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PATTERN AND PROCESS IN WETLANDS OF VARYING STANDING CROP: THE IMPORTANCE OF SCALE

by

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submitted in partial fulfillment of the requirements
for the degree of Doctor of Philosophy
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ABSTRACT

Predicting diversity is a central theme of ecology. In this thesis, two aspects of diversity were explored, number of vegetation types and species richness. In this thesis, a vegetation type is defined to include all communities having the same set of numerically dominant species. For each diversity measure, patterns along a wetland standing crop gradient were determined and the underlying processes explored. The common theme throughout this exploration was the importance of scale in setting the limits for general models of pattern and process in community ecology.

In the first chapter, I examined the relationship between number of vegtation types and standing crop in wetlands. Fifteen individually homogeneous wetland sites which represented a broad standing crop gradient were sampled in eastern Canada. In each site, fifteen 0.25 m^2 quadrats were randomly sampled and species presence in each of nine subquadrats and quadrat standing crop were determined. A Spearman Rank Correlation test demonstrated a significant positive relationship between the mean vegetational similarity of wetland sites and standing crop ($r_s = 0.39$; $p < 0.0001$). Further, Detrended Correspondence Analysis demonstrated that low standing crop sites had little similarity in terms of species composition while very high standing crop sites had similar species composition. Thus, there appears to be an inverse relationship between number of vegetation types and standing crop.

In chapter 2, I investigated the relationship between species richness and standing crop at two levels of organization: the among vegetation types level and the within vegetation type level. Each of the fifteen sites described above was relatively homogeneous in terms of the dominant species present. However, as a group, the sites comprised a wide range of vegetation types. A second order polynomial regression indicated a significant bitonic relationship between species richness and standing crop at the among vegetation types scale, that is, when all fifteen sites were combined. At the within vegetation type level, however, no significant relationships were observed ($p > 0.05$). The results indicated that the model of species richness proposed by Grime had predictive

power at a coarse-grained level of organization, among vegetation types, but did not survive the transition to a finer-grained level of organization, the within vegetation type level. Therefore, the higher level processes which structure species richness patterns among vegetation types are not the same processes that determine richness patterns within a vegetation type.

Numerous forces, abiotic or biotic, can maintain or alter vegetation states and species richness at different levels of organization. In the third chapter, I tested whether these "assembly forces" had the potential to duplicate the patterns observed in chapters 1 and 2 in a large microcosm experiment. In this study, I created artificial wetland microcosms with an identical species mixture and manipulated the following variables to determine their impact on wetland vegetation states and species richness: vegetation history, length of growing season, substrate texture, litter accumulation, water depth, and fluctuating water levels. These variables were manipulated at two fertility levels to: (i) determine whether high fertility reduced the effects assembly forces had on the range of wetland vegetation types observed, as predicted in chapter 1, and (ii) test whether high fertility levels reduced species richness, as predicted in chapter 2. Water depth, fluctuating water levels, and litter significantly affected wetland species composition at both fertility levels. In addition, in each of the twelve artificial habitats, species richness was higher in the low fertility treatment than was observed in the corresponding high fertility treatment. Relatively small habitat differences also affected species richness. However, high fertility did not reduce the effects of the assembly forces on wetland vegetation species composition, except that small, rare species were eliminated. The high fertility result was unexpected based upon observations of natural wetlands in which the natural range of habitat differences produced many vegetation types at low fertility but only a few states at high fertility.

Chapter 4 investigated the effects of a disturbance involving the complete removal of above ground vegetation in five wetlands of varying standing crop found on the Ottawa River. The study was designed to test whether the effects of the removal treatment on the two diversity measures were dependent on (i) position of the wetland site along the standing crop gradient, (ii) the level of organization considered, and (iii) the length of the recovery period following the removal treatment. A parallel experiment was also conducted to determine the relative

importance of various stress and disturbance factors in the wetlands considered in this study. The results indicated that the wetland standing crop gradient and the diversity patterns observed along this gradient were likely the result of an underlying natural disturbance gradient. The disturbance experiment indicated that the low standing crop wetlands with a history of disturbance were less affected by a single disturbance event than were high standing crop wetlands at the relatively fine-grained guild and species levels of organization. However, the effects on species richness and other higher level variables were small and short-lived indicating that the effects of the disturbance treatment were scale dependent. A longer, more intense disturbance regime is likely required to explore the processes underlying the diversity patterns found in chapters 1 and 2.

In chapter 5, I considered the results from chapters 1 to 4 with regards to the conservation value, potential threats, and proper management techniques for wetlands, particularly for low standing crop wetlands. In addition to the fifteen wetlands surveyed in chapter 1, additional low standing crop wetland sites from the Georgian Bay area in Ontario and the Tusket River Valley in Nova Scotia were surveyed. The results revealed that low standing crop wetlands had many more nationally rare species than did high standing crop wetlands, in addition to the higher species richness and higher number of vegetation types discussed above. If the ultimate goal of nature conservation is to preserve genetic diversity as stated in the World Conservation Strategy, then these results strongly suggest that low standing crop wetlands have a much higher conservation value than presently accounted for in wetland evaluation systems. The results of the microcosm experiment revealed that low standing crop wetlands may be severely threatened by eutrophication and by an invasive Eurasian weed, *Lythrum salicaria*. In each of the five wetland sites examined in the field experiment, *L. salicaria* exhibited dramatic increases in abundance over the three year observation period. Further, the disturbance treatment at each site did not slow the invasion of *L. salicaria*, but instead increased the rate of invasion in at least one site. I conclude that low standing crop wetlands, despite their high conservation value, are severely threatened and must be protected from the effects of eutrophication and invasion by *Lythrum salicaria*.

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In conducting ecological research, particularly in wetlands, one encounters many hazards and endures often unpleasant working conditions. These included: mosquitoes with breakfast (literally), deer flies the size of small birds, extreme heat and humidity, heretofore unknown rapids, pneumonia (sorry Kevin), a horse with a taste for human flesh, dobermans, cows (see chapter 4), extreme cold, short-sighted duck hunters, mud, and a certain doctoral student with a penchant for tipping canoes. Despite the above, I could always count on the tireless assistance of my field assistants. A special thanks goes to Kim Lemky, Kim Boutilier, Dann McCann, Joyce Belcher, Cheryl McJannet, Barbara Minish, Irene Wisheu, Kevin Stone, Cathy Keddy, Mirek Sharp, and Dan Brunton.

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Four blind men are led into a courtyard to experience an elephant for the first time. The first grasps the trunk and declares that elephants are fire hoses. The second touches an ear and maintains that elephants are rugs. The third walks into its side and believes that elephants are a kind of wall. The fourth feels a leg and decides that elephants are pillars."

Traditional Buddhist Proverb

GENERAL INTRODUCTION

"The eventual goal of science is to provide a single theory that describes the whole universe", writes Stephen Hawking in a recent book entitled *A Brief History of Time*. Do scientists really have theories that are sufficient to make predictions about everything from microbes to man, superstrings to the universe, or the weather the day after tomorrow? Sadly, the answer is no. The truth is that science can only answer certain types of questions. At the lowest levels of matter, energy and the building blocks of which they are made up, science is at its very best in providing general theories and accurate predictions, as was evidenced in Hawking's book. However, as one climbs through successive layers to chemistry and biology, science begins to lose more and more of its precision. By the time science reaches human behaviour and beyond, general theories and practical predictions have been left far behind. For all the detailed understanding which now exists at the level of sub-atomic particles, this understanding has not proven useful in predicting the next earthquake or in determining the cause of cancer. Just as it is inconceivable that literary scholars would attempt to interpret the works of Shakespeare by reference to the alphabet, scientists cannot explain phenomena at one level of organization by reference to lower levels. Much of the rancorous debate in science in general, and in ecology in particular, could be avoided by specifying the levels of organization where general models do or do not apply. In this thesis, I explore how patterns and processes in wetlands vary between different levels of organization ranging in scale from those affecting the abundance of individual species in a m^2 quadrat to those affecting the structure and composition of wetlands in eastern North America.

The most important influence on the content of this thesis was a book by Allen and Starr (1982) entitled, *Hierarchy: Perspectives for Ecological Complexity*. In this book, Allen and Starr began by acknowledging that ecology is inherently complex because there are too few parts to average their behaviour reliably (as with gas laws) and too many parts to manage each separately with its own equation (as with the orbits of planets). The complexity of these so called middle number systems is related to the interaction of different levels of organization. Therefore, to account for complexity, ecological models must be hierarchical. Hierarchy may be understood as "a system of behavioral interconnections wherein the higher levels constrain and control the lower levels" (Allen and Starr 1982).

As O'Neill *et al.* (1982) point out in *A Hierarchical Concept of Ecosystems*, if ecologists focus on interactions among individual organisms, ecosystems seem relatively constant backgrounds that provide the context within which interesting phenomena occur. If ecologists instead focus on succession, then ecosystems appear to change continuously through time. Of course, both impressions are correct, depending on the temporal and spatial scale of our observations.

Diversity is an important phenomenon in ecology which exists at many levels of organization. At the global scale, one can consider how annual evapotranspiration and other climatic variables affect diversity. At a more local scale, one can consider how frequency of disturbance affects diversity when comparing between different wetlands (the among vegetation types level). At an even more local scale, one can consider the effects of microsite differences on diversity within a given wetland (the within vegetation type level). Hierarchy theory predicts that the processes affecting diversity patterns at a lower level of organization will have no effect at higher levels of organization. Similarly, diversity patterns observed at one level of organization will not likely survive the transition to other levels of organization. In the first two chapters of this thesis, I use the concept of hierarchy theory to explore patterns of diversity in wetlands at different levels of organization. Specifically, I explore how two measures of diversity, number of vegetation types and number of species, vary with wetland standing crop when a wide range of wetlands are considered (among vegetation types level). I then test whether the observed relationship between species richness and standing crop at the among vegetation types level survives the transition to a finer-grained level of organization, the within vegetation type level. Chapters 3 and 4 explore the consequences of different processes on the two measures of diversity and test whether these effects are dependent on the level of organization considered. Finally, chapter 5 considers the implications of the results of the first four chapters for the conservation and management of wetlands.

CHAPTER 1

THE RELATIONSHIP BETWEEN THE NUMBER OF WETLAND VEGETATION TYPES AND STANDING CROP

"Ought we, for instance, to begin by discussing each separate species - man, lion, ox, and the like - taking each kind in hand independently of the rest, or ought we rather to deal first with the attributes which they have in common in virtue of some common element of their nature, and proceed from this as a basis for the consideration of them separately?"

Aristotle, *De Partibus Animalium*

INTRODUCTION

In presenting his 1986 Robert H. MacArthur Award lecture, May (1986) argued that "the largely unanswered question for the 20th century (and maybe the 21st)-is to understand how many species there are". The answer, it seems, depends in part on the scale of investigation. At the global scale, Currie and Paquin (1987) demonstrated that realized annual evapotranspiration explained 76% of the variation in the number of tree species observed at a given latitude and longitude. At a more local scale, variation in the number of plant species can be predicted by local differences in standing crop (or biomass)(Grime 1973, 1979; Al Mufti *et al.* 1977; Day *et al.* 1988). An equally important, but less explored question, addresses the factors that control the number of community types or vegetation types in a landscape. The questions raised about number of vegetation types are analagous to number of species: what are the patterns, what are the independent variables that predict them, and what are the underlying mechanisms which create and maintain the observed patterns (see May 1986). To explore these questions, a vegetation type is defined to include all communities having the same dominant species (*sensu* Moore and Keddy 1989). These communities need not be contiguous.

Previous studies have indicated that standing crop gradients are useful predictors of attributes of plant communities such as species richness (e.g., Al-Mufti *et al.* 1977) and number of rare species (Chapter 5; Moore *et al.* 1989). Standing crop has the added advantage as an independent variable in that it is easily observed and measured. The objective of this chapter is to utilize the dependent variable, number of vegetation types, and test whether it also varies predictably with standing crop. Since wetlands often have broad standing crop gradients (e.g., Wheeler and Giller 1982; Vermeer and Berendse 1983; Day *et al.* 1988), wetlands will be used as a convenient model system in which to explore the relationship between number of vegetation types and standing crop.

An inverse relationship between number of vegetation types and standing crop is a central assumption of the "centrifugal organization model" proposed by Keddy (1989a) for herbaceous vegetation (see Rosenzweig and Abramsky 1986). In this model, the number of vegetation types increases from one or a few at high standing crop

(Figure 1.1, centre) to many at low standing crop (Figure 1.1, periphery). The postulated mechanism is that light is the major limiting resource in fertile, undisturbed sites, and thus there has been morphological convergence such that these high standing crop sites are dominated by large, canopy-forming species which are highly competitive. As standing crop decreases (i.e., as adversity and/or disturbance increase) and light is no longer a limiting resource, the number of potential life forms increases (e.g., carnivorous species, isoetids, annuals). To date, two aspects of the model have been tested and verified - first, the assumption that competition intensity is positively correlated with standing crop (Wilson and Keddy 1986; Gaudet and Keddy 1988) and second, the predictions that the number of life forms and the number of rare species are negatively correlated with standing crop (Moore *et al.* 1989; Boutin and Keddy, in press). This chapter tests the central prediction of the model, that there is an inverse relationship between number of vegetation types and standing crop.

To test the hypothesis that the number of observed wetland vegetation types declines with increasing standing crop, fifteen wetland sites were surveyed in eastern Canada which together encompassed a broad range of standing crop. Since it is operationally difficult to decide at what point two sites belong to the same vegetation type, and since I wish to avoid the long standing but unproductive community unit/continuum controversy, the hypothesis will be tested by testing whether similarity of wetland sites, in terms of species composition, increases as standing crop increases.

METHODS

Study Locations

Three primary study locations were chosen in eastern Ontario (Presqu'ile and Westmeath) and western Quebec (Luskville), Canada. In general, each location included low (<150 g/m^2), moderate (150 - 500 g/m^2), high (500 - 1000 g/m^2) and very high standing crop (>1000 g/m^2) wetlands. The Presqu'ile study area (44°0'N, 77° 43'W) is a peninsula located on the north Lake Ontario shoreline within Presqu'ile Provincial Park. The sites surveyed included infertile wet meadows, a fen, a Carex marsh and a Typha marsh. The Westmeath study area (45° 47'N, 76°50'W) is a riverine shoreline located on the Ottawa River 22 km southwest of the City of Pembroke. At this location, open beach wetlands and sheltered marshes located in Bellows Bay were surveyed. A Typha marsh located 15 km south of Wesmeath was also surveyed. The Luskville study area (45°31'N, 76°6'W) is also a riverine shoreline located 5 km west of Luskville, Quebec on the Ottawa River. The survey included open beach wetlands, sheltered riverine marshes, and a Typha marsh. The low standing crop wetland sites were each dominated by species of varying life form (annuals, slow-growing perennials, isoetids)(Table 1.1). High standing crop wetlands were dominated by species of similar life form (tall, fast-growing perennials capable of clonal spread)(Table 1.1).

Wetland Surveys

The descriptive surveys described below were done at Presqu'ile (12-14 September, 1986), Westmeath (25-26 August, 1987) and Luskville (18-19 August, 1987). At each location five sites were selected, each chosen to represent a different standing crop level. In each site, fifteen quadrats were randomly placed over an area of approximately 100 m^2 and the vegetation sampled using a 0.5 m x 0.5 m quadrat with nine equivalent subdivisions. The presence of each species in each subdivision was recorded and the vegetation clipped at ground level, dried to constant biomass at 60°C, and weighed. All voucher specimens were deposited at the Agriculture Canada herbarium (DAO) or University of Ottawa herbarium (OTT).

Data Analyses

I. Similarity of Wetland Sites Versus Standing Crop

In this analysis the hypothesis was tested that the similarity of wetland sites in terms of species composition was correlated with standing crop. The raw data matrix consisted of 225 quadrats with a total of 141 species. From this data matrix, a quadrat dissimilarity matrix (225 x 225) was calculated using the quantitative symmetric formula:

$$D_{jk} = 1 - (1/2)\{\ [\text{minimum}\ (X_{ij}, X_{ik}) / (X_{ij})] +$$
$$[\text{minimum}\ (X_{ij}, X_{ik}) / (X_{ik})]\ \}$$

where D_{jk} is the dissimilarity between two quadrats j and k, based upon the abundance (X)(number of subquadrats species is found in; maximum = 9) of species i = 1 to N (Faith *et al.* 1987). The quantitative symmetric measure has been shown to have a robust monotonic relationship with similarity of quadrats even when species turnover between sites is high (Faith *et al.* 1987), as is the case in this data set. In addition, this measure has the desirable properties of: (1) having a minimum value of zero when both quadrats contain the same species with the same relative abundances and a constant maximum value of one when no species are shared, and (2) having a built in data standardization in which quadrats are standardized to equal totals (Faith *et al.* 1987). It was chosen not to standardize species to equal maximum abundances in the total data set because it is the numerically dominant species which were used to define the vegetation types in this study.

The quadrats were then ordered in terms of standing crop, and dissimilarity (D_j) of each quadrat to each of the nearest ten other neighbours on the standing crop gradient was summed and the mean calculated. There was an additional important constraint upon the selection of the ten nearest neighbours: neighbours from the same wetland site were not considered to ensure that intra-site comparisons were ignored when performing this calculation. To test whether similarity of wetland sites increased as standing crop increased, a correlation was tested for between quadrat similarity ($S_j = 1 - D_j$) and standing crop using the Spearman Rank Correlation test (Siegel 1956).

II. Sampling Scale Considerations

Sampling scale is a key consideration when testing ideas and hypotheses which are themselves scale dependent. Consider the possible following scenario. Suppose that the low standing crop sites had high pattern diversity at a small spatial scale, while the high standing crop sites also had high pattern diversity, but at a much larger spatial scale. Given the sampling design chosen in this study (i.e., equivalent quadrat size ($0.25m^2$), equivalent site size ($100\ m^2$)), then it is likely that an inverse relationship would be found between number of vegetation types and standing crop as predicted. However, in this scenario the relationship is at least partially a function of the fact that more vegetation types are being sampled at low standing crop (i.e., several per site) than at high standing crop (i.e., one per site). A more severe test is to test for an inverse relationship between number of vegetation types and standing crop only when each portion of the standing crop gradient has been sampled with equal intensity. To test whether sampling intensity was the same across the standing crop gradient the following test was performed: (i) mean within-site similarity was determined for each wetland site by calculating the mean similarity between all possible pairs of the fifteen quadrats sampled within each site (the quantitative symmetric formula (see above) was used to calculate dissimilarity (D) between each pair of quadrats; similarity was calulated using the formula, $S = 1 - D$), and (ii) testing whether mean within-site similarity varied predictably across the standing crop gradient using the Spearman Rank Correlation test (Siegel 1956). Only if no correlation was found, could the possibility be ruled out that an inappropriate sampling scale unduly influenced the results.

III. Detrended Correspondence Analysis

An alternative method to eliminate the possible effects of sampling scale on the results is to only consider mean species composition for each site, and then to compare similarity between groups of wetland sites at different points along the standing crop gradient. Each group must then have the same number of sites to ensure that sampling intensity is equal across the gradient. To determine whether vegetation similarity increased as standing crop increased the following test was conducted: (i) a Detrended Correspondence Analysis (DCA; Gauch 1982) was performed using the 141 x 225 (species x quadrat) raw data matrix, (ii) wetland sites were grouped in terms of mean standing crop by dividing the fifteen sites into classes of three sites each, and calculating mean euclidean distances in two-dimensional DCA space between site centroids within each class, and (iii) testing whether low standing crop wetland sites were more widely scattered in two-dimensional DCA space than were high standing crop wetland sites by performing a Kruskal-Wallis test (Siegel 1956) on the site-site euclidean distances amongst sites, within each of the five standing crop classes. The DCA analysis was performed using the ECOSURVEY program package (Carleton 1985).

RESULTS

I. Similarity of Wetland Sites Versus Standing Crop

Figure 1.2 shows that the similarity of vegetation among wetland sites was positively correlated with standing crop ($r_s = 0.39$, $n = 224$, $p < 0.0001$). This result supported the prediction that the number of wetland vegetation types declined with increasing standing crop.

