (eds.). Ecological Communities: Conceptual Issues and the Evidence. Princeton U. Press, Princeton.

Bazzaz, F.A. 1979. The physiological ecology of plant secession. Ann. Rev. Ecol. Syst. 10:351-371.

Bloom, A.J., F.S. Chapin III, and H.A. Mooney. 1985. Resource limitation in plants - an economic analogy. Ann. Rev. Ecol. Syst. 16:363-392.

Buckley, R. 1982. Transplants along the vegetation gradient on central Australian sand ridges. Australian Journal of Ecology 7:421-422.

Cain,S.A. 1947. Characteristics of natural areas and factors in their development. Ecol. Monogr. 17:185-200.

Chapin III, F.S. 1980. The mineral nutrition of wild plants. Ann. Rev. Ecol. Syst. 11:233-260.

Chesson, P.L. and R.R. Warner. 1981. Environmental variability promotes coexistence in lottery competitive systems. Am. Nat. 117:923-943.

Chesson, P.L. 1982. The stabilizing effect of a random environment. J. Math. Biol. 15:1-36.

Clements, F.E. 1916. Plant succession: an analysis of the development of vegetation. Publ. Carneg. Inst. 242.

Clements, F.E., J.E. Weaver and H.C. Hanson. 1929. Plant

Competition: An Analysis of Community Functions. Carnegie Inst. of Washington.

Colinvaux, P. 1986. Ecology. John Wiley & Sons, N.Y.

Colwell, R.K. and E.R. Fuentes. 1975. Experimental studies of the niche. Ann. Rev. Ecol. Syst. 6:281-311.

Colwell, R.K. and D.W. Winkler. 1984. A null model for null models in biogeography. In: D.R. Strong Jr., D.S. Simberloff, L.G. Abele and A.B. Thistle (eds.). Ecological Communities: Conceptual Issues and the Evidence. Princeton U. Press, Princeton.

Connell, H.H 1972. Community interactions in marine rocky intertidal shores. Ann. Rev. Ecol. Syst. 3:169-192.

Connell, H.H 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. Am. Nat. 122:661-696.

Connor, E.F. and D. Simberloff. 1978. Species number and compositional similarity of the Galapogos flora and avifauna. Ecol. Monogr. 48:219-248.

Connor, E.F. and D. Simberloff. 1979. The assembly of species communities: chance or competition? Ecol. 60:1132-1140.

Connor, E.F. and D. Simberloff. 1984. Neutral models of species' co-occurrence patterns. In: D.R. Strong Jr., D.S. Simberloff, L.G. Abele and A.B. Thistle (eds.). Ecological Communities: Conceptual Issues and the Evidence. Princeton U. Press, Princeton.

Curtis, J.T. 1955. A prairie continuum in Wisconsin. Ecology

36:558-566.

Dale, M.R.T. 1984. The contiguity of upslope and downslope boundaries in a zoned community. Oikos 43:92-96.

Day, R.T., P.A. Keddy, J.M. McNeill and T. Carleton. In press. A multivariate description of marshes along the Ottawa River (Canada) and exploration of the Grime-Huston diversity model. J. Ecol.

Diamond, J.M. 1975. Assembly of species communities. In: M.L. Cody and J.M. Diamond (eds.). Ecology and Evolution of Communities. Belknap Press, Cambridge, Mass.

Diamond, J.M. 1979. Community structure: is it random, or is it shaped by species differences and competition? In: R.M. Anderson, B.D. Turner and L.D. Taylor (eds.). Population Dynamics. Blackwell, Oxford.

Diamond, J.M. and T.J. Case. 1986. Preface. In: J.M. Diamond and T.J. Case (eds.). Community Ecology. Harper & Row, N.Y.

Diamond, J.M. 1986. Overview: Laboratory experiments, field experiments, and natural experiments. In: J.M. Diamond and T.J. Case (eds.). Community Ecology. Harper & Row, N.Y.

Dore, W.G. and J. McNeill. 1980. Grasses of Ontario. Canadian Government Publishing Centre, Hull, Quebec, Canada.

Egler, F.E. 1947. Arid southwest Oahu vegetation, Hawaii. Ecol. Monogr. 17:383-435.

Feller, W. 1968. An Introduction to Probability Theory and Its Applications. Volume I. Third Edition. John Wiley & Sons, N.Y.

Fenner, M. 1978. A comparison of the abilities of colonizers and

closed-turf species to establish from seed in artificial swards. J. Ecol. 66:953-963.