II. Sampling Scale Considerations

Figure 1.3 shows that within-site similarity was, however, positively correlated with standing crop ($r_s = 0.471$, $p < 0.05$). Therefore, it is possible that the observed correlation between similarity of wetland sites and standing crop was at least partially due to the greater range of vegetation being sampled at the low standing crop end of the gradient. In other words, at an equivalent spatial scale of 100 m^2, pattern diversity was higher within low standing crop sites than in high standing crop sites.

III. Detrended Correspondence Analysis

Prior to the DCA analysis, the fifteen wetland sites were divided into five standing crop classes with three sites each. Figure 1.4 obtained from the DCA indicates that the sites with low standing crop (sites L1, P1, W1; class I) had little similarity in terms of species composition while sites of very high standing crop (sites L5, P5, W5; class V) had similar species composition. Comparison of mean distances between centroids shows that these differences were statistically significant ($p < 0.05$; Figure 1.5). The sites within each of the three middle standing crop classes (II, III, IV) were moderately similar in species composition. The results from the DCA indicate that when the effect of higher pattern diversity within low standing crop sites was removed (Figure 1.3), there still existed a significant positive relationship between the similarity of wetland sites and standing crop.

DISCUSSION

The current challenge in plant ecology is to develop general principles and models to establish a broad theoretical basis for vegetation science (Prentice and van der Maarel 1987). Rigler (1982) has stated that this challenge can best be met by focussing our efforts on state variables that are easily measured, ubiquitous and have predictable properties (see also Lewontin 1974; Peters 1980; Keddy 1987, 1989a,b). This will in turn require that we define the scale of observation which our models describe and choose state variables accordingly (Allen and Starr 1982; Allen 1987; Noy-Meir and van der Maarel 1987). However, plant ecologists have too often focussed on the specifics of a particular system rather than planning for generality (Austin 1986; Keddy 1989a). In this study, I have chosen to examine the relationship between the state variable, number of vegetation types, and standing crop at a landscape scale defined as the among vegetation types (*sensu* Moore and Keddy 1989) level of organization. The eventual goal is to develop a series of nested models incorporating appropriate state variables (e.g., species abundance, number of vegetation types) at successively higher levels of organization (e.g., within vegetation type, between vegetation types; see Chapter 2).

Vegetation Types

Inspection of Table 1.1 shows that the most common species found at each wetland site differed amongst low standing crop wetland sites but were similar in high standing crop wetland sites (see Figures 1.2, 1.4 and 1.5). However, two avenues of research need to be further pursued to verify this conclusion. First, since only 15 wetland sites were examined in this study, it is clear that more wetland sites need to be sampled to better characterize the range of vegetation types that exist for different regions of the standing crop gradient. Second, recent research has emphasized that many species in a given system have convergent morphologies and life-histories, such that the disappearance of any one species and its replacement by another similar species has no effect on the overall functioning of the community (for a discussion, see Terborgh and Robinson 1986). However, by emphasizing species composition in these analyses, it is possible that communities of very similar form and function were classified as having little similarity. This was likely the case with the high standing crop cattail marshes in which two sites were dominated by *Typha xglauca* (*T. angustifolia* x *T. latifolia*) and the third was dominated by *T. latifolia*. Both species are large clonal perennials having high growth rates (Shipley and Keddy 1989) and high competitive ability (Gaudet and Keddy 1988). These characteristics indicate a competitor strategy (sensu Grime 1977, 1979) and are typical of species found in nutrient rich sites with little disturbance. Therefore, if I had instead classified species on the basis of morphology and life-history, then these sites would have been much more similar than was indicated in Figures 1.2, 1.4 and 1.5. Future studies may gain more generality by classifying communities according to form and function rather than species composition.

In low standing crop wetlands there appears to be a wide variety of species morphologies and life-history strategies. For instance, site 1 at Luskville was dominated by obligate annuals (e.g., *Lindernia dubia*) and functional annuals (e.g., *Leersia oryzoides*) with high growth rates (e.g., *L. oryzoides*; Shipley and Keddy 1989) and poor competitive ability (e.g., *L. oryzoides*; Gaudet and Keddy 1988). According to Grime's (1977, 1979) C-S-R model (see also Southwood 1988) these species exhibit a ruderal life-history strategy typical of highly disturbed habitats. Personal observations suggest that this site is annually disturbed by intense ice scour and sand deposition (see Chapter 4). Conversely, site 1 at Presqu'ile was dominated by small perennial species, several of which were evergreen or partially evergreen (e.g., *Dicanthelium acuminatum*). This strategy is typical of stress tolerators (*sensu* Grime, 1977, 1979) in nutrient poor habitats.

Centrifugal Organization Model

The convergence in taxonomy, morphology and life history amongst species in high standing crop wetlands suggests that only a few vegetation types are possible. Keddy (1989a) has suggested that in low standing crop habitats which are disturbed or stressed (*sensu* Grime 1979), release from intense competition for light (see Figure 4.3) has created conditions in which a wide array of life forms and morphologies can survive (Table 5.1). These results support the centrifugal organization model (Keddy 1989a) in which number of vegetation types is inversely correlated with standing crop (Figure 1.1).

Pattern and Process: Implications For Future Research

This chapter introduced the state variable number of vegetation types. An inverse relationship between number of vegetation types and standing crop was demonstrated using wetlands as a model system. Recently, Inouye and Tilman (1988) demonstrated that old field plots of varying initial species composition appeared to be converging through time after addition of nitrogen fertilizer. This was not the case in unfertilized plots. Willis (1963) also found similar patterns after experimental fertilization of sand dune vegetation. These studies provide evidence that the patterns observed in this chapter may also apply to other herbaceous systems. The results of this chapter suggest three important questions, each of which will be explored in the following chapters:

(1) Do other diversity measures such as species richness and number of rare species exhibit similar patterns along a wetland standing crop gradient? Are the observed patterns scale dependent?

(2) What were the underlying processes which produced the observed inverse relationship between number of vegetation types and standing crop?

(3) What are the implications of the results presented in this chapter for the conservation and management of wetlands, particularly low standing crop wetlands

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Table 1.1. The three most common species[1] in descending order found in each of fifteen wetland sites sampled in this study. Mean standing crop for each site (n = 15) and site standing crop class are also shown.

Standing Crop (g/m^2)	Class	Location and Site No.	Species
16.0	I	Westmeath I	*Scirpus americanus* *Carex lenticularis* *Salix lucida*
71.2	I	Presqu'ile I	*Scleria verticillata* *Dicanthelium acuminatum* *Rhyncospora capitellata*
130.8	I	Luskville I	*Leersia oryzoides* *Lindernia dubia* *Eleocharis erythropoda* *Salix interior*[2]
160.0	II	Luskville II	*Eleocharis erythropoda* *Leersia oryzoides* *Lythrum salicaria*
218.0	II	Westmeath II	*Scirpus americanus* *Hypericum boreale* *Fimbristylis autumnalis*
268.0	II	Presqu'ile II	*Cladium mariscoides* *Potentilla anserina* *Equisetum variegatum*
335.2	III	Presqu'ile III	*Scirpus americanus* *Calamogrostis canadensis* *Cladium mariscoides*
369.2	III	Luskville III	*Scirpus americanus* *Lythrum salicaria* *Eleocharis palustris*
498.4	III	Luskville IV	*Agrostis stolonifera* *Scirpus fluviatilis* *Sparganium eurycarpum*
527.6	IV	Westmeath IV	*Carex vesicaria* *Lemna minor* *Hydrocharis morsus-ranae*

652.0	IV	Westmeath III	*Scirpus acutus* *Potentilla palustris* *Polygonum amphibium*
692.4	IV	Presqu'ile IV	*Carex lanuginosa* *Carex aquatilis* *Hydrocharis morsus-ranae*
1109.6	V	Luskville V	*Typha xglauca* *Rumex verticillatus* *Galium sp.*
1263.2	V	Westmeath V	*Typha xglauca* *Lemna minor* *Sium sauve*
1686.4	V	Presqu'ile V	*Typha latifolia* *Lemna minor* *Leersia oryzoides*

---

[1] nomenclature as in Gleason and Cronquist (1963) except *C. lanuginosa* Michx., *D. acuminatum* (Swartz) Gould and Clark, and *T.* x*glauca* Godron.

[2] these species had the same abundance.

FIGURE CAPTIONS

Figure 1.1. Centrifugal organization of vegetation types along a standing crop gradient ranging from 0 at the periphery to >1000 g/m^2 in the centre. The dominant genera for each wetland vegetation type are shown. Superscripts refer to patterns identified by [1]Wisheu and Keddy (1989), [2]Keddy (1981, 1983), [3]Moore *et al.* (1989), [4]Day *et al.* (1988), [5]Moore *et al.* (1989), [6]Moore *et al.* (1989), and [7]Keddy (unpublished data).

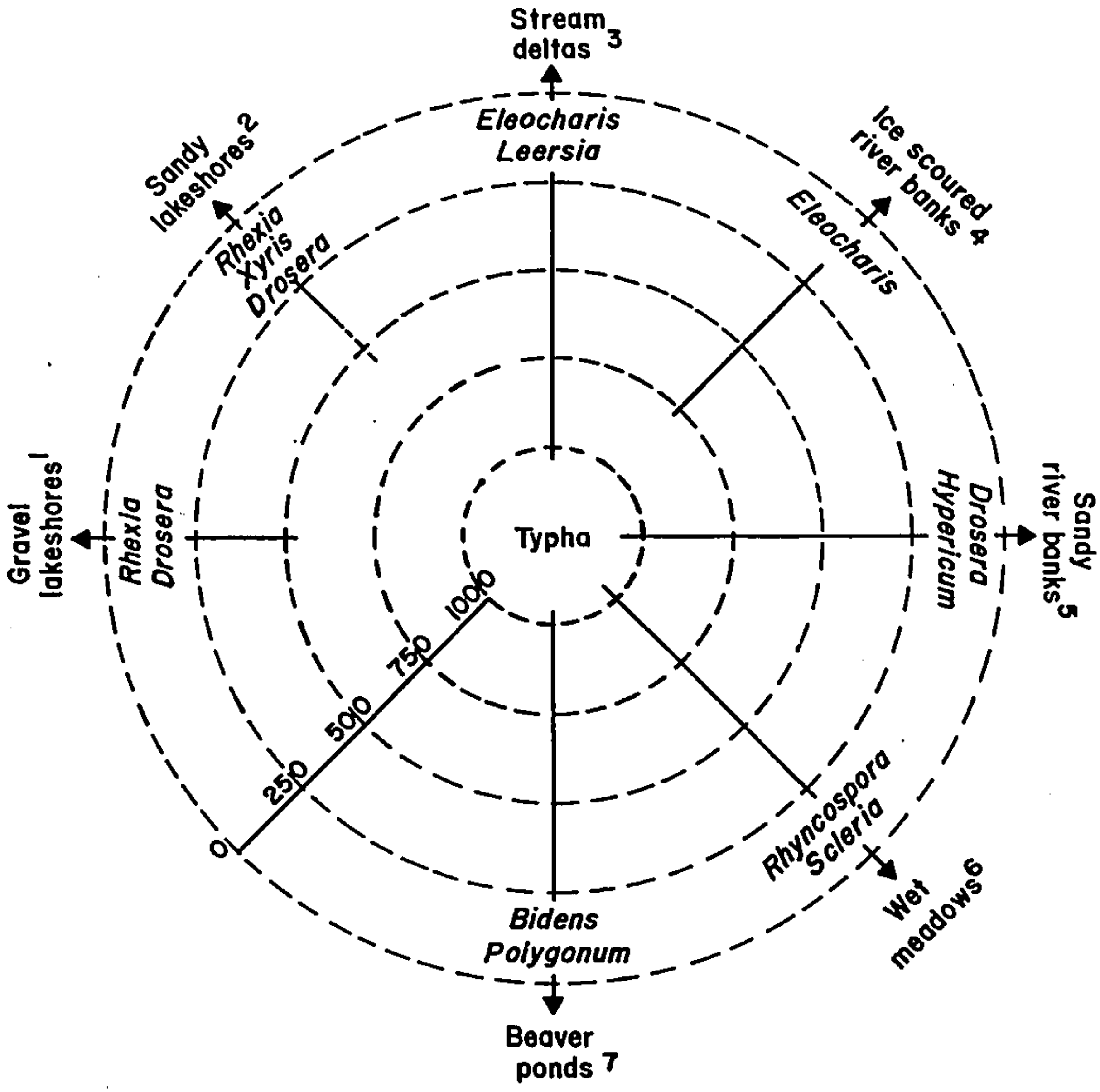
Figure 1.2. Mean similarity of quadrats in terms of species composition plotted against standing crop. Quadrat similarity was calculated by comparing each quadrat with the ten other quadrats having the most similar standing crop. (Intra-site comparisons were excluded from the calculations, Spearman Rank Correlation Coefficient, $n = 224$, $r_s = 0.39$, $p < 0.0001$).

Figure 1.3. Mean within-site similarity of quadrats in terms of species composition plotted against standing crop. Quadrat similarity was calculated by comparing all possible combinations of the 15 quadrats sampled at each site. The Spearman Rank Correlation Coefficient indicated a significant correlation ($n = 15$, $r_s = 0.47$, $p < 0.05$).

Figure 1.4. Two-dimensional DCA model with fifteen wetland site centroids and standing crop isoclines. Each isocline separates the standing crop classes indicated in Table 1.1.

Figure 1.5. Mean euclidean distance in two-dimensional DCA space between wetland site centroids within each of the five standing crop classes. Classes which are significantly different from one another do not share a common letter (a, b, or c).

FIGURE 1.1



Stream deltas 3
Eleocharis
Leersia
Sandy lakeshores 2
Rhexia
Xyris
Drosera
Ice scoured river banks 4
Eleocharis
Gravel lakeshores 1
Rhexia
Drosera
Typha
Drosera
Hypericum
Sandy river banks 5
0
250
500
750
1000
Rhyncospora
Scleria
Wet meadows 6
Bidens
Polygonum
Beaver ponds 7

FIGURE 1.2

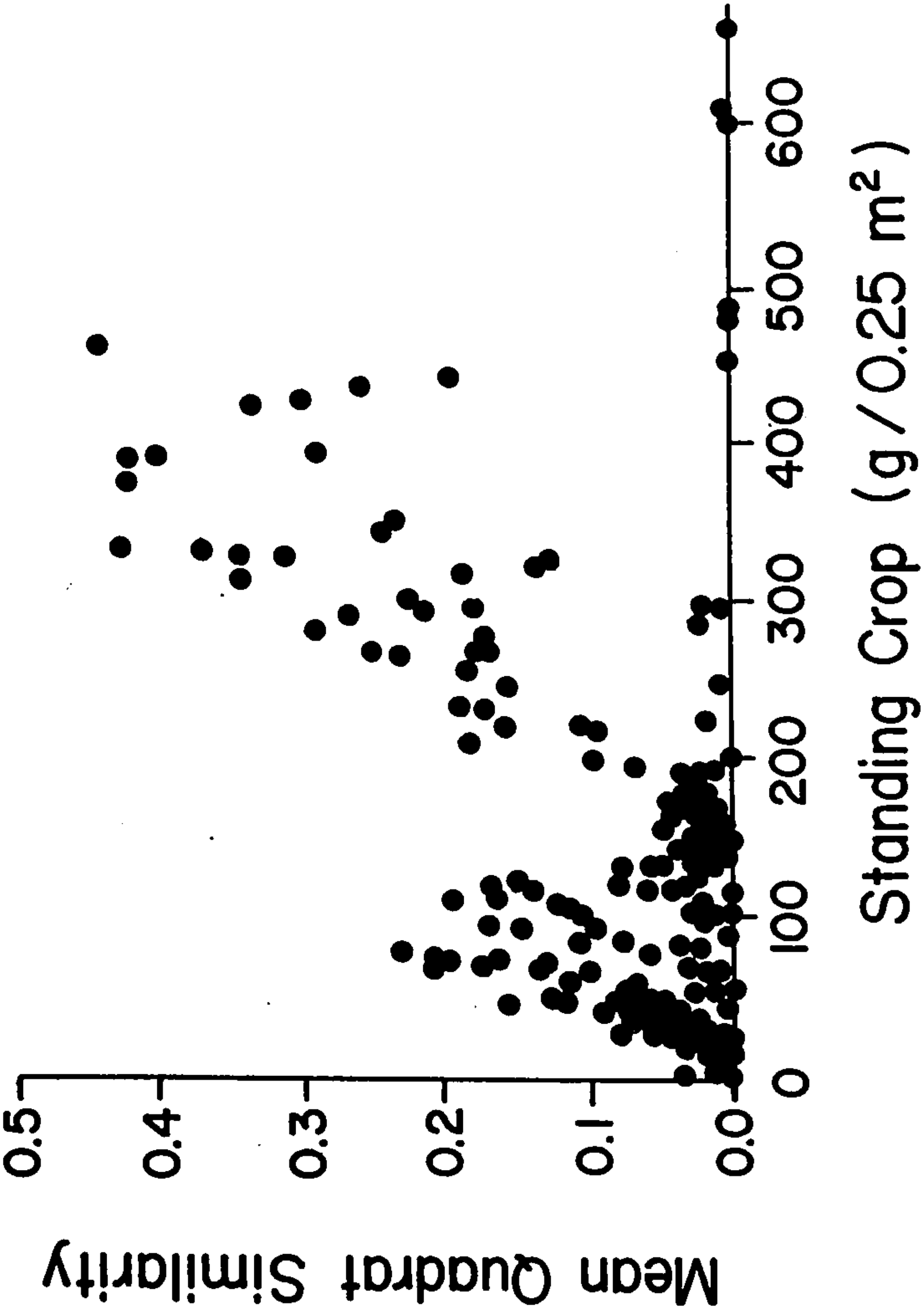
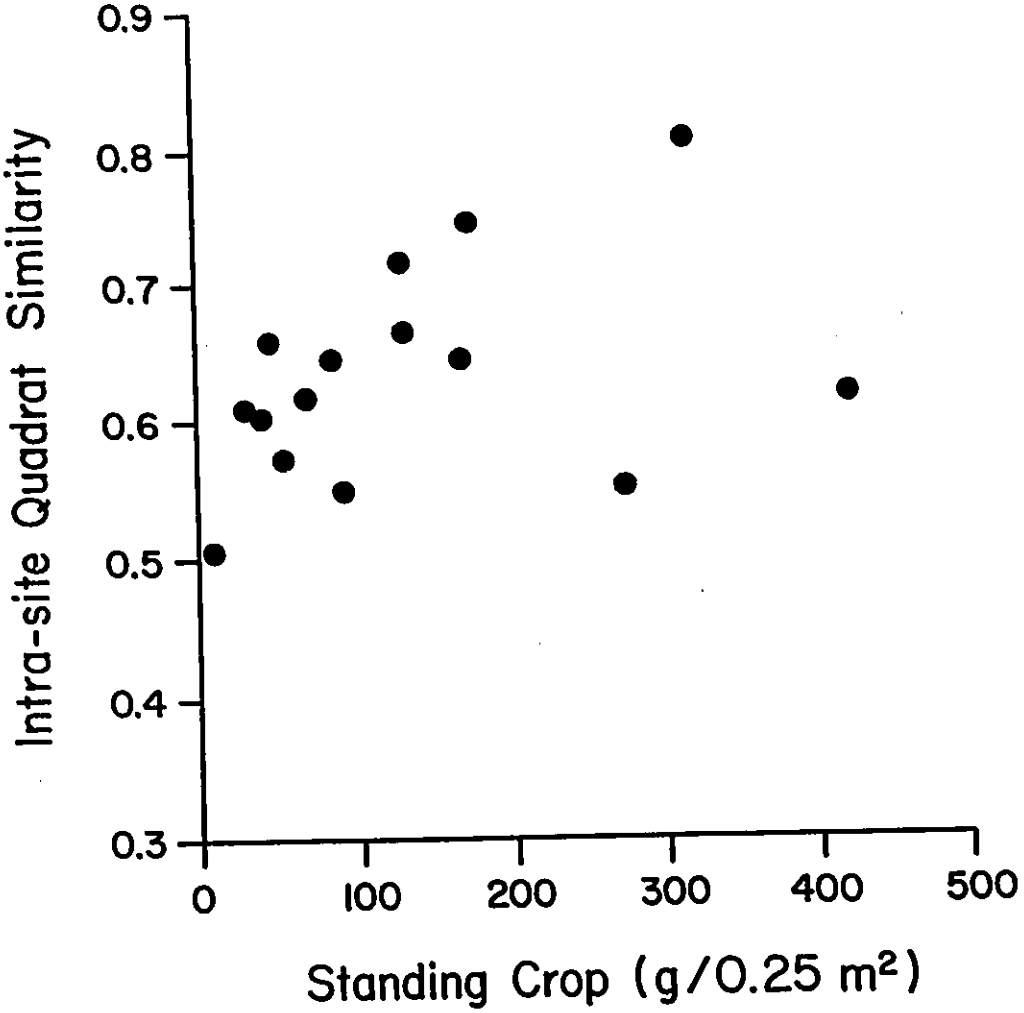

Mean Quadrat Similarity
0.0
0.1
0.2
0.3
0.4
0.5
0
100
200
300
400
500
600
Standing Crop (g / 0.25 m²)

FIGURE 1.3



Intra-site Quadrat Similarity
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0
100
200
300
400
500
Standing Crop (g/0.25 m²)

FIGURE 1.4

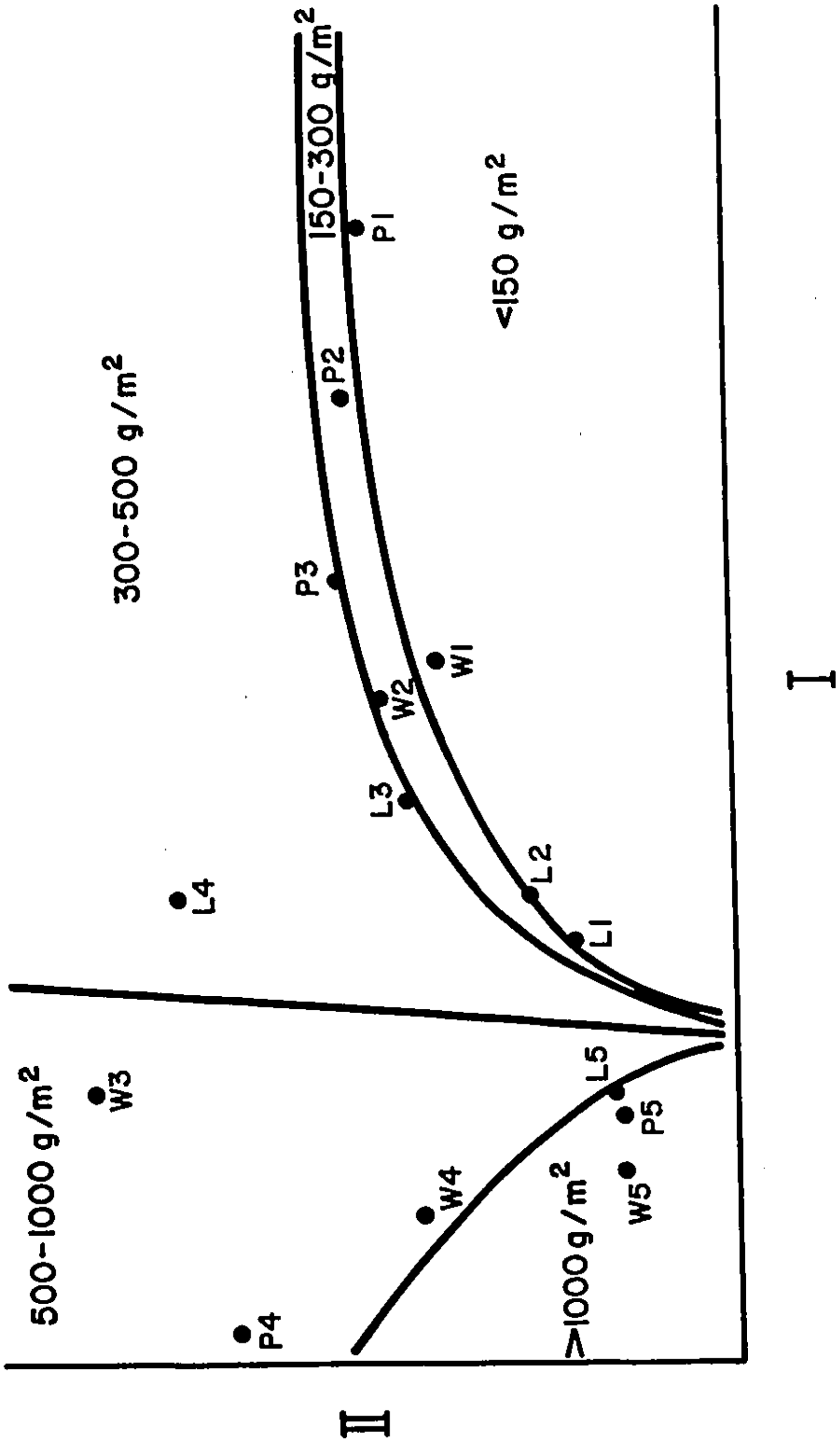
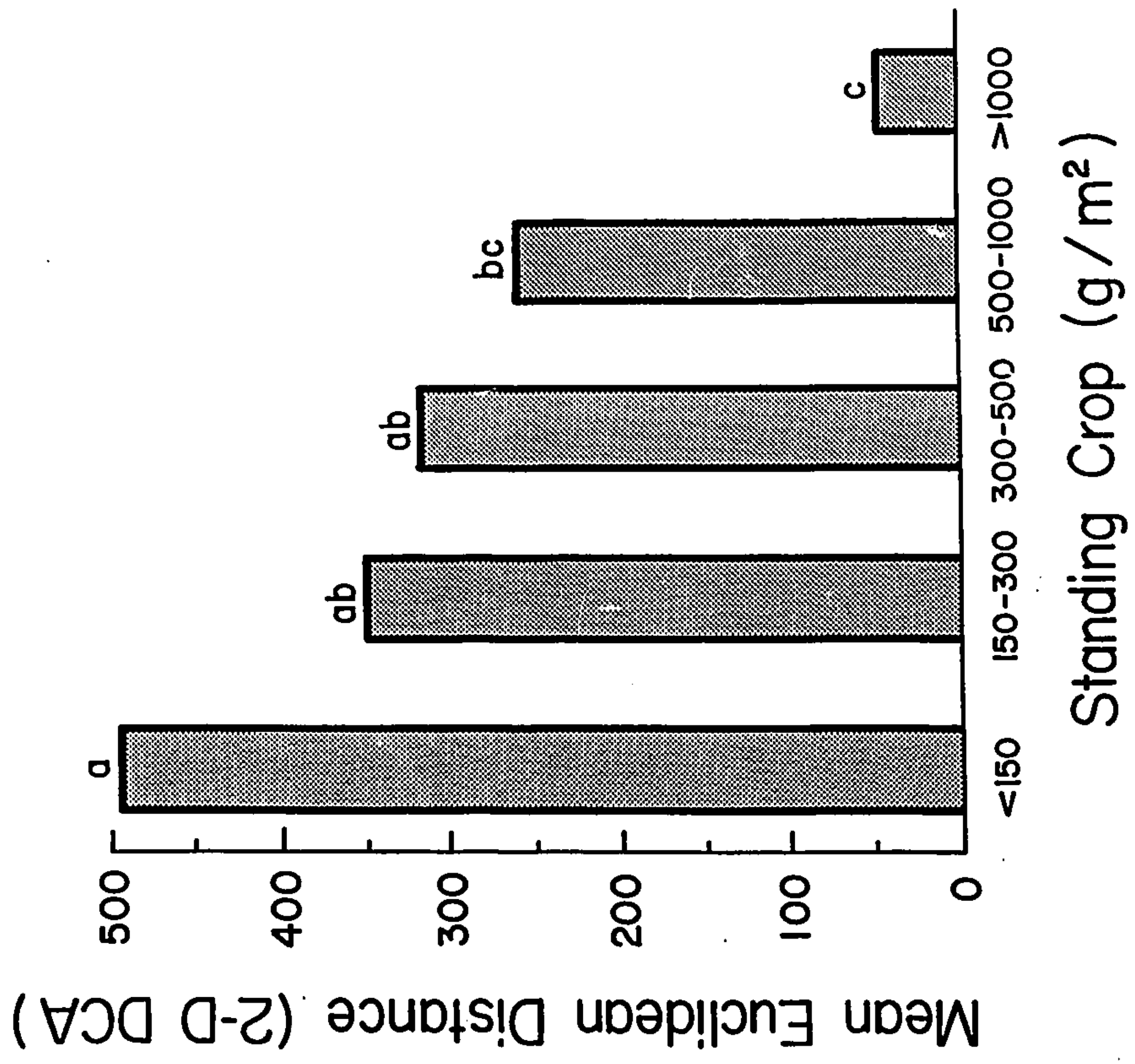

150-300 g/m²
<150 g/m²
300-500 g/m²
500-1000 g/m²
>1000 g/m²
P1
P2
P3
P4
P5
W1
W2
W3
W4
W5
L1
L2
L3
L4
L5
I
II

FIGURE 1.5


Mean Euclidean Distance (2-D DCA)
0
100
200
300
400
500
a
ab
ab
bc
c
<150
150-300
300-500
500-1000
>1000
Standing Crop (g/m²)

CHAPTER 2

THE RELATIONSHIP BETWEEN SPECIES RICHNESS AND STANDING CROP IN WETLANDS: THE IMPORTANCE OF SCALE

"By formalizing scale considerations we can unravel complexity".

Allen (1987)

INTRODUCTION

In this chapter, another diversity measure, species richness, is considered along the same wetland standing crop gradient considered in chapter 1. Specifically, this chapter explores the species richness model proposed by Grime (1973, 1979) which predicts high species richness at moderate standing crop and low species richness at high and low standing crop (more recently, related models have been proposed by Connell (1978), Huston (1979) and Tilman (1982)). Grime's model of species richness is of considerable significance because it can be generalized to many vegetation systems (e.g., Al-Mufti *et al.* 1977; Willems 1980; Wheeler and Giller 1982; Bond 1983; Vermeer and Berendse 1983; Walker and Peet 1983; Day *et al.* 1988; Wisheu and Keddy 1989) and appears to be a general empirical relationship in plant ecology. Therefore, the model needs to be carefully scrutinized to determine the degree of generality that it achieves and to determine the scale in which accurate predictions can be made.

The studies of Grime's model of species richness cited above have each utilized systems with a variety of vegetation types. For instance, Al-Mufti *et al.* (1977) utilized a standing crop gradient that included such different vegetation types as grasslands and the herbaceous plant communities in forest understories. It is unclear whether a demonstrable species richness-standing crop relationship exists at finer levels of organization. In this chapter, Grime's species richness model is considered at two levels of organization: (i) the 'among vegetation types' level which is defined as being relatively heterogeneous (i.e., coarse-grained) with different areas having different dominant species, and (ii) the 'within vegetation type' level which is defined as being a relatively homogeneous area (i.e., fine-grained) with the same dominant species throughout.

These two contrasting levels of organization need to be separated when considering patterns and processes in plant communities. For instance, models concerning zonation (e.g., Pielou and Routledge 1976; Pielou 1979; Keddy 1983; Wilson and Keddy 1985) or competition intensity gradients (e.g., Wilson and Keddy 1986) consider the among vegetation types level of organization while other models concerning population interactions (e.g., Aarssen *et al.* 1979; Grover 1988) consider the within vegetation type level of organization.

The purpose of this chapter was to test whether Grime's model can make effective predictions of species richness along within vegetation type standing crop gradients in wetlands. This test had two steps: (1) constructing a species richness-standing crop curve from a polynomial regression that included data from a wide array of vegetation types, and (2) testing whether the correlation between species richness and standing crop predicted from the among vegetation types data could be detected within each vegetation type.

METHODS

Study Locations

The study locations and the descriptive survey carried out at each location are described in chapter 1. Each site was relatively homogeneous as determined by the most common species present (Table 1.1). Together, the sites comprised a variety of vegetation types as can be seen by comparing the dominant species found at each site (Table 1.1).

Data Analyses

I. Among Vegetation Types

The data from the fifteen sites were combined for a total of 225 quadrats and a second order polynomial regression was performed between species richness (#sp/0.25 m^2) and standing crop (g/0.25 m^2) using the SPSSX statistical package.

II. Within Vegetation Type

Each of the fifteen sites was then analyzed separately to test for a linear relationship between richness and standing crop within each site. Low standing crop sites (<26g/0.25 m^2; as empirically derived from the second order polynomial regression performed on all 225 quadrats) were tested for a significant positive linear regression and high standing crop sites (>26g/0.25 m^2) were tested for a significant negative linear regression. All analyses were performed using the SPSSX statistical package.

RESULTS

I. Among Vegetation Types

Figure 2.1 indicates that species richness was initially low (3 - 13 species) at very low standing crop (<15 g/0.25 m^2), rapidly increased to maximum richness (3 - 24 species) at moderate standing crop (15-125 g/0.25 m^2), after which richness declined gradually to eventually reach a constant low level (2 - 5 species) at very high standing crop (>375 g/0.25 m^2). The second order polynomial regression equation,

$$y = -0.91 + 16.52(\log_{10}(x + 1)) - 5.81(\log_{10}(x + 1)^2)$$

where x is standing crop (g/0.25 m^2) and y is species richness (#sp/0.25 m^2), was found to be highly significant (multiple $r = 0.59$, $r^2 = 0.34$, $p < 0.0001$). Both the first and second order variables contributed significantly to the regression equation ($p < 0.0001$) indicating that there was a significant bitonic relationship between species richness and standing crop when the data from all fifteen sites were included.

II. Within Vegetation Type

Figure 2.2 shows that within each vegetation type, species richness does not appear to have a predictable relationship with standing crop. As shown in Table 2.1, none of the linear regressions for the fifteen sites were significant at $p = 0.05$. (Based on the among vegetation types model, sites with less than 26 g/0.25m^2 were tested for a positive slope and sites with greater than 26 g/0.25m^2 were tested for a negative slope).

III. Alternative Tests Using Equivalent Sample Sizes

One difficulty in interpreting these results is that the sample size ($n = 225$) was much greater in the among vegetation types regression than in the within vegetation type regressions ($n = 15$). Therefore, the significant relationship between species richness and standing crop among vegetation types, but not within, may simply be a consequence of differences in sample sizes.

Two techniques were used to eliminate the effects of sample size (see Heads and Lawton 1983). The first was to equate sample sizes by randomly selecting fifteen samples from the among vegetation types data set. Even with the much reduced sample sizes, ten of fifteen draws gave significant second order polynomial regressions ($p < 0.05$) between species richness and standing crop (Figure 2.3). This is in sharp contrast with the previous section where none of the fifteen within vegetation type regressions were significant even though sample sizes were equivalent to the regressions derived from the random draws.

Another technique of equating sample sizes was to divide the among vegetation types data set into fifteen approximately equal standing crop classes on a logarithmic scale. For each class mean species richness and mean standing crop were calculated. As before, the second order polynomial regression was highly significant (multiple $r = 0.90$; $r^2 = 0.81$; $p < 0.0001$)(Figure 2.4). Together these results are strong evidence that lack of a significant relationship between species richness and standing crop in the fifteen within vegetation type comparisons was not due to reduced sample sizes but was an inherent attribute of the within vegetation type level of organization.

DISCUSSION

When comparing among vegetation types, the data indicate that as standing crop increased, species richness initially increased to reach a maximum at moderate standing crop, after which richness gradually declined (Figure 2.1). This relationship between species richness and standing crop has also been found in many other wetland systems (Wheeler and Giller 1982; Vermeer and Berendse 1983; Day *et al.* 1988; Moore *et al.* 1989; Wisheu and Keddy 1989) and is likely a general trend in herbaceous plant systems (Grime 1973, 1979; Tilman 1982; but see Vermeer and Verhoeven 1987). However, the data presented here demonstrated that patterns found at this level of organization may not be found at another (Figure 2.2). In addition, even at the same level of organization, the two measures of diversity considered in this thesis, number of vegetation types and species richness, exhibited different patterns along the standing crop gradient. The relationship between species richness and standing crop was observed to be bitonic with maximum richness occurring at moderate standing crop, while number of vegetation types was observed to be inversely correlated with standing crop.

The Importance of Scale

It has been shown that Grime's model describes among vegetation types, but not within vegetation type, variation in species richness. This result illustrates Allen and Starr's (1982) point about choosing the appropriate scale for ecological models. It also suggests the potential for sterile debates when one school of thought operates on the among vegetation types scale, while another operates on the within vegetation type scale (Figure 2.5).

The data presented here dealt only with patterns between two variables. It is also probable that processes are fundamentally different at these two scales. Shipley and Keddy (1987) have explored the confusion which can arise by inferring process from pattern. Nonetheless, some comments on process are necessary.

At the among vegetation types level, Grime postulated that stress, disturbance and dominance control species richness. Recent experimental studies of wetland communities have shown that competition intensity does vary predictably among vegetation types with different standing crop (Wilson and Keddy 1986), and that competitive ability is strongly correlated with plant size (Gaudet and Keddy 1988). These processes are likely less important at the within vegetation type level where there is less variation in standing crop and morphology. At the within vegetation type level, variables associated with lower level processes are likely to be more useful. The most promising of these would likely be those variables associated with processes creating patchiness. Examples include temporal variation in perturbation and gap regeneration (Grubb 1977), spatial variability in seed predation (Janzen 1970) and dispersal (Grubb 1977), localized herbivory (Lubchenco 1978), and microsite variation (Harner and Harper 1976).

It is concluded that general models in plant ecology, like other general models, will have scale limitations. Some of the criticisms levelled at general models (e.g., Harper 1982; Grubb 1985) can be viewed as misunderstandings of these inherent constraints of models. Such criticisms could be rephrased to become valuable contributions to general theory if they were presented as attempts to define the scale where a general model does not apply rather than simple rejections of the model entirely. Then a nested hierarchy of models could be constructed, with specific sub-models incorporated within more general models (Keddy 1989). Determining the appropriate scale for different models is a process as important as developing general models for plant ecology.

The results of this chapter suggest the following questions, each of which will be explored in chapters 3 and 4:

(1) The standing crop gradient observed in chapters 1 and 2 is likely the result of an underlying soil fertility gradient (see Table 5.2) or disturbance gradient (see Chapter 4) or a combination of both. Are either of these variables in isolation sufficient to recreate the diversity patterns observed in chapters 1 and 2 at the among vegetation types level of organization?

(2) Can localized disturbance events or microsite differences account for the observed variation in species richness observed at the among vegetation types level of organization?

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Wisheu, I.C. and P.A. Keddy. 1989. The conservation and management of a threatened Coastal Plain plant community in Eastern North America (Nova Scotia, Canada). Biol. Conserv. 48: 229-238.

Table 2.1. The location and mean standing crop (g/0.25 m^2) for each of the fifteen wetland sites sampled in this study. It was predicted that low standing crop sites (<26 g /0.25 m^2) would have a positive species richness-standing crop relationship whereas high standing crop sites (>26g/0.25 m^2) would have a negative relationship. The slope (r) and significance level of r are indicated.

Location	Mean S.C	r	p
Luskville			
Site 1	32.7	-0.16	0.58
Site 2	40.0	-0.34	0.22
Site 3	92.3	-0.30	0.27
Site 4	124.6	-0.06	0.82
Site 5	277.7	-0.11	0.69
Presqu'ile			
Site 1	17.8	-0.18	0.52
Site 2	67.0	-0.18	0.51
Site 3	86.8	-0.06	0.84
Site 4	173.1	0.42	0.12
Site 5	421.6	-0.20	0.47
Westmeath			
Site 1	4.0	0.47	0.08
Site 2	54.5	0.17	0.55
Site 3	163.0	-0.25	0.37
Site 4	131.9	-0.06	0.84
Site 5	315.8	0.23	0.40

FIGURE CAPTIONS

Figure 2.1. Species richness plotted against standing crop in a broad range of wetland vegetation types located in Ontario (Presqu'ile and Westmeath) and Quebec (Luskville)(n = 224 0.25 m^2 quadrats). The second order polynomial regression,

$$y = -0.91 + 16.52(\log_{10}(x + 1)) - 5.81(\log_{10}(x + 1)^2)$$

where x is standing crop (g/0.25 m^2) and y is species richness (#sp/0.25 m^2), was found to be highly significant (multiple $r = 0.59$, $r^2 = 0.34$, $p < 0.0001$).