Fenner, M. 1985. Seed Ecology. Chapman & Hall, London.

Fitter, A.H. and R.K.M. Hay. 1983. Environmental Physiology of Plants. Academic Press, N.Y.

Fisher, R.A. 1920. Some remarks on the methods formulated in a recent article on 'The qualitative analysis of plant growth'. Ann. appl. Biol. 7:376-372.

Gilpin, M.E. and J.M. Diamond. 1984. Are species co-occurrences on islands non-random, and are null hypotheses useful in community ecology? In: D.R. Strong Jr., D.S. Simberloff, L.G. Abele and A.B. Thistle (eds.). Ecological Communities: Conceptual Issues and the Evidence. Princeton U. Press, Princeton.

Gleason, H.A. 1926. The individualistic concept of the plant association. Bull. Torry Bot. Club. 53:7-26.

Gleason,H.A. 1939. The individualistic concept of the plant association. Am. Midl. Natur. 21:92-1,10.

Gleason, H.A. and A. Cronquist. 1963. Manual of vascular plants of northeastern United States and adjacent Canada. Willard Grant Press, Boston, USA.

Gower, J.C. 1966. Some distance properties of latent root and vector methods used in multivariate analysis. Biometrica 53:325-338.

Gower, J.C. 1971. A general coefficient of similarity and some of its properties. Biometrics 27:857-874.

Grace, J.B. and R.G. Wetzel. 1981. Habitat partitioning and competitive displacement in cattails (Typha): experimental field studies. Am. Nat. 118:463-474.

Grant, P.R. and I Abbott. 1980. Interspecific competition, island biogeography, and null hypotheses. Evol. 34:332-341.

Grime, J.P. and R. Hunt. 1975. Relative growth-rate: its range and adaptive significance in a local flora. J. Ecol. 63:393-422.

Grime, J.P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. Am. Nat. 111:1169-1194.

Grime, J.P. 1979. Plant Strategies and Ecological Processes. John Wiley & Sons, Chichester.

Gross, K.L. 1984. Effects of seed size and growth form on seedling establishment of six monocarpic perennial plants. J. Ecol. 72:369-387.

Grubb, P.J. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. Biol. Rev. 52:107-145.

Gurevitch, J. 1986. Competition and the local distribution of the grass Stipa meomexicana. Ecol. 67:46-57.

Harper, J.L., P.H. Lovell and K.G. Moore. 1970. The shapes and sizes of seeds. Ann. Rev. Ecol. Syst. 1:327-356.

Harris, S.W. and W.H. Marshall. 1963. Ecology of water level manipulations on a northern marsh. Ecol. 44:331-343.

Harris, R.J. 1975. A Primer of Multivariate Statistics.

Academic Press, N.Y.

Hill, M.O. and H.G. Gauch, Jr. 1980. Detrended correspondence analysis: an improved ordination technique. Vegetatio 42:47-58.

Hutchinson, G.E. 1975. A Treatise on Limnology, vol III. Limnological Botany. John Wiley & Sons, N.Y.

Karson, M.J. 1982. Multivariate Statistical Methods. Iowa State Univ. Press, Iowa, USA.

Keddy, P.A. 1982. Quantifying within-lake gradients of wave energy: interrelationships of wave energy, substrate particle size and shoreline plants in Axe Lake, Ontario. Aquatic Botany 14:41-58.

Keddy, P.A. 1983. Shoreline vegetation in Axe Lake, Ont.: effects of exposure on zonation patterns. Ecol. 64:331-344.

Keddy, P.A. 1985. Wave disturbance on lakeshores, and the within-lake distribution of Ontario's Atlantic Coastal Plain flora. Can. J. Bot. 63: 656-660.

Kozlowski, T.T. 1984. Responses of woody plants to flooding. In: Kozlowski, T.T. (ed.). Flooding and Plant Growth. Academic Press.

Lefkovitch, L.P. 1984. A nonparametric method for comparing dissimilarity matrices, a general measure of biogeographical distance, and their application. Am. Nat. 123:484-499.

Lefkovitch, L.P. 1985. further nonparametric tests for comparing dissimilarity matrices based on the relative neighborhood graph. Math. Biosciences 73:71-88.

Legendre, L. and P. Legendre. 1983. Numerical Ecology. Elsevier, Amsterdam.

Levins, R. and R. Lewontin. 1982. Dialectics and reductionism in ecology. In: E. Saarinen (ed.). Conceptual Issues in Ecology. D. Reidel Publishers, Dardrecht, Holland. pp.107-138.