Figure 2.2. Species richness versus standing crop at the within vegetation type level in each of fifteen sites located in Quebec (circles = Luskville, sites 1-5) and Ontario (squares = Presqu'ile, sites 1-5; triangles = Westmeath, sites 1-5). Linear regressions performed for each site were all found to be non-significant ($p > 0.05$).

Figure 2.3. Species richness plotted against standing crop in each of fifteen random draws (n = 15 quadrats) from the total data set (n = 224). * indicates a significant ($p < 0.05$) second order polynomial regression between species richness and standing crop. N.S. indicates a non-significant polynomial regression.

Figure 2.4. Mean species richness plotted against mean standing crop for fifteen equivalent standing crop classes as calculated on a logarithmic scale. In each class mean species richness and standing crop were calculated and a significant second order polynomial regression was tested for. The polynomial regression,

$$y = -1.10 + 15.54(\log_{10}(x + 1)) - 5.23(\log_{10}(x + 1)^2)$$

where x is mean standing crop (g/0.25 m^2) and y is mean species richness (#sp/0.25 m^2), was found to be highly significant (multiple $r = 0.90$, $r^2 = 0.81$, $p < 0.0001$).

Figure 2.5. Different patterns and processes are found at different levels of organization. For instance, zonation patterns along environmental gradients are concerned with the among vegetation types level of organization while

patterns of recruitment in gaps are concerned with the within vegetation type level of organization. Similarly, important processes vary between the among vegetation types (e.g., competition intensity gradients, stress gradients) and the within vegetation type (e.g., recruitment, competitive hierarchies) levels of organization.

FIGURE 2.1

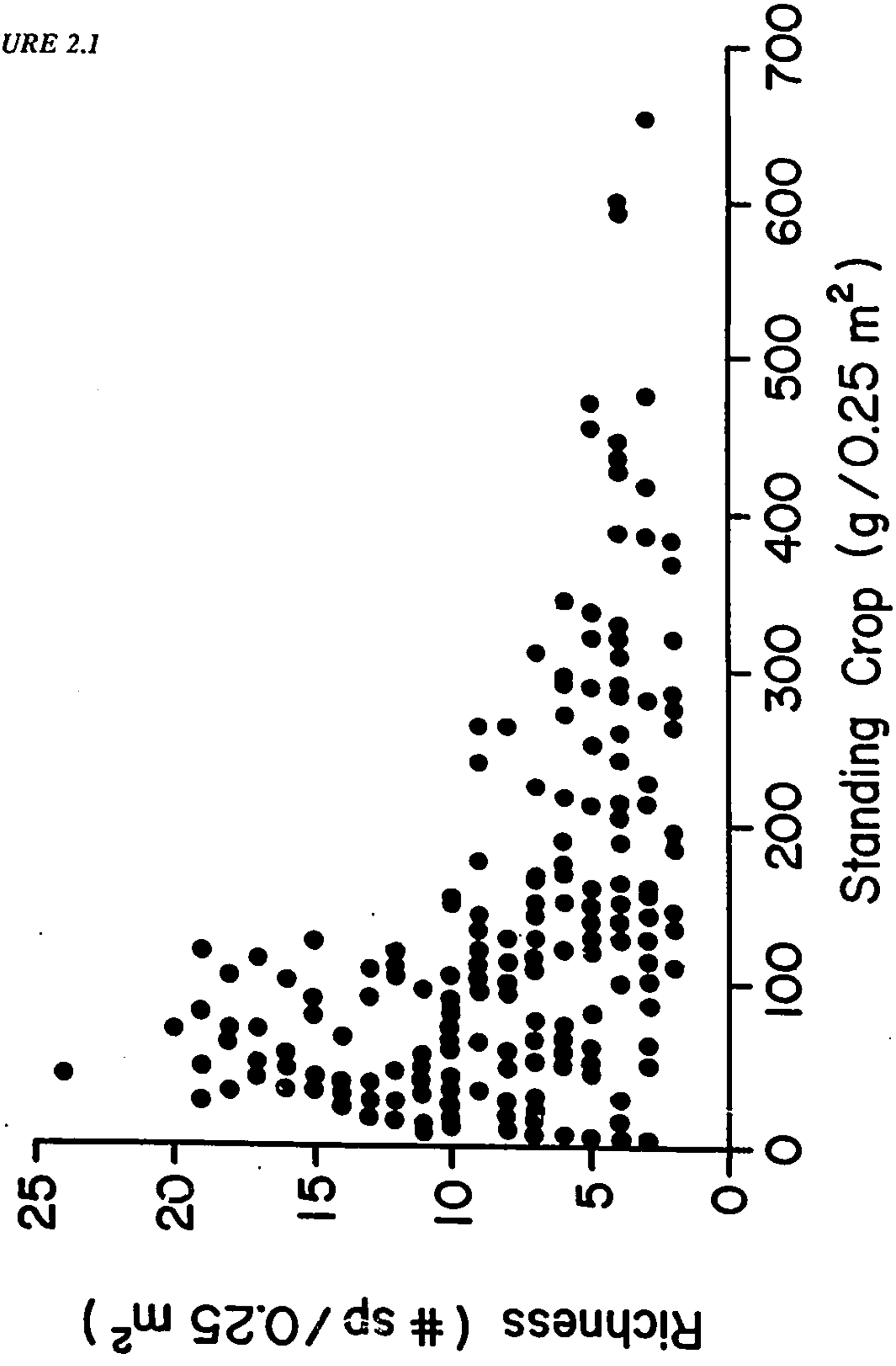
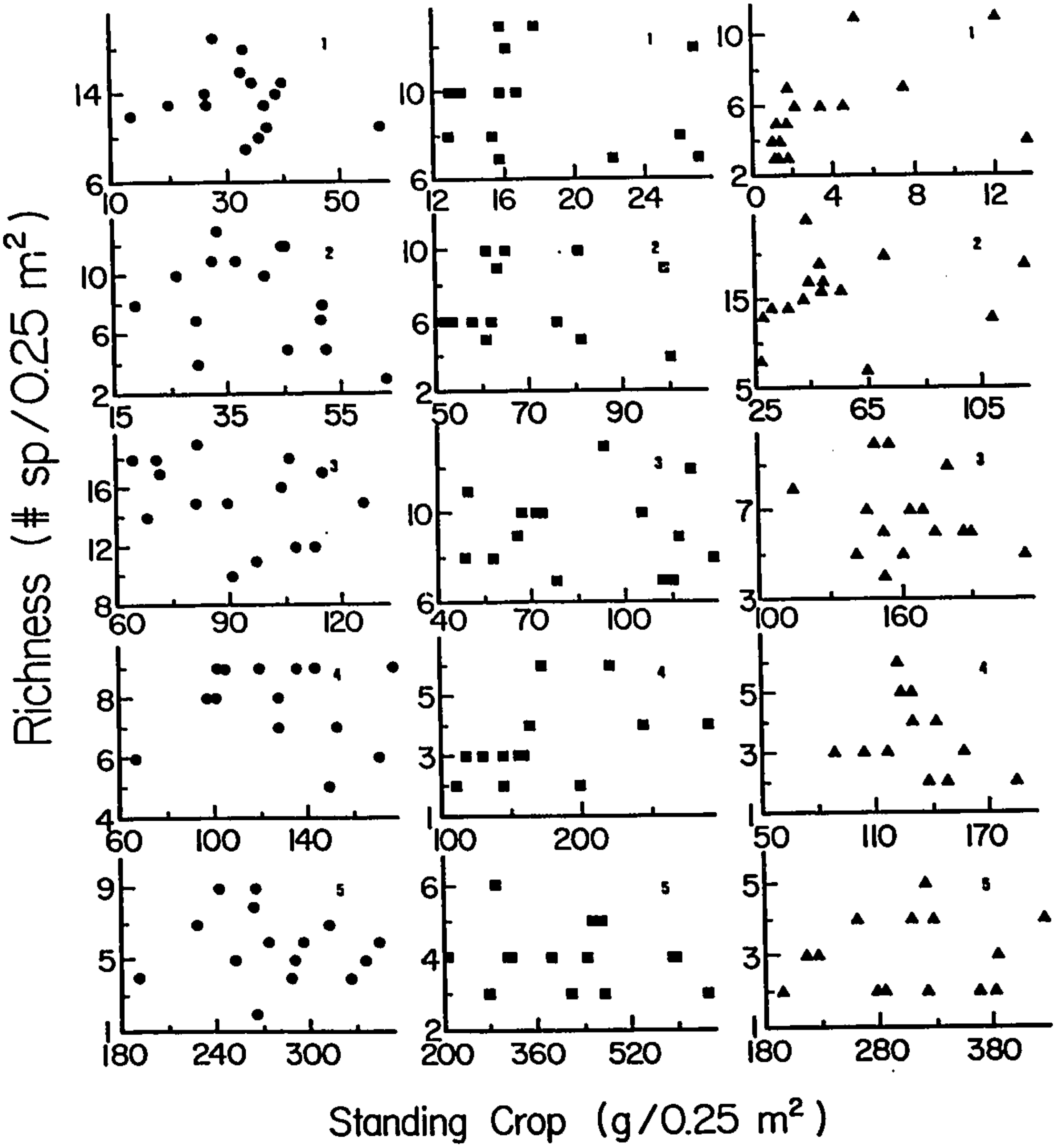

Richness (# sp/0.25 m^2)
0
5
10
15
20
25
Standing Crop (g/0.25 m^2)
0
100
200
300
400
500
600
700

FIGURE 2.2



Richness (# sp/0.25 m²)
Standing Crop (g/0.25 m²)
1
1
1
2
2
2
3
3
3
4
4
4
5
5
5
6
14
10
30
50
6
10
12
16
20
24
2
6
10
0
4
8
12
2
6
10
15
35
55
2
6
10
50
70
90
5
15
25
65
105
8
12
16
60
90
120
6
10
40
70
100
3
7
100
160
4
6
8
60
100
140
1
3
5
100
200
1
3
5
50
110
170
1
5
9
180
240
300
2
4
6
200
360
520
1
3
5
180
280
380

FIGURE 2.3

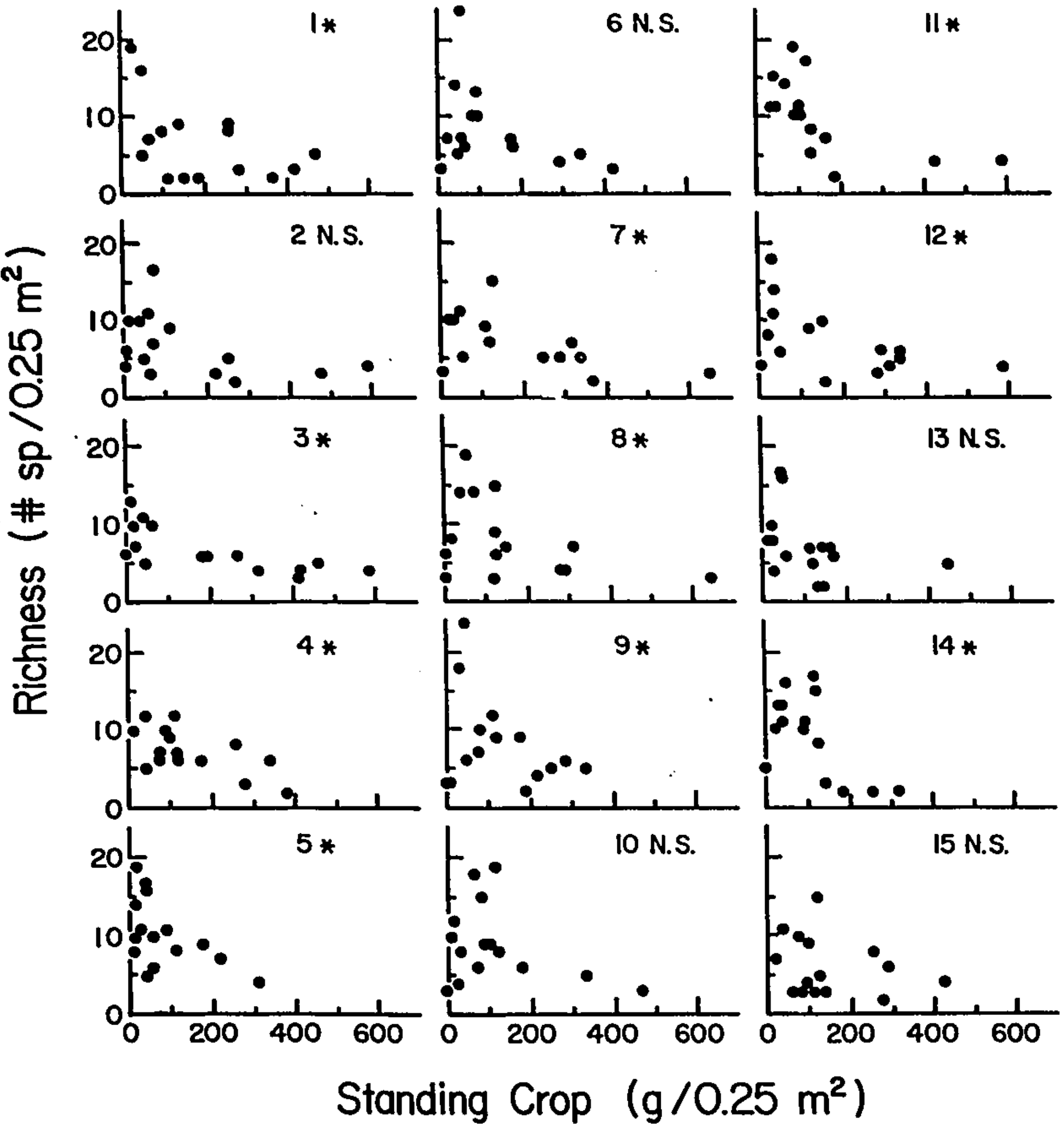

1*
6 N.S.
11*
2 N.S.
7*
12*
3*
8*
13 N.S.
4*
9*
14*
5*
10 N.S.
15 N.S.
0
10
20
0
200
400
600
Richness (# sp/0.25 m²)
Standing Crop (g/0.25 m²)

FIGURE 2.4

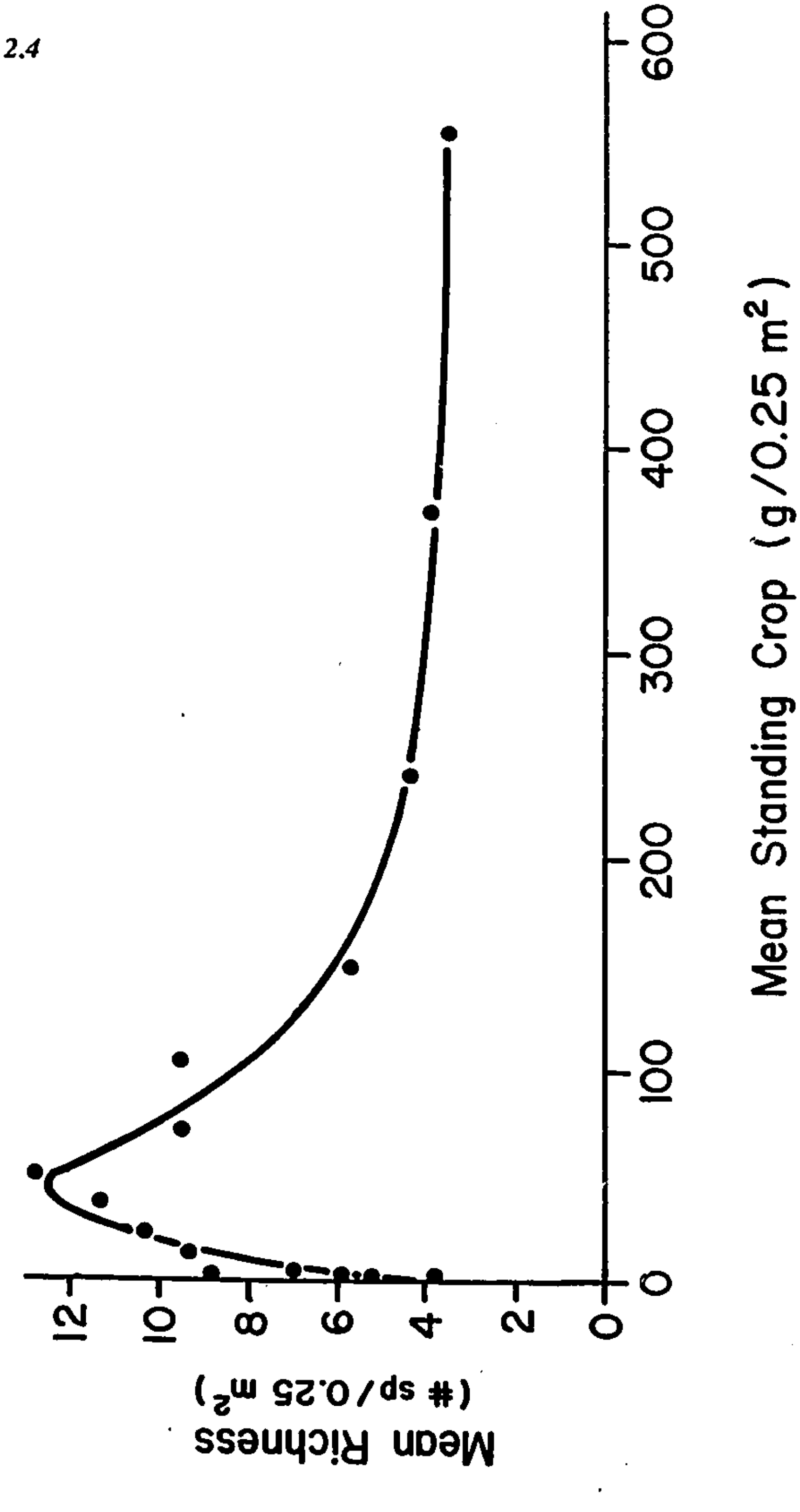
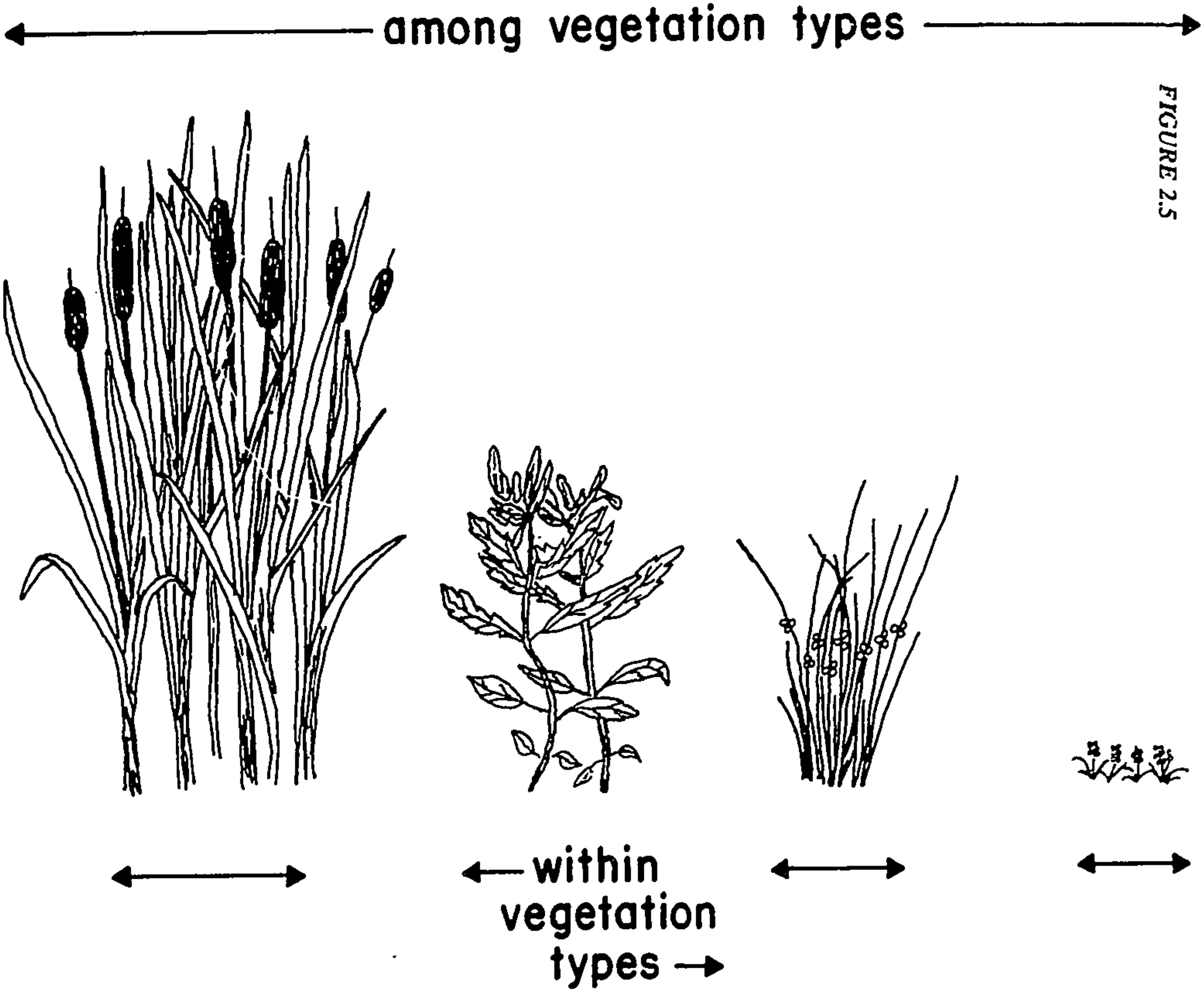

Mean Richness
(# sp/0.25 m²)
0
2
4
6
8
10
12
0
100
200
300
400
500
600
Mean Standing Crop (g/0.25 m²)

FIGURE 2.5



CHAPTER 3

ASSEMBLY FORCES: THEIR IMPORTANCE IN THE ESTABLISHMENT AND MAINTENANCE OF WETLAND VEGETATION STATES

"The most incomprehensible fact about Nature is that it is comprehensible."

Albert Einstein

INTRODUCTION

Ecological communities are constantly subjected to a variety of forces, both natural and man-made, that influence the structure and dynamics of the system. One major objective of community ecology is to determine which forces maintain communities in a given state and which forces drive communities to alternative states (Paine 1969; Sutherland 1974; Peterman 1980; Holling 1977, 1986). In several systems, these forces are known and their importance in maintaining or establishing specific community states are understood. For example, in Minnesota old fields, rates of supply of the limiting nutrient, nitrogen, and the past history of the vegetation are two major forces determining the observed community states (Tilman 1987; Inouye and Tilman 1988). In the fouling communities at Beaufort, North Carolina, the order of larval recruitment and the presence or absence of important consumers determined the states observed (Sutherland 1974). However, in most systems it is difficult to establish cause and effect relationships between potential forces and observed community states because the actions and interactions of these forces are complex.

Assembly forces can be defined as including any force, biotic (e.g., coral reef predators, invasive exotics) or abiotic (e.g., nitrogen supply rates, fire), upon which the establishment and maintainance of community states depends. All environmental variables may ultimately be important in maintaining community states; however, only assembly variables are those which can account for a significant portion of the variance between different community states. In this chapter, I explore a variety of forces which could potentially establish, maintain or alter states in wetland herbaceous communities.

In wetlands, numerous potential assembly forces exist. These include fertility (Morgan and Phillip 1986; Vermeer and Verhoeven 1987; Day *et al* 1988), exposure to waves (Keddy 1985), fluctuating water levels (Keddy and Reznicek 1986), hurricanes (Vogl 1980), litter accumulation (van der Valk 1986), invasion by exotic species (Moore and Keddy 1989) and many others (see Spence 1967; Hutchinson 1975). However, very few of these forces have been experimentally manipulated and thus their potential to establish and maintain community states is unknown. In this study, artificial wetland microcosms were created with an initially identical species mixture to explore how potential assembly forces the establishment and maintenance of different wetland community states. These included: vegetation history, length of growing season, substrate texture, litter accumulation, water depth and fluctuating water levels.

Chapter 1 indicated that in herbaceous wetlands in eastern Canada, there was an inverse relationship between the number of wetland vegetation types and standing crop. This observation suggested that increased soil fertility in high standing crop sites may have the potential to reduce the effects that assembly forces would otherwise have on the range of vegetation types observed. That is, given the same range of variability in habitat conditions, fewer vegetation types will be observed at high fertility and standing crop. Chapter 2 found that another measure of diversity, species richness, was also reduced at high fertility and standing crop when a range of vegetation types were considered. To test whether soil fertility was the underlying cause of the diversity patterns observed in chapters 1 and 2, each of the wetland treatments in the microcosm experiment was duplicated at high and low fertility.

METHODS

General

This study used a replicated microcosm approach, which permitted the manipulation of specific variables. Each microcosm consisted of a high-density polyethylene container (internal dimensions: 630 x 420 x 260 mm) filled to a height of 130 mm with sterilized 002 grade washed concrete sand. All microcosms were connected to a central water source via vinyl plastic tubing and were watered twice daily during the growing season with City of Ottawa treated water. Water inlet valves of diameter 6 mm were located at a height of 220 mm in each microcosm. Controlled water depths were maintained by means of a 6 mm outlet valve located at the designated depth opposite the inlet valve. The microcosm study was conducted at an outdoor compound located at Carleton University, Ottawa, Canada (45°25'N, 75°45'W). This compound was relatively flat, received full sun exposure and was regularly mown to minimize weed species dispersal near the experiment. Black plastic sheeting was also placed between microcosms and around the immediate perimeter of the experiment and covered with sand to further reduce weed species dispersal into the microcosms.

Experimental Design

The microcosm study was designed to explore two or three levels for each of the six potential assembly forces under investigation (e.g., no litter, light litter, heavy litter). The "control" treatment was the same for each of the forces under investigation (i.e., constant water depth of 0 cm with no alterations to the substrate surface). Altogether, the microcosm study included twelve artificial wetland habitats, each of which was duplicated at two fertility levels ('infertile' and 'fertile'). At the end of the two year experiment, standing crop in the infertile treatments was similar to that observed for the "moderate" standing crop sites described in chapters 1 and 2. Conversely, the fertile treatments produced standing crop levels which were equivalent to the "high" and "very high" sites described in chapters 1 and 2. In each of five blocks, the 24 treatments were completely randomized. The habitats were created by manipulating a single specified variable as described below:

A. Water Depth

Constant water depths of -5 cm (submersed), 0 cm (at substrate surface), and +5 cm (emersed) were used to create three wetland habitat treatments.

B. Fluctuating Water Depths

Two habitat treatments were created by manipulating water depths throughout the growing season. In the first treatment, water depth was high at the beginning of the growing season (-5 cm) and was lowered to 0 cm in mid-July. The second habitat treatment was similarly treated except that the water depth was further lowered to +10 cm in late August.

C. Texture

Two habitat treatments were created by placing stones of different sizes on the substrate surface. The water depth was maintained at a constant 0 cm in both habitats. In the first treatment, rounded cobblestones 2.5 to 7.5 cm in diameter were placed as close together as possible in a single layer on the soil surface. In the second treatment, small pebbles 0.5 to 1.25 cm in diameter were scattered on the soil surface to a depth of 1.25 cm.

D. Litter

Two habitat treatments were created by scattering differing amounts of litter on the substrate surface in treatments which were maintained at a constant water depth of 0 cm. The litter was collected from a riverine shoreline in late May, 1987 and was composed primarily of *Scirpus fluviatilis* with minor amounts of *S. americanus*, *Eleocharis smallii*, and *Typha angustifolia*. In the first habitat treatment, 50 g of litter (167 g/m^2) was spread evenly across the soil surface to form a litter layer 0.5 cm deep. In the second habitat treatment, 150 g of litter (500 g/m^2) was spread on the surface to form a litter layer 1.5 cm deep.

E. Length of Growing Season

Two habitat treatments which had a constant water depth of 0 cm were sown at later dates to simulate reduced growing seasons. The first was sown 14 days later than all other treatments, while the second was sown 28 days later.

F. Invasion by a Clonal Perennial

In one habitat treatment, four *Typha angustifolia* shoots were added at the beginning of the second growing season to determine the effects of invasion by a large, clonal perennial on the observed wetland community states and species richness. This treatment was maintained at 0 cm water depth before and after the addition of *T. angustifolia*.

The experiment was constructed from 27 May, 1987 to 4 June, 1987 and was allowed to equilibrate for one week prior to the sowing of seed mixtures.

Seed Mixtures

Seeds of twenty wetland species of varying morphology and life-history were collected in the fall of 1986 and placed in dark storage at 4°C in sand which was 75% saturated (Table 3.1). Subsequent germination trials conducted for 14 days in April, 1987 in a growth chamber (25°C/15°C during a 12 hour light/12 hour dark regime) revealed that the species selected were at least 20% viable.

A total of 120 equivalent seed mixtures were made up during the period 20 May to 4 June, 1987. To prepare the mixtures, seeds of each species were removed from storage, counted into equal lots, mixed with previously counted seeds and placed back in cold, dark storage in sand prior to sowing. Between 11 June and 13 June, 1987, the seed mixtures were evenly scattered over the soil surface of each treatment. In the two litter treatments, the litter was added immediately after sowing; all other treatment conditions were established prior to sowing. Seeds of several species were observed to float for up to seven days after sowing in the flooded treatments.

Fertilization

On 22 June, 1987 all 'fertile' treatments were fertilized with a complete hydroponic mixture (7-11-27 and 15-0-0)(Table 3.2) at a rate of 37.4 g for each fertilizer per microcosm (124.5 g/m^2). The fertilizer additions were then repeated every 21 days at a reduced rate of 9.3 g per microcosm (31.0 g/m^2) until the end of the growing season (26 August, 1987). The rate of fertilization used for the 'fertile' treatments had been shown to be an optimal rate for maximum biomass accumulation in a calibration experiment conducted using *Lythrum salicaria* as a phytometer. This fertilization regime was repeated for the 1988 growing season.

The 'infertile' treatments did not receive any fertilizer additions until 10 August, 1987 at which time 0.58 g per microcosm was added for each fertilizer (1.9 g/m^2). The fertilizer additions were repeated in 1987 on 24 August and in 1988 on 23 June, 20 July, 11 August and 15 September. The rate of fertilization used for the 'infertile' treatments was previously found to stimulate low to moderate growth of *Lythrum salicaria* in a calibration experiment (as compared to a no fertilizer treatment).

Overwintering

On 4 October, 1987 plants in each microcosm were tied together in the centre to minimize seed dispersal outside the container. Flowering stalks were also shaken periodically to disperse seeds within the microcosm. All containers were then flooded to a depth of -10 cm between 19-25 November in order to simulate natural wetland conditions and to form a protective ice cover during the winter. From 1-5 December, straw was packed around each microcosm to prevent freezing from the sides. All treatments were restored to growing season conditions on 18 May, 1988.

Surveys

All microcosms were surveyed between 5-13 August, 1987 and between 22-30 August, 1988 using a non-destructive point sampling technique. In each microcosm, a 50 cm x 25 cm quadrat was placed above the centre of the container. The quadrat had intersecting steel wires at each 5 cm interval for a total of 50 sampling points. Sampling was conducted by dropping a 2 mm thick steel rod from each wire intersection to ground level and counting the number of contacts each species made with the rod. Relative above-ground abundance for each species was then estimated by summing the total number of contacts for each container.

Data Analyses

The sampling data were summarized in the form of a 20 x 240 table (species x microcosms in 1987 and 1988). The data were then ordinated using detrended correspondence analysis (DCA; Hill and Gauch 1980). For each treatment, 95% confidence limits were calculated using the results from the first two DCA axes (n = 5 replicates)(1988 data only). The variables having a significant effect on wetland species composition were determininted by comparing the 95% confidence limit envelope for each treatment to the 95% confidence limit envelope from the 0 cm constant water depth treatment. The comparisons were conducted separately for each fertility level. The same procedure was used to determine whether fertility significantly affected species composition in each of the 12 habitat treatments. The analytical technique is an extension of the multivariate approach with the added advantage that hypotheses concerning possible treatment effects can be tested with a geometric statistical analysis.

To test whether more wetland vegetation types existed at low fertility, each microcosm was classified by two-way indicator species analysis (TWINSPAN). The analysis was repeated separately for 1987 and 1988. The DCA and TWINSPAN analyses were conducted using the ECOSURVEY program package (Carleton 1985).

A two-factor ANOVA was used to test the effects of fertility and habitat treatment on species richness. Scheffe's procedure for multiple contrasts was used to determine for which treatments and fertility levels, significant effects were being exerted. These analyses were performed with the STATGRAPHICS version 3.0 software package.

RESULTS

Assembly Forces

The comparison of treatment 95% confidence limit envelopes on the data produced by the first two DCA axes indicated that a constant water depth treatment of -5 cm, both fluctuating water level treatments, and the heaviest litter treatment (500 g/m^2) each had significant ($p < 0.05$) effects on species composition with each fertility level, when compared to the 0 cm constant water depth treatment (Figure 3.1; Table 3.3). In addition, the infertile surface texture treatment with cobblestones had a significantly different species composition from the infertile 0 cm constant water depth treatment. The first two axes of the DCA accounted for 78% of the variation in the data set indicating that an examination of the remaining axes of variation was unnecessary to compare treatments.

Fertility

A. Total Abundance

After two growing seasons, the total abundance of plants was 4 to 18 times higher in the fertile treatments than in the corresponding infertile treatments (Figure 3.2). The two litter treatments followed by the two surface texture treatments (cobblestones and pebbles) had the highest total abundance in the infertile treatments, possibly indicating that these treatments were providing additional nutrients. The two treatments which had a shorter growing season in 1987 had reduced total abundance at both fertility levels after the first growing season. However, by the end of the second growing season these two treatments, when compared to the 0 cm constant water depth treatment, had similar total abundance levels.

B. Species Richness

In each of the twelve habitat treatments, species richness was higher in the infertile treatments than was found in the corresponding fertile treatments after two growing seasons (Figure 3.3). The differences in richness between fertile and infertile treatments was significant ($p < 0.05$) for all habitat treatments except the constant water depth of -5 cm treatment, the two fluctuating water level treatments, and the treatment which had a reduced growing season (28 days). In addition, the constantly flooded water depth (-5 cm) treatment and the two fluctuating water level treatments had significantly reduced species richness when compared to the 0 cm constant water depth treatment. The constant water depth of +5 cm treatment had significantly higher species richness when compared to the 0 cm constant water depth treatment (Figure 3.3)

C. Species Composition

The comparison of 95% confidence limit envelopes for each habitat treatment using the data produced by the first two DCA axes indicated few significant differences in species composition between high and low fertility levels (Figure 3.1; Table 3.4). The only two treatments with species composition differences between fertility levels were the 0 cm and +5 cm constant water depth treatments. The DCA, from which the above analyses were conducted, downweighted the contribution of rare species in the analysis in order to specifically emphasize differences due to numerically dominant species. Therefore, there were few major differences in the numerically dominant species between fertility levels for each habitat treatment. However, as indicated in figure 3.3, species richness was generally higher in low fertility treatments, thus indicating that rare species were more frequent at this fertility level. These rare species were generally small in stature (e.g., *Gnaphalium uliginosum*, *Hypericum majus*, *Penthorum sedoides*).

To test whether fertile conditions reduced the number of wetland vegetation types observed across the 12 habitat treatments, a TWINSPAN classification was conducted using all 120 microcosms. It was found that the number of TWINSPAN groups detected in the analysis was slightly higher in infertile treatments after two growing seasons (Figure 3.4). However, this difference was more pronounced after the first growing season. Therefore, given sufficient time, there is no evidence to suggest that the number of vegetation types observed for all 12 habitat treatments will be higher under infertile conditions.

DISCUSSION

Assembly Forces

This study demonstrated that water depth, fluctuating water levels, litter, and surface texture are all capable of influencing species composition in artificially created herbaceous wetlands. However, the use of detrended correspondence analysis to recover underlying community patterns has been the subject of recent criticism (e.g., Kenkel and Orloci 1986; Minchin 1987). The criticisms were directed at the general lack of robustness and erratic performance of detrended correspondence analysis in data sets with high species turnover, irregular sampling of gradients, and bimodal or multimodal species response curves. However, in this study species turnover was relatively low with all microcosms having at least one species in common, gradient sampling was regular (e.g., water depth = -5 cm, 0 cm, +5 cm; litter = none, low, high), and species were observed to have unimodal distributions along the artificially created gradients. Kenkel and Orloci (1986) and Minchin (1987) indicated that in these cases, detrended correspondence analysis gives a consistently superior performance to other ordination methods such as correspondence analysis, principal coordinates analysis and gaussian ordination.

In the surface level (0 cm) constant water depth treatment, the most abundant species were leafy perennials, particularly *Lythrum salicaria* and *Bidens cernua* (Figure 3.5). However, when a 1.5 cm thick litter layer was added to this treatment (heavy litter treatment), emergence of *L. salicaria* was inhibited. Other species such as *Carex crinita*, a narrow leaved, tussock species, *Scirpus acutus*, a leafless perennial, and *Epilobium ciliatum*, an erect dicot species increased in abundance as a result (Figure 3.5). This shift in species composition may be due to the fact that *L. salicaria* has an absolute light requirement for germination (Shamsi 1974). Further, the morphology of species such as *C. crinita* and *S. acutus* may provide a more effective means of penetrating the leaf litter than is the case with *L. salicaria*. This situation is analogous to the effects of tree leaf litter on herbaceous vegetation in deciduous woodlands studied by Sydes and Grime (1981). In this study, it was found that tree litter had the least inhibitory effect on species with the most effective means of penetrating the leaf litter.

In the treatments that were flooded for all (constant water depth of -5 cm) or part (-5 cm to 0 cm, -5 cm to +10 cm) of the growing season, a leafy annual species, *Bidens cernua*, was the dominant species (Figure 3.5). *B. cernua* was the only species which could both germinate (underwater or floating) and emerge above the water surface before the seed reserves were exhausted. *B. cernua* is commonly found in a wide variety of wetland habitats, including beaver ponds that are flooded throughout the growing season (Keddy, pers. obs.). In the treatments that were flooded for part of the growing season, another leafless perennial, *Eleocharis smallii*, germinated underwater but did not grow until the water levels were dropped to the soil surface level (0 cm). *E. smallii* is commonly found on seasonally flooded riverine shorelines (Day *et al.* 1988).

In this experiment, several potential assembly forces such as a shorter growing season or invasion by a clonal perennial did not have any effect on wetland species composition. However, the shorter growing season treatment could only be maintained during the first growing season. Had this treatment been maintained over several growing seasons, effects on species composition might have been more likely. Similarly, invasion by a clonal perennial (*Typha angustifolia*) had little effect on species composition because the shoots of *T. angustifolia* did not become established. Other treatments including litter loading to a depth of 0.5 cm, a constant water depth of +5 cm, and a pebble surface layer also had no effect on species composition. In these cases, the treatments may not have been severe enough to affect species composition. For example, when the thickness of the litter layer was increased to 1.5 cm, species composition was significantly altered.

Species Richness

In most of the twelve habitat treatments, species richness was significantly lower in the fertile treatments than was found in the corresponding infertile treatments (Figure 3.3). This result suggests that large differences in fertility may reproduce the among vegetation types pattern of species richness along the standing crop gradient (see chapter 2), even when a wide range of habitat treatments are considered. The likely mechanism for this result was that species of small stature and cover were competitively eliminated by large, rapidly growing species such as *Lythrum salicaria* under high fertility conditions (Gaudet and Keddy 1988).