Lieffers, V.J. and J.M. Shay. 1981. The effects of water level on the growth and reproduction of Scirpus maritimus var. paludosus. Can. J. Bot. 59:118-121.

Lubchenco, J. 1980. Algal zonation in the New England rocky intertidal community: an experimental analysis. Ecology 61:333- 344.

MacArthur, R.H. 1972. Geographical Ecology. Harper & Row, N.Y.

Mason, H.L. 1947. Evolution of certain floristic associations in western North America. Ecol. Monogr. 17:201-210.

McConnaughay, K.D.M. and Bazzaz, F.A. 1987. The relationship between gap size and performance of several colonizing annuals. Ecol. 68:411-416.

McCullagh, P. and J.A. Nelder. 1983. Generalized Linear Models. Chapman & Hall, London.

McIntosh, R.P. 1967. The continuum concept of vegetation. Bot. Rev. 33:130-187.

McIntosh, R.P. 1975. H.A. Gleason - 'individualistic ecologist' 1882-1975. His contributions to ecological theory. Bull. Torry Bot. Club 102:253-273.

Miller, T.E. 1982. community diversity and interactions between the size and frequency of disturbance. Am. Nat. 120:533-536.

Mitchley, J. and P.J. Grubb. 1986. Control of relative abundance of perennials in chalk grassland in southern England. I. Constancy of rank order and results of pot- and field-experiments on the role of interference. J. Ecol. 74:1139-1166.

Mirkin, B.M. 1987. Paradigm change and vegetation classification in Soviet phytocoenology. Vegetatio 68:131-138.

Moore, D.R.J. 1985. Dormancy and germination responses to various water levels and their relationship to species distributions in a lakeshore plant community. MSc. Thesis, University of Ottawa, Ottawa, Ontario, Canada.

Murphy, G.I. 1968. Pattern in life history and the environment. Am. Nat. 102:390-404.

Newman, E.I. 1983. Interactions between plants. In:Physiological Plant Ecology III. Responses to the Chemical and Biological Environment. O.L. Lange, P.S. Nobel, C.B. Osmond and H. Ziegler (eds.). Springer-Verlag, Berlin.

Nicholson, A. and B. Aroyo. 1975. A case study in hydrarch zonation. Vegetatio 30:207-212.

Niklas, K.J. 1986. Evolution of plant shape: design constraints. TREE 1:67-72.

Paine, R.T. 1984. Ecological determinism in the competition for space. Ecology 65:1339-1348.

Peters, R.H. 1982. Useful concepts for a predictive ecology. In: E. Saarinen (ed.). Conceptual Issues in Ecology. D. Reidel Publishers, Dardrecht, Holland. pp:215-228.

Pianka, E.R. 1978. Evolutionary Ecology, 2nd Edition. Harper & Row, N.Y.

Pielou, E.C. and R.D. Routledge. 1976. Salt marsh vegetation: latitudinal variation in the zonation patterns. Oecol. 24:311-321.

Pielou, E.C. 1977. Mathematical Ecology. John Wiley and Sons, New York, N.Y. USA.

Rabinowitz, D. 1978a. Abundance and diaspore weight in rare and common prairie grasses. Oecol. 37:213-219.

Rabinowitz, D. 1978b. Early growth of mangrove seedlings in Panama, and an hypothesis concerning the relationship of dispersal and zonation. J. Biogeogr. 5:113-133.

Roughgarden, J. 1979. Theory of Population Genetics and Evolutionary Ecology: an Introduction. Macmillan, N.Y.

Roughgarden, J. 1983. Competition and theory in community ecology. Am. Nat. 122:583-601.

Salisbury, E.J. 1942. The Reproductive Capacity of Plants. Bell, London.

Schaffer, W.M. 1974. Optimal reproductive effort in fluctuating environments. Am. Nat. 108:783-790.

Schoener, T.W. 1983. Field experiments on interspecific competition. Am. Nat. 122:240-285.

Sharitz, R.R. and J.F. McCormick. 1972. Population dynamics of two competing annual plant species. Ecology 54:723-740.

Shipley, B. and P.A. Keddy. In press. The community-unit and individualistic concepts as falsifiable hypotheses. Vegatatio.

Silander, J.A. and J. Antonovics. 1982. Analysis of interspecific interactions in a coastal plant community - a perturbation approach. Nature 298:557-510.

Silvertown, J.W. 1983. The distribution of plants in limestone pavement: tests of species interaction and niche separation against null hypotheses. J. Ecol. 71:819-828.