Figure 3.3 also indicates that relatively small differences in water depth or the presence of a fluctuating water level regime can have significant effects on species richness, independent of microcosm fertility level. This result suggests that microsite differences may account for the observed variation in species richness within vegetation types (see chapter 2).

Number of Vegetation Types

This experiment found little evidence to suggest that wetland species composition differed between fertility levels of the same habitat treatment, except that small, rare species were not found at high fertility. Field observations, however, have indicated little similarity in species composition between fertile and infertile wetland sites (see chapter 1). This discrepancy may be the result of natural fertile and infertile wetland sites having other habitat differences, which was not the case in the microcosm experiment. However, nutrient additions in previously infertile wetlands not only reduced species richness, but also led to major changes in the species that dominated the wetlands (Willis 1963; Morgan and Phillip 1986). For example, Willis (1963) found that when nutrients were added to several dune pasture plots, species composition changed from a mixture of small cryptogams to a thick, tall growth of *Festuca rubra*. The control plots experienced no such changes in species composition. Alternatively, species composition similarity between corresponding high and low fertility treatments may have been the result of the initial limited species pool or because the immigration of other wetland species was prevented during the course of the experiment.

In wetlands, it has been observed that there was an inverse relationship between number of vegetation types and standing crop and fertility (see chapter 1). Fertile, undisturbed sites were usually dominated by large, clonal species such as *Typha spp.* or *Phragmites communis* which formed dense, nearly monospecific stands. Conversely, in infertile or disturbed sites, a vast array of life forms and morphologies were found including annuals, isoetids and carnivorous plants.

The microcosm experiment results indicated that an inverse relationship between number of vegetation types and fertility was apparent after one growing season as predicted (Figure 3.4). However, this relationship had all but disappeared by the end of the second growing season. In essence, fertility did not dampen the effects of the assembly forces, and thus more vegetation types occurred at high fertility than would have been predicted by the centrifugal organization model. Several possibilities could account for this anomaly:

(1) In nature, there are fewer unique habitats at high fertility and the number of observed vegetation types simply corresponds to the number of available habitats. This possibility would indicate that competitive exclusion is not the mechanism controlling the centrifugal organization of wetland vegetation types as suggested by Keddy (1989). In this scenario, the results of the microcosm experiment were as expected. However, Moore *et al.* (1989) observed *Typha* stands in such contrasting high fertility habitats as riverine bays, sandy lakeshores, and interdunal swales. The corresponding infertile habitats at each of these sites had unique vegetation types associated with each.

(2) There may have been insufficient time for competitively superior species to have eliminated inferior species and thus reduce the number of vegetation types at high fertility. However, Figure 3.4 indicates that the trend is towards an equivalent number of vegetation types at both fertility levels, not the opposite. Nevertheless, the possibility exists that founder effects, which are simply a function of initial habitat conditions, are still the primary mechanism controlling species composition in fertile and infertile sites after two growing seasons (see Noble and Slatyer 1980; Grace 1987). If the centrifugal organization model is correct, the expectation is that fertile treatments will begin to converge in composition as competitive exclusion eliminates and replaces

inferior species. Since competitive exclusion is likely to be more rapid at high fertility (Wilson and Keddy 1986), convergence will proceed more quickly at this fertility level. This scenario is similar to one found by Christensen and Peet (1985) for forests during secondary succession. In their study, it was found that chance variables, such as site history and seed rain, played important but transient roles in determining composition of young tree stands. These chance variables had little effect on species composition in older stands.

(3) Another variable, not included in the microcosm experiment, is required in the centrifugal organization model to explain, in nature, the observed inverse relationship between number of vegetation types and fertility. A likely candidate is disturbance. In the microcosm experiment, none of the habitat treatments were disturbed. However, in nature disturbance is an important phenomenon affecting community structure in wetlands (e.g., drawdowns, Meeks 1969; fluctuating water levels, Keddy and Reznicek 1986; grazing, Walker and Wehrhahn 1971; invasion by an exotic species, Moore and Keddy 1989). If species composition in infertile sites is more sensitive to the effects of disturbance, then over time there is likely to be a greater divergence in composition of infertile sites than would occur in the fertile sites. Thorhaug (1980) has shown that plant communities under stress (e.g., infertility) have a very slow recovery period after perturbation, while fertile communities (e.g., a marsh) often have high recovery rates.

This chapter has demonstrated that the manipulation of single variables, or assembly forces, can have significant effects on species composition of wetland communities. Further, this chapter has shown that increasing fertility differences may account for the observed variation in species richness at the among vegetation types level of organization, while microsite differences may account for the observed variation in species richness at the within vegetation types level of organization. Finally, this chapter has shown that fertility did not reduce or dampen the effects of the assembly forces on wetland species composition as was predicted from the field observations discussed in chapter 1. Whether this result was due to the absence of a perturbation regime in the microcosm experiment was tested by imposing various disturbances on riverine shoreline plant communities of differing fertility and standing crop. The results of this experiment will be discussed in chapter 4.

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Table 3.1. The species used in the microcosm experiment and their associated morphologies and life-histories.

Species Name	Characteristics	Life-History
Acorus calamus	Monocot with vertical leaf blades	Perennial
Aster nemoralis	Erect dicot	Perennial
Bidens cernua	Erect dicot of variable size	Annual
Carex crinita	Tussock, monocot	Perennial
Eleocharis smallii	Large monocot reed	Perennial
Epilobium ciliatum	Erect dicot	Perennial
Eupatorium perfoliatum	Tall, erect dicot	Perennial
Glyceria canadensis	Erect grass	Perennial
Gnaphalium uliginosum	Small, creeping dicot	Annual
Hypericum majus	Small, creeping dicot	Perennial
Juncus filiformis	Small, leafless monocot	Perennial
Lythrum salicaria	Tall, erect dicot	Perennial
Myrica gale	Shrub	Perennial
Panicum longifolium	Small, rosette grass	Perennial
Penthorum sedoides	Small, erect dicot	Perennial
Rumex verticillatus	Large rosette dicot	Perennial
Scirpus acutus	Tall, leafless monocot	Perennial
Typha angustifolia	Tall, erect monocot	Perennial
Verbena hastata	Tall, erect dicot	Perennial
Xyris difformis	Small, rosette monocot	Perennial

[1] nomenclature as in Gleason and Cronquist (1963) except *E. smallii* Britton and *X. difformis* Chapman.

Table 3.2. Hydroponic fertilizer mixtures used in the microcosm experiment. Both mixtures were used in equal proportions.

Mixture	Element	Relative Percentage
7-11-27	Nitrogen	7.0
	Magnesium	3.75
	Phosphorus	11.0
	Potash	27.0
	Sulphur	4.8
	Iron	0.1
	Manganese	0.085
	Zinc	0.03
	Boron	0.027
	Copper	0.0041
	Molybdenum	0.009
15-0-0	Calcium	19.0
	Nitrate	15.0
	Magnesium	3.98

Table 3.3. Summary of the effects of the 12 habitat treatments on wetland species composition in the microcosm experiment. Effects were tested by comparing 95% confidence limit envelopes using the data generated by the first two axes of a detrended correspondence analysis (DCA). Statistical effects were tested for between treatments for each potential assembly force. In cases where the * symbols are not vertically aligned, significant differences ($p < 0.05$) were observed.

Fertility Level	Habitat Treatment	DCA I	DCA II
Infertile	Constant Water Depth, 0 cm	*	*
	Constant Water Depth, -5 cm	*	*
	Constant Water Depth, +5 cm	*	*
	No Fluctuating Water Levels	*	*
	Fluctuating Water Levels, -5 to 0 cm	*	*
	Fluctuating Water Levels, -5 to +10 cm	*	*
	No *Typha* Added	*	*
	Typha Added	*	*
	No Litter	*	*
	Light Litter	* *	*
	Heavy Litter	*	*
	Surface Texture, Sand	*	*
	Surface Texture, Pebbles	* *	*
	Surface Texture, Cobbles	*	*
	Full Growing Season	*	*
	Reduced Growing Season By 14 Days	*	*
	Reduced Growing Season By 28 Days	*	*
Fertile	Constant Water Depth, 0 cm	*	*
	Constant Water Depth, -5 cm	*	*
	Constant Water Depth, +5 cm	*	*
	No Fluctuating Water Levels	*	*
	Fluctuating Water Levels, -5 to 0 cm	*	*
	Fluctuating Water Levels, -5 to +10 cm	*	*
	No *Typha* Added	*	*
	Typha Added	*	*

No Litter	*	*
Light Litter	*	* *
Heavy Litter	*	*
Surface Texture, Sand	*	*
Surface Texture, Pebbles	*	*
Surface Texture, Cobbles	*	*
Full Growing Season	*	*
Reduced Growing Season By 14 Days	*	*
Reduced Growing Season By 28 Days	*	*

Table 3.4. Summary of the effects of fertility on species composition in 12 habitats. Effects were tested by using the data generated by a detrended correspondence analysis (DCA) and comparing 95% confidence limit envelopes (* = significant effect; N.S. = not significant effect).

Habitat Treatment	DCA I	DCA II
Constant Water Depth, 0 cm	N.S.	*
Constant Water Depth, -5 cm	N.S.	N.S.
Constant Water Depth, +5 cm	N.S.	*
Fluctuating Water Levels, -5 to 0 cm	N.S.	N.S.
Fluctuating Water Levels, -5 to +10 cm	N.S.	N.S.
Typha Added	N.S.	N.S.
Light Litter	N.S.	N.S.
Heavy Litter	N.S.	N.S.
Surface Texture, Pebbles	N.S.	N.S.
Surface Texture, Cobbles	N.S.	N.S.
Reduced Growing Season By 14 Days	N.S.	N.S.
Reduced Growing Season By 28 Days	N.S.	N.S.

FIGURE CAPTIONS

Figure 3.1. 95% confidence limits (n = 5) of species composition after two growing seasons in twelve artificially created wetland habitats plotted from a two-dimensional DCA model. The results from the two fertility levels are shown. The treatment abbreviations are explained more fully in Table 3.3.

Figure 3.2. Total above-ground abundance (#contacts for all species/microcosm) after two growing seasons for twelve artificially created wetland habitats at two levels of fertility.

Figure 3.3. Species richness (#species/microcosm) after two growing seasons for twelve artificially created wetland habitats at two levels of fertility. A * symbol indicates for which treatments fertility had a significant effect on species richness (p = 0.05). In addition, four habitat treatments (constant water depth of +5 cm and -5 cm, and the two fluctuating water level treatments) had signficantly different richness levels when compared to the 0 cm constant water depth treatment (p = 0.05).

Figure 3.4. Number of TWINSPAN groups produced at six division levels for 60 microcosms (12 habitat treatments x 5 replicates) at each of two fertility levels after the first and second growing season. The raw data matrix for this analysis was 20 species (#contacts for each species/microcosm) by 240 microcosms (1987 and 1988 data, two fertility levels).

Figure 3.5. Species composition in twelve habitat treatments at two fertility levels after two growing seasons in the microcosm experiment. The five most common species are shown for each treatment. The abbreviations are as follows: (i) Bc = *Bidens cernua*, (ii) Cc = *Carex crinita*, (iii) Ec = *Epilobium ciliatum*, (iv) Es = *Eleocharis smallii*, (v) Gc = *Glyceria canadensis*, (vi) Ls = *Lythrum salicaria*, (vii) Rv = *Rumex verticillatus*, (viii) Sa = *Scirpus acutus*, (ix) Ta = *Typha angustifolia*, and (x) Vh = *Verbena hastata*.

FIGURE 3.1 a

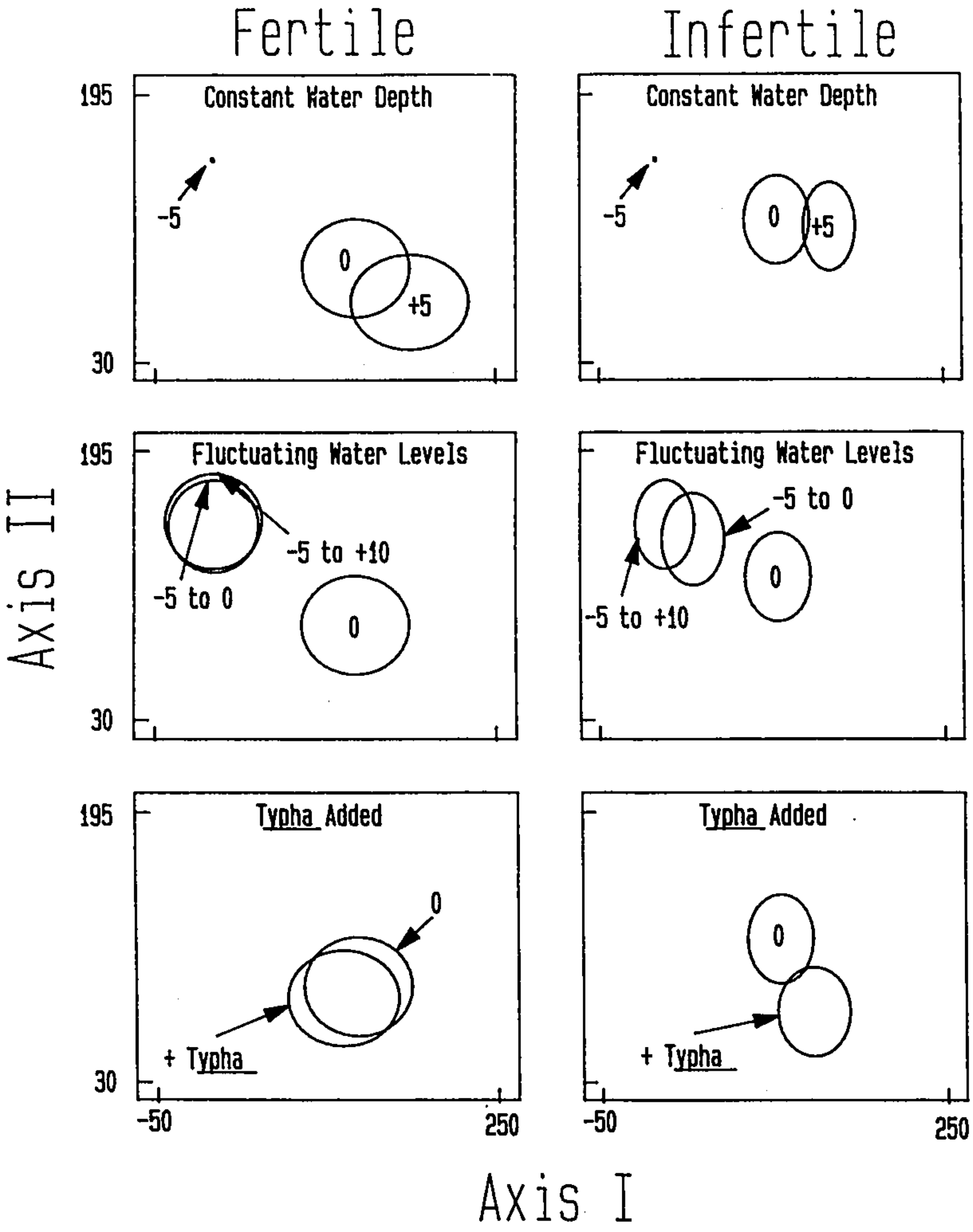

Fertile
Infertile
Constant Water Depth
Constant Water Depth
-5
0
+5
-5
0
+5
Fluctuating Water Levels
Fluctuating Water Levels
-5 to +10
-5 to 0
0
-5 to 0
0
-5 to +10
Typha Added
Typha Added
0
+ Typha
0
+ Typha
195
30
195
30
195
30
-50
250
-50
250
Axis II
Axis I

FIGURE 3.1 b

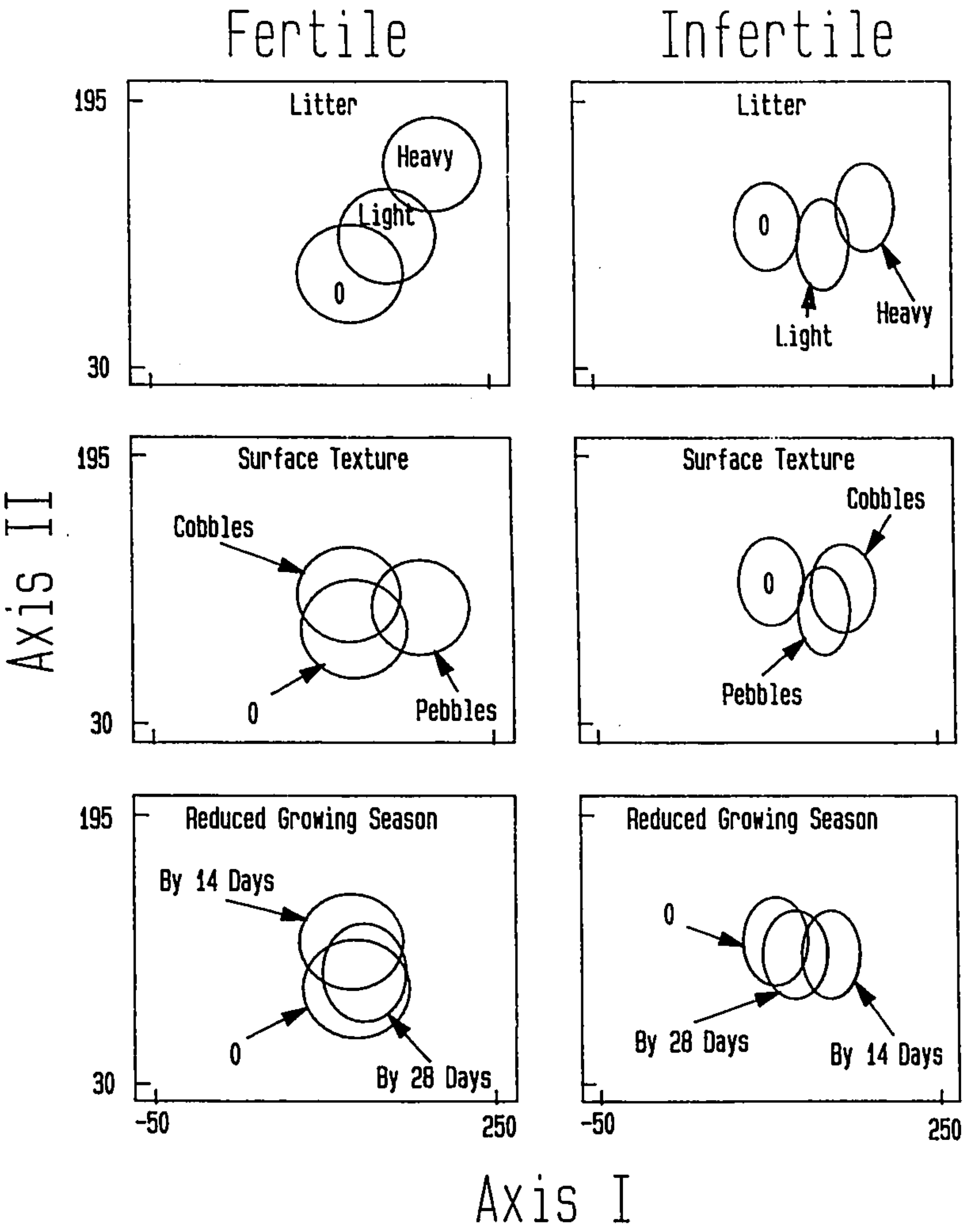

Fertile
Infertile
Litter
Heavy
Light
0
Litter
0
Light
Heavy
Surface Texture
Cobbles
0
Pebbles
Surface Texture
Cobbles
0
Pebbles
Reduced Growing Season
By 14 Days
0
By 28 Days
Reduced Growing Season
0
By 28 Days
By 14 Days
195
30
195
30
195
30
-50
250
-50
250
Axis II
Axis I

FIGURE 3.2

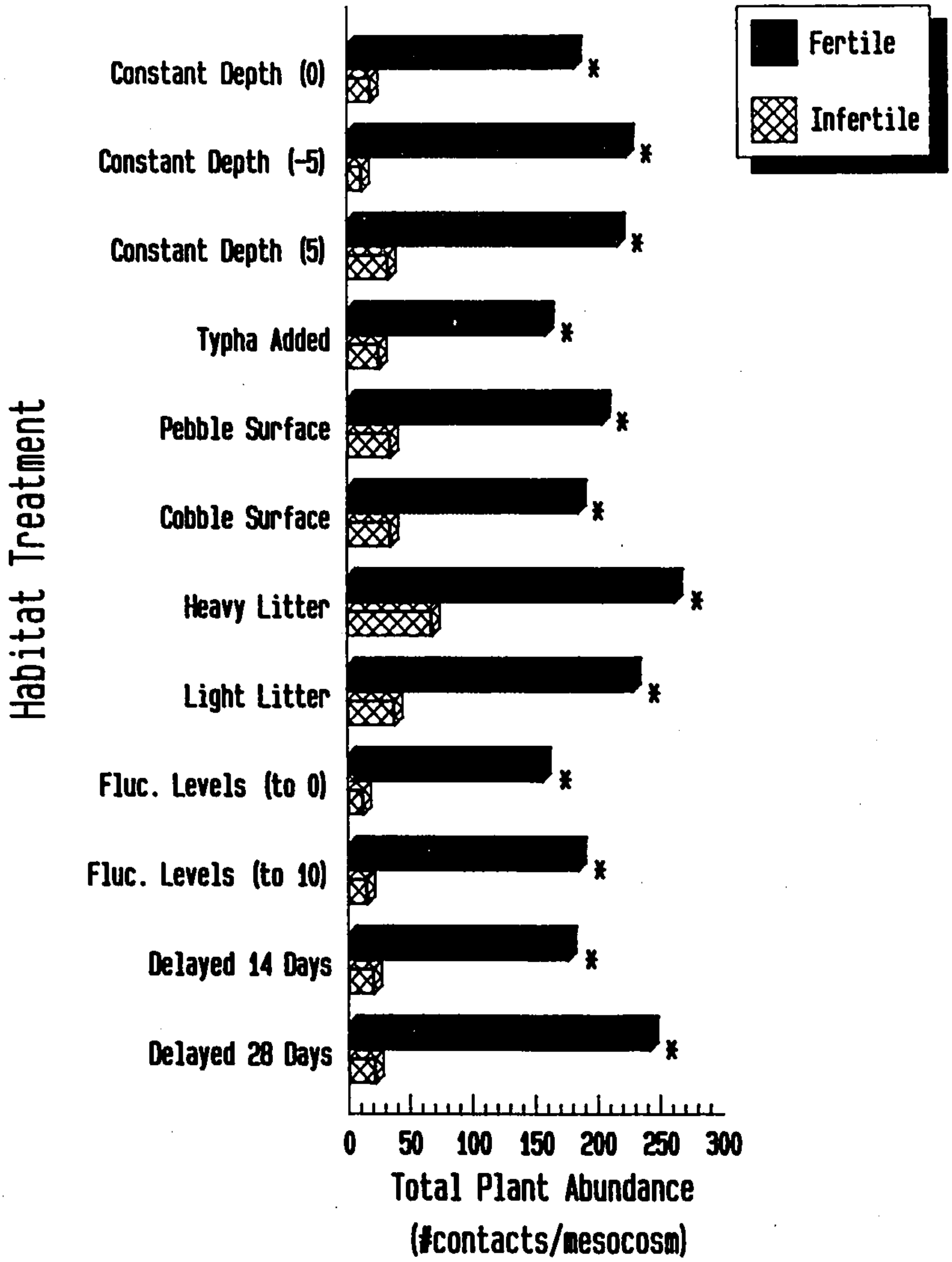

Fertile
Infertile
Habitat Treatment
Constant Depth (0)
Constant Depth (-5)
Constant Depth (5)
Typha Added
Pebble Surface
Cobble Surface
Heavy Litter
Light Litter
Fluc. Levels (to 0)
Fluc. Levels (to 10)
Delayed 14 Days
Delayed 28 Days
*
0
50
100
150
200
250
300
Total Plant Abundance
(#contacts/mesocosm)

FIGURE 3.3

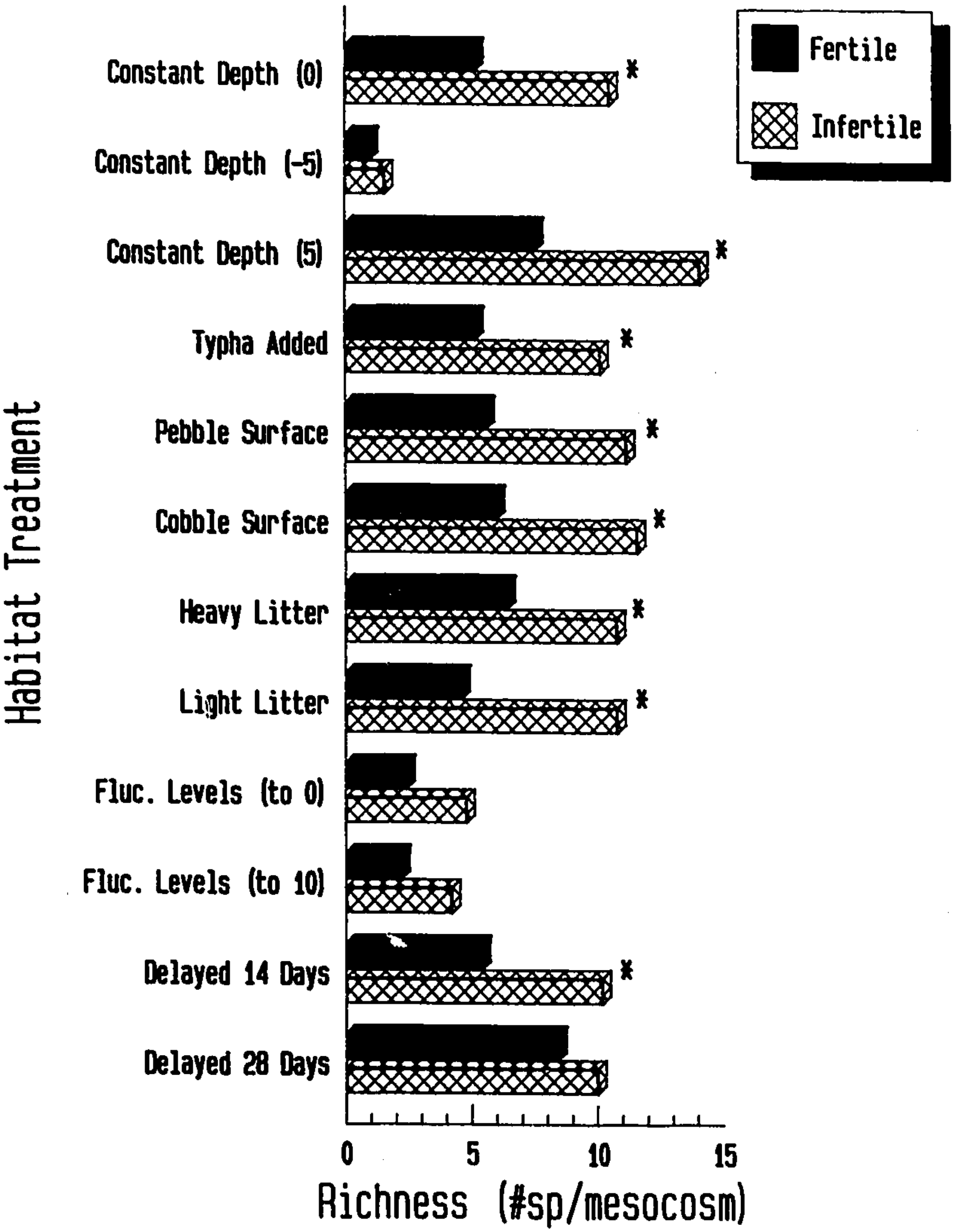

Fertile
Infertile
Constant Depth (0)
Constant Depth (-5)
Constant Depth (5)
Typha Added
Pebble Surface
Cobble Surface
Heavy Litter
Light Litter
Fluc. Levels (to 0)
Fluc. Levels (to 10)
Delayed 14 Days
Delayed 28 Days
*
Habitat Treatment
0
5
10
15
Richness (#sp/mesocosm)

FIGURE 3.4

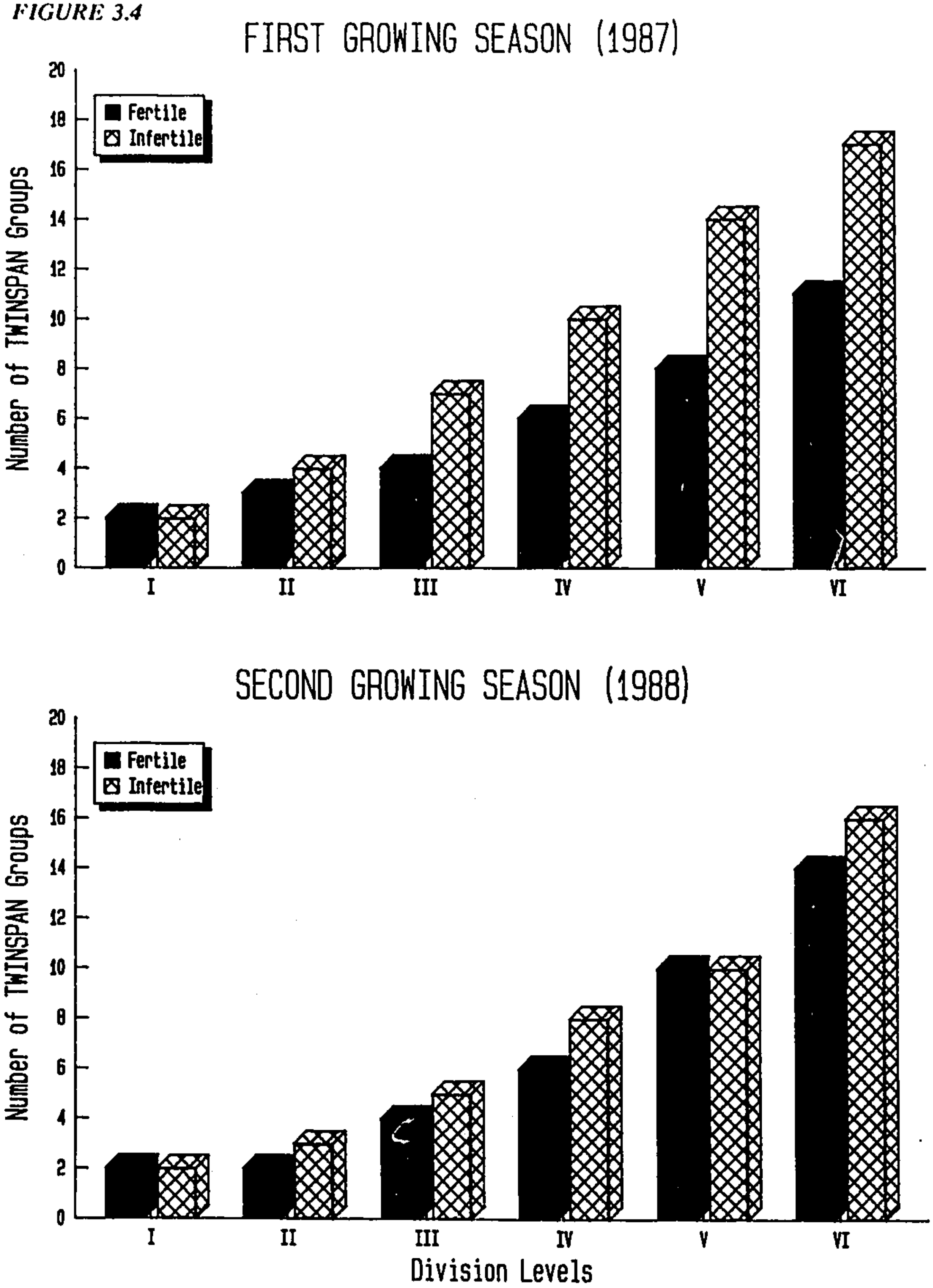

FIRST GROWING SEASON (1987)
Number of TWINSPAN Groups
0
2
4
6
8
10
12
14
16
18
20
■ Fertile
▨ Infertile
I
II
III
IV
V
VI
SECOND GROWING SEASON (1988)
Number of TWINSPAN Groups
0
2
4
6
8
10
12
14
16
18
20
■ Fertile
▨ Infertile
I
II
III
IV
V
VI
Division Levels

*FIGURE 3.5*a

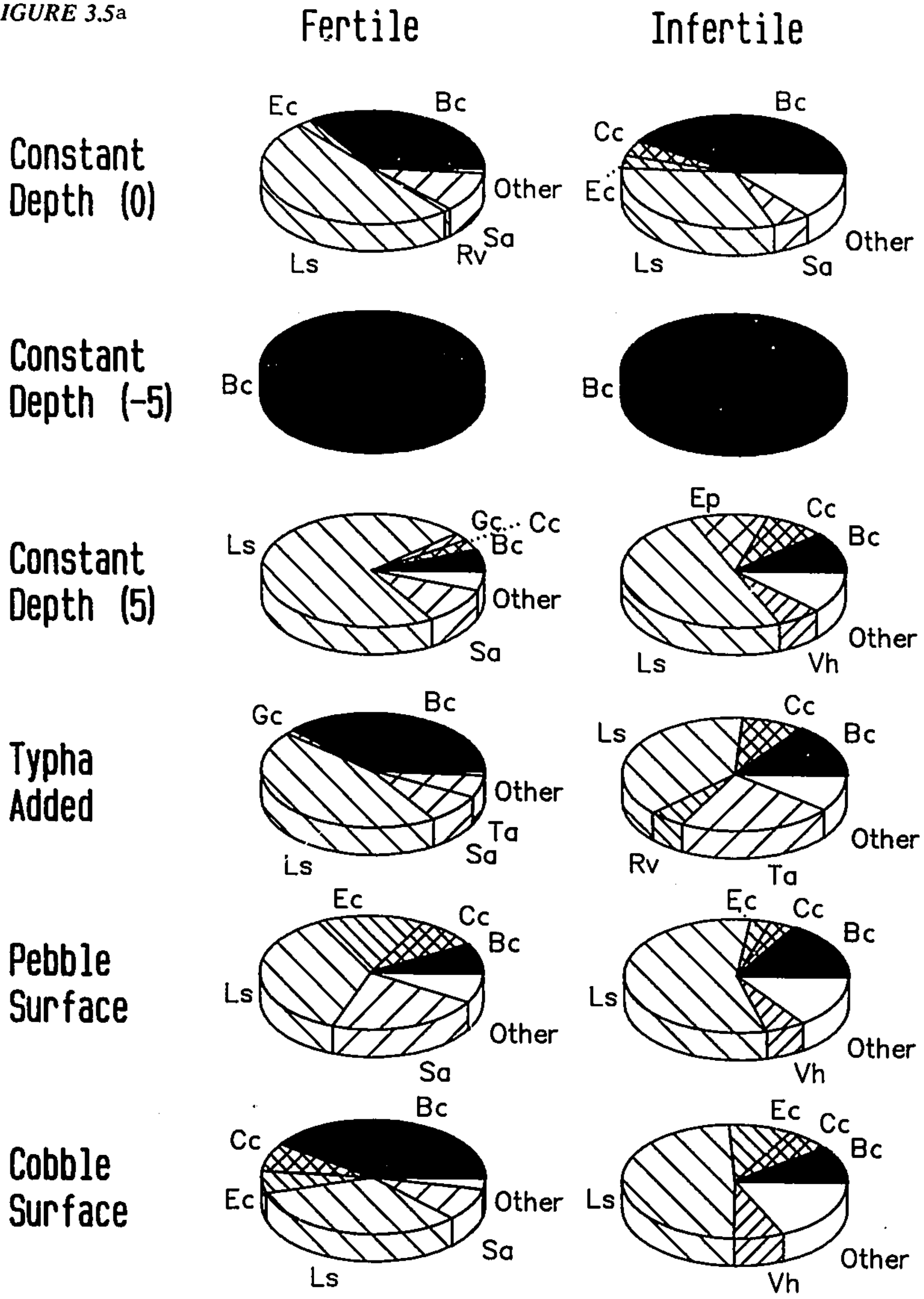
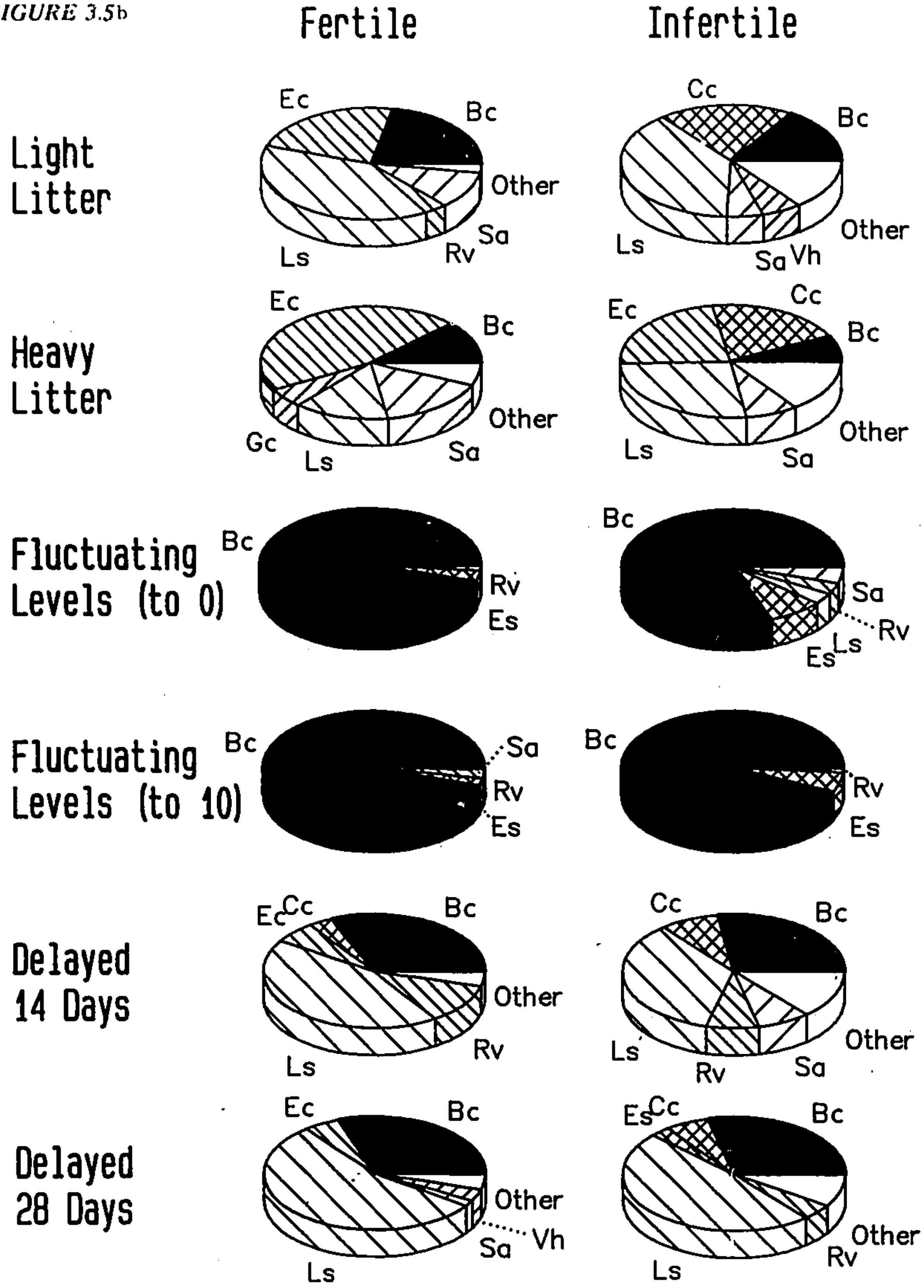

Fertile
Infertile
Constant Depth (0)
Ec
Bc
Other
Sa
Rv
Ls
Cc
Bc
Ec
Other
Sa
Ls
Constant Depth (-5)
Bc
Bc
Constant Depth (5)
Ls
Gc
Cc
Bc
Other
Sa
Ep
Cc
Bc
Other
Vh
Ls
Typha Added
Gc
Bc
Other
Ta
Sa
Ls
Ls
Cc
Bc
Other
Ta
Rv
Pebble Surface
Ec
Cc
Bc
Ls
Other
Sa
Ec
Cc
Bc
Ls
Other
Vh
Cobble Surface
Bc
Cc
Ec
Other
Sa
Ls
Ec
Cc
Bc
Ls
Other
Vh

FIGURE 3.5b


Fertile
Infertile
Light Litter
Ec
Bc
Other
Sa
Rv
Ls
Cc
Bc
Other
Vh
Sa
Ls
Heavy Litter
Ec
Bc
Other
Sa
Ls
Gc
Ec
Cc
Bc
Other
Sa
Ls
Fluctuating Levels (to 0)
Bc
Rv
Es
Bc
Sa
Rv
Ls
Es
Fluctuating Levels (to 10)
Bc
Sa
Rv
Es
Bc
Rv
Es
Delayed 14 Days
Ec
Cc
Bc
Other
Rv
Ls
Cc
Bc
Other
Sa
Rv
Ls
Delayed 28 Days
Ec
Bc
Other
Vh
Sa
Ls
Es
Cc
Bc
Other
Rv
Ls

CHAPTER 4

DISTURBANCE OF WETLAND VEGETATION: EFFECTS OF STANDING CROP AND THE LEVEL OF ORGANIZATION UNDER CONSIDERATION

"The description of the physical state of DNA, even to the details of quantum mechanics, would give no more clue to the meaning of the strand than the chemistry of this ink would give a clue to the meaning of my words."