Simberloff, D. 1978. Using island biogeographic distributions to determine if colonization is stochastic. Am. Nat. 112:713-726.

Simberloff, D. 1982a. A succession of paradigms in ecology: essentialism to materialism and probiblism. In: E. Saarinen (ed.). Conceptual Issues in Ecology. D. Reidel Publishers, Dordrecht, Holland. pp.139-153.

Simberloff,D. 1982b. reply . In: E. Saarinen (ed.). Conceptual Issues in Ecology. D. Reidel Publishers, Dordrecht, Holland. pp.139-153.

Snow, A.A. and S.W. Vince. 1984. Plant zonation in an Alaskan salt marsh I. Distribution, abundance and environmental factors. Jour. Ecol. 72:651-667.

Smith, H. 1982. Light quality, photoperception, and light strategy. Ann. Rev. Plant Physiol. 33:481-518.

Spence, D.H.N. 1982. The zonation of plants in freshwater lakes. Adv. Ecol. Res. 12:37-125.

Stearns, C. 1976. Life-history tactics: a review of the ideas. Quart. Rev. Biol. 51:3-47.

Terborgh, J. 1971. Distribution on environmental gradients:

theory and a preliminary interpretation of distributional patterns in the avifauna of the Cordillera Vicabamba, Peru. Ecol. 52:23-40.

Tilman, D. 1982. Resource competition and community structure. Princeton U. Press, Princeton.

Turkington R. and L.W. Aarssen. 1984. Local-scale differentiation as a result of competitive interactions. In: R. Dirzo and J. Sarukhan (eds.). Perspectives on Plant Population Biology. Sinauer Associates Inc., Sunderland, MA. USA. pp.107-127.

Underwood, A.J. 1978a. The detection of non-random patterns of distribution of species along an environmental gradient. Oecol. 36:317-326.

Underwood, A.J. 1978b. A refutation of critical tidal levels as determinants of the structure of intertidal communities on British shores. Journal of Experimental Marine Biology and Ecology 33:261-276.

van der Valk, A.G. 1981. Succession in wetlands: a Gleasonian approach. Ecol. 62:688-696.

van Hulst, R. In press a. From population dynamics to vegetation dynamics: plant succession as a species replacement process. In: Succession. D.G. Lewin (ed.). Chapman & Hall, London.

van Hulst, R. In press b. Invasion models of vegetation dynamics. Vegetatio.

Vince, S.W. and A.A. Snow. 1984. Plant zonation in an Alaskan salt marsh II. An experimental study of the role of edaphic conditions. Jour. Ecol.72:669-684.

Walker, B.H. and C.F. Wehrhahn. 1971. Relationships between derived vegetation gradients and measured environmental variables in Saskatchewan wetlands. Ecol. 52:88-95.

Weiner, J. 1986. How competition for light and nutrients affects size variability in Ipomoea tricolor populations. Ecol. 1425-1427.

Weiner, J. and S.C. Thomas. 1986. Size variability and competition in plant monocultures. Oikos 47:211-222.

Weins, J.A. 1984. On understanding a non-equilibrium world: myth and reality in community patterns and processes. In: D.R. Strong Jr., D.S. Simberloff, L.G. Abele and A.B. Thistle (eds.). Ecological Communities: Conceptual Issues and the Evidence. Princeton U. Press, Princeton.

Whittaker, R.H. 1951. A criticism of the plant association and climatic climax concepts. Northwest Sci. 25:17-31.

Whittaker, R.H. 1956. Vegetation of the Great Smoky Mountains. Ecol. Monogr. 26:1-80.

Whittaker, R.H. 1962. Classification of natural communities. Bot. Rev. 28:1-160.

Whittaker, R.H. 1967. Gradient analysis of vegetation. Biol. Rev. 42:207-264.

Whittaker, R.H. 1975. Communities and Ecosystems, 2nd edition. Macmillan Publishing Co., New York, USA.

Wilson, S.D. and P.A. Keddy. 1985. Plant zonation on a shoreline gradient: physiological response curves of component species. J. Ecol. 73:851-860.

Wilson, S.D. and P.A. Keddy. 1986a. Species competitive ability and position along a natural stress/disturbance gradient. Ecol. 67:1236-1242.

Wilson, S.D. and P.A. Keddy. 1986b. Measuring diffuse competition along an environmental gradient: results from a shoreline plant community. Am. Nat. 127:862-869.

Wright, S.J. and C.C. Biehl. 1982. Island biogeographic distributions: testing for random, regular and aggregated patterns of species occurrence. Am. Nat. 119:345-357.