Pattee (1978)

INTRODUCTION

Disturbance effects are a function of its size, frequency and magnitude and the spatial (e.g., organism size) and temporal (e.g., organism lifespan) dimensions of the system under consideration (Sousa 1984; White and Pickett 1985; Pickett *et al.* 1989). Within any given system there are various levels of organization and corresponding state variables that may be affected by disturbance (Allen and Starr 1982; O'Neill *et al.* 1986; Pickett *et al.* 1989). At one hierarchical extreme (the community level), disturbance can affect state variables such as species/number relationships and standing crop (Kohlmaier 1989). At the other extreme, disturbance can affect the presence, absence or abundance of particular species (the species level) (O'Neill *et al.* 1986). In between these two levels of organization is the guild level of organization where disturbance can affect the abundance of groups of species that are functionally related (Terborgh and Robinson 1986).

Individual species may vary in their response to a disturbance treatment because of differing sensitivities to disturbance, differing recovery and growth rates, or because of temporary changes in the competitive hierarchy (Denslow 1985). However, these effects are not necessarily translated to higher levels of organization because a reduction in the abundance of some species may be "balanced" by an increase in the abundance of other species, such that overall community structure and function remains unaffected. Thus, the effects of a disturbance acting at one level of organization are not, as a rule, transmitted to higher levels of organization. This statement is one of the foundations of hierarchy theory as proposed by Allen and Starr (1982). Conversely, in cases where the severity of the disturbance is such that community level changes do occur (e.g., a decrease in community biomass), then hierarchy theory would predict that lower level variables (e.g., abundance of species A) will already have been seriously disrupted. Therefore, one of the basic tenets of hierarchy theory is the following prediction:

(1) *The magnitude and duration of disturbance effects will increase as the level of organization considered decreases.*

In this study, I tested this prediction by performing a disturbance treatment (removal of above ground biomass) and monitoring the effects of this treatment at each of three levels of organization: the species, guild and community levels in five natural wetland sites.

System responses to a disturbance are dependent not only on the level of organization examined but also on the history of the system itself (O'Neill *et al.* 1986). In this study, the effects of the disturbance treatment were examined in five wetland sites located at different points along a standing crop gradient. According to Grime (1979), high standing crop sites are likely to be have had a history of limited disturbance and should therefore be sensitive to the effects of a disturbance treatment. Low standing crop sites can, however, vary widely in their history of disturbance. If one considers Grime's C-S-R model, low standing crop sites may exist in areas with low disturbance and high stress or in areas of high disturbance and low stress. *A priori*, one cannot make a prediction concerning the expected effects of a disturbance on a low standing crop community without first knowing its disturbance history. Therefore, an experiment was also conducted to determine the relative importance of various stress and disturbance factors in the low standing crop communities used in this study. Based on the outcome of this experiment, one of two predictions can be made:

> *(2A) If the standing crop gradient is the result of an underlying gradient of disturbance, the effects of the disturbance treatment will increase as site standing crop increases.*
>
> *(2B) If the standing crop gradient is the result of an underlying gradient of stress, the effects of the disturbance treatment will be severe at all points along the gradient, but particularly in the low standing crop sites because of low species growth rates* (Shipley and Keddy 1988).

METHODS

Study Location

The study location was located along the Ottawa River near Luskville, Quebec (45°31'N, 76°6'W), approximately 60 km northeast of Ottawa, Canada. This section of the Ottawa River is one of the few remaining areas on the river with a gently sloping shoreline that has remained relatively undisturbed by agriculture, industry or recreation. A wide (100 - 500 m) emergent macrophyte zone extends for approximately 3 km from an exposed sand spit to a large, sheltered bay. At this study area, five sites of varying standing crop and equivalent water depth were selected. The five sites were the same sites utilized in the Luskville wetland survey described in chapters 1 and 2. Site 1 was located on the tip of the sand spit and was a low standing crop wetland (mean = 32.7 g/0.25 m^2) exposed to intense wave action and ice scour. Site 2 was located on the lee side of the sand spit and although not as exposed as site 1, this site was also a low standing crop wetland (mean = 40.0 g/0.25 m^2). Site 3 was a moderate standing crop wetland (mean = 92.3 g/0.25 m^2), approximately 150 m from site 1 in a small bay which was partially protected from wave action by the sand spit. Sites 4 and 5 were both located in a large sheltered bay approximately 1.5 km downstream of the sandspit. Site 4 was a high standing crop wetland (mean = 124.6 g/0.25 m^2) and was located slightly closer to the main river flow than was the very high standing crop (mean = 277.7 g/0.25 m^2) site 5 wetland.

In 1986, community species composition in each of the five sites was relatively homogeneous over large areas (>25 m^2), making each site amenable to large scale field experiments. In addition, there were marked differences in richness, evenness, species composition, and species life-history patterns among sites. In 1986, site 1 was dominated by small, facultative and obligate annual species, particularly *Leersia oryzoides*, while site 2 was dominated by a small, interstitial reed species, *Eleocharis erythropoda*. Sites 3 and 4 were dominated by erect perennial species (e.g., *Lythrum salicaria*, *Scirpus americanus*, *S. fluviatilis*) and site 5 was dominated by the tall, clonal perennial species, *Typha* x*glauca* (see table 1.1).

Description of Standing Crop Gradient

Soil samples, ground-level light intensity readings, and a measure of ice scour and wave action intensity were taken in 1986 to further characterize conditions at each of the five sites. Five soil samples were taken from each of ten 0.25 m^2 quadrats randomly located on the perimeter of each site and sent to Agri-Food Laboratories (503 Imperial Rd., Guelph, Ontario) to determine NO_3, P, K and Mg levels. Ground-level light intensity readings were taken at the four corners and centre of each control plot (n = 5)(control plots are described below) at each site between 1230 and 1400 hours on 25 September, 1986. To determine relative disturbance intensity along the standing crop gradient, the following experiment was conducted: (i) 50 pegs with a length of 20 cm and a diameter of 0.6 cm were sunk 10 cm into the ground at each site on 28 October, 1986, and (ii) broken, missing and intact pegs were enumerated at each site from 16 to 24 June, 1987 as an indicator of relative disturbance intensity from ice scour and wave action during the spring high water period.

In addition to the above, a preliminary experiment was conducted to determine the relative importance of stress from soil infertility versus disturbance (sand deposition, wave and wind action, ice scour) to site standing crop and community composition. In this experiment, ramets of three species of differing morphology were placed at each site in pots with two soil type treatments: (i) soil collected from the site in which the pots were placed ('native' soil), and (ii) soil collected from the most fertile site at the study location, site 5 ('fertile' soil). The species used were *Eleocharis erythropoda*, a clonal reed that was abundant at site 2, *Lythrum salicaria*, a tall perennial that was abundant at site 3, and *Scirpus fluviatilis*, a tall, clonal perennial that was abundant at site 4. At each of the five sites from 19 to 26 August, 1986, six replicate pots of each treatment (3 species x 2 soil types) were arranged in a latin square design and the pots sunk to ground level in an area cleared of surrounding vegetation. Prior to potting, collected ramets for each species were sorted, weighed (fresh weight), and randomly assigned to each site and treatment. Ramets were replaced as necessary until 24 September, 1986 and the experiment was harvested 8 September, 1987. The number of survivors for each treatment was noted and ramet shoot and root biomass were determined by drying each to constant biomass at 60°C. The results from site 5 were not included in the analyses because most ramets had either been trampled or eaten by cows which had escaped from a nearby pasture.

Disturbance Experiment

This experiment investigated the effects of a disturbance treatment involving the complete removal of above ground vegetation midway through the growing season at each site. At each of the five sites, 15 - 25 permanent quadrats were arranged in a grid design. Each site was divided into five blocks, containing one replicate of the control and of each treatment. In each quadrat, a 1 m x 1 m area was used to assess treatment effects. Each quadrat had a double buffer zone - the inner 25 cm zone also received the treatment but was not recorded and the outer 25 cm zone received no treatment (Figure 4.1).

Estimates of species cover prior to receiving treatments in each quadrat were used as a covariate in the analyses of this experiment to remove confounding effects of spatial heterogeneity (Fowler 1981). Species composition was determined in each quadrat using a non-destructive optical point cover sampling technique which has been described as providing the best and least biased estimate of species composition from the range of techniques available (Greig-Smith 1964). The surveyer used at each permanent quadrat was 1 m x 1 m and defined 400 points on the ground - 20 rows of 20 points each. At each point, the identity of the species directly underneath the crossed threads of the plotter were recorded, together with the coordinates of the point. In cases of overlapping species, all species encountered were recorded; thus in some quadrats total cover exceeded 100%. However, for any given point no species was recorded more than once because vertical, leafless ramets had the potential for an infinite number of contacts. Litter and bare ground were not distinguished in the surveys. Voucher specimens for all species encountered in the pre-and post-treatment surveys were collected and sent to the Biosystematics Research Centre of Agriculture Canada for verification and were deposited in their herbarium (DAO) or in the University of Ottawa herbarium (OTT).

Following the pre-treatment survey, a complete removal treatment was performed (31 July to 11 August, 1986) at each site. This treatment involved clipping and removing all of the above ground vegetation in each of five replicates at each site. A control treatment in which no vegetation was removed was randomly assigned to each block (n = 5) in which a complete removal treatment was performed. In addition to the complete removal treatment, single species removal treatments were conducted for the most abundant species at each site. The species removal treatments were conducted for reasons not central to this thesis and will not be considered any further here.

Treatment effects were assessed by repeating the non-destructive survey described above several times during the following two growing seasons. Post-treatment surveys were conducted from 29 September to 9 October, 1986, 21-29 July, 1987, and 11-19 July, 1988. The first post-treatment survey did not include sites 4 and 5 because an early frost had heavily damaged the vegetation in these sites. However, the results of this survey and periodic observations during the latter part of the 1986 growing season indicated that only site 1 underwent significant changes in species composition from the mid to latter part of the growing season. For this reason, site 1 was also surveyed on 9 September, 1987. Site 5 could not be surveyed in July, 1988 because of extensive damage from trampling by cows which had escaped from a nearby pasture.

To determine if the effects of the complete removal treatment were scale dependent, the data were organized into three levels of organization: community, guild and species level variables. The three community level variables considered were richness (number of species/m^2), total abundance of species (number of contacts/m^2) and evenness. Evenness was calculated using the following formula as detailed in Legendre and Legendre (1983):

$$R = H/H_{max} = -(\sum_{i=1} p_i \log p_i)/\log n$$

where p_i is the relative frequency of species i and n is the total number of species in the quadrat. The guild level classification was developed by Boutin and Keddy (in press) based on a multivariate classification of 43 species of wetland plants grown under standardized field conditions. From the results of the classification analyses, Boutin and

Keddy determined that there were seven major functional guilds in wetland plant communities: obligate ruderals, faculative ruderals, interstitial (or gap) reeds, clonal interstitials, interstitial tussocks, matrix stress tolerators, and matrix clonal dominants. The obligate ruderal guild includes all species which are true annuals while the facultative ruderal guild includes perennial species but only those which have high growth rates and set seed in the first growing season. The three interstitial species guilds include perennial species which have compact above-ground growth forms and shallow below-ground structures. The interstitial reed guild consists of species with numerous, but essentially leafless, aerial shoots. The interstitial tussock guild includes large perennial species which are highly clumped while the clonal interstitial guild includes species which are neither reed-like nor tussock-like and which are weakly spreading. The matrix clonal dominant guild includes species which are tall, robust and capable of vigorous lateral spread, characteristics that frequently produce large monospecific stands in fertile habitats. The matrix stress tolerators have a similar growth form but are smaller and do not form dense canopies. Of the 43 species classified by Boutin and Keddy, 31 occurred in the five experimental wetland sites described above, including nearly all of the most abundant and common species at each site. The remaining species encountered during the field experiment were classified into one of the seven functional groups on the basis of personal observations, reference to herbarium vouchers, and reference to Gleason and Cronquist (1963). This latter group of species had their classification confirmed by Dr. Paul Keddy. Following the classification step, the relative abundance of each guild was determined by calculating the total number of contacts for each guild and dividing by the total number of contacts for all seven guilds for each quadrat and sampling date. Similarly, at the species level of organization, the relative abundance of each species for each quadrat and sampling date was calculated.

This study was designed to test whether the effects of the removal treatment were dependent on (i) position of the wetland site along the standing crop gradient, (ii) the level of organization considered, and (iii) the date of sampling. For each site and variable (3 community level variables, 7 guild level variables, 4 - 10 species level variables depending on the site), a two-factor Analysis of Covariance (factors = treatment, date; covariate = pre-treatment level) was performed (Zar 1974). For the guild level and species level variables an arcsine transformation was performed to ensure that the data had an underlying normal distribution (Zar 1974). Scheffe's procedure for multiple contrasts was used to determine for which sampling dates the complete removal treatment was exerting significant effects. All analyses were performed with the STATGRAPHICS version 3.0 software package.

For each level of organization and for each of two sampling dates (one and two growing seasons after the removal treatment) a correlation between the magnitude of removal treatment effects and site standing crop was tested for. For the community level of organization, the three variables calculated for each site were considered together in the correlation test (total number of contacts, richness, evenness). For the guild and species levels of organization, the number of variables selected for inclusion in the correlation test varied between sites and was based on the number of guilds and species which were deemed to be important components (defined below) of the site. The following test procedure was used: (1) For each selected variable, mean control and treatment levels were calculated for each site and sampling date; the guilds and species selected for each site were those that had at least 10% relative abundance in at least one treatment on at least one sampling date. (2) The data were transformed by the following equation to determine the magnitude of removal effects on the relative abundance of each selected variable (Ravera 1989):

$$Z_t = (x_0 \cdot y_t)/(x_t \cdot y_0)$$

where x_0 is the mean value for the variable in the control treatment during the pre-treatment survey, x_t is the mean value in the control treatment during the post-treatment survey, y_0 is the mean value measured in the removal treatment during the pre-treatment survey, and y_t is the mean value measured in the removal treatment during the post-treatment survey. The Z value is independent of initial variable levels and is independent of variations resulting from natural temporal changes. A Z value of 1.0 indicates no removal treatment effects while values above or below one indicate an increase or decrease in the variable, respectively. In this study, it is the magnitude of the variable change after the removal treatment which is important, rather than the direction of the change. Therefore, all calculated Z values less than one were recalculated using the formula, $Z_t' = 1/Z_t$. For site 1, Z values were calculated without the data from the pre-treatment survey (i.e., $Z_t = y_t/x_t$) because this community was essentially an annual community and thus the data from the post-treatment surveys were independent of the data from the pre-treatment survey. (3) A Spearman Rank Correlation coefficient (r_s)(Siegel 1956) was calculated between Z values and mean site standing crop for each level of organization. The calculation was performed separately for the 1987 (all five sites) and 1988 (sites 1 to 4) growing seasons.

RESULTS

Description of Standing Crop Gradient

The data in figure 4.2 indicate that, in general, soil nutrient levels increased as site standing crop increased. Soil nutrient differences were most pronounced between the sites occurring on or near the sand spit (sites 1, 2 and 3) and those occurring in the sheltered bay (sites 4 and 5). However, caution should be exercised when interpreting this data since soil samples were taken on only one date and soil nutrient levels may vary seasonally. In addition, it is not known if the observed soil nutrient levels were limiting (see experiment below). Figure 4.3 indicates that there was an inverse relationship between light intensity at ground level and site standing crop as would be expected given that high standing crop sites were observed to have higher, denser canopies. Figure 4.4 indicates that site 1 was exposed to intense disturbance from ice scour and wave action during the winter of 1986 and spring of 1987, while the remaining sites were relatively unaffected. There was also deposition of fresh sediment on low standing crop sites with approximately 5 cm of sand being deposited on the soil surface of site 1, and 2 to 4 cm of sand deposited on the site 2 soil surface.

Figure 4.5 indicates that the low soil fertility at site 1 (see figure 4.2) was relatively unimportant when compared to the effects of other environmental variables, since no ramets of any of the test species survived in either soil treatment. In sites 2 to 4, survivorship of the three test species was relatively unaffected by site or soil type. However, two-factor ANCOVAs (factors = site, soil type; covariate = initial ramet fresh weight) conducted for each test species revealed that total shoot and root biomass increased significantly for *Lythrum salicaria* and *Scirpus fluviatilis* as site standing crop increased; soil treatment had no effect on these species (Figure 4.6). Conversely, *Eleocharis calva* biomass was not affected by site position on the standing crop gradient, but did increase significantly with the 'fertile' soil treatment in site 4 (Figure 4.6).

Disturbance Experiment

At the community level of organization, most observed effects ($p < 0.05$) were restricted to the first sampling date after the complete removal treatment for sites 1, 2 and 3 (sites 4 and 5 were not sampled on this date). Within one growing season, there were few observable effects of the removal treatment at any of the sites (Figure 4.7). Figure 4.7 also indicates that the low standing crop control treatments at sites 1 and 2 underwent dramatic increases in the total number of species contacts and richness during the two year experiment.

Few changes in guild composition occurred as a result of the removal treatment at any of the sites (Figure 4.8). However, at each site significant minor changes in guild composition did occur. Those effects that were observed generally did not persist beyond October, 1986 in the low standing crop sites (sites 1, 2 and 3). In sites 4 and 5, changes in guild composition tended to be more persistent. For instance, in site 4 the matrix clonal dominant guild was found to have a significantly higher abundance one and two growing seasons after the removal treatment.

At the species level of organization, significant removal treatment effects were more frequently observed than was found with the two higher levels of organization (Figure 4.9). Figure 4.9 further indicates that the most abundant species at each site in 1986 (site 1 = *Leersia oryzoides*, site 2 = *Eleocharis erythropoda*, site 3 = *Lythrum salicaria* and *Scirpus americanus*, site 4 = *Scirpus fluviatilis*, site 5 = *Typha xglauca*) were all significantly affected by the removal treatment with all but *L. salicaria* experiencing a significant decrease in abundance. As well, there was a suggestion that the removal treatment had a longer-lasting effect on species from the high standing crop sites (sites 4 and 5).

Figure 4.10 indicates a significant correlation between species Z values and site standing crop one growing season after the removal treatment ($r_s = 0.802$; $p < 0.01$). Therefore, the effects of the complete removal treatment at the species level of organization increased as standing crop increased. Figure 4.10 also indicates that this relationship was evident two growing seasons after the removal treatment ($r_s = 0.584$; $p < 0.05$). At the next highest level of organization, the guild level, the magnitude of removal treatment effects increased as standing crop increased for the first growing season after the treatment ($r_s = 0.477$; $p < 0.05$)(Figure 4.11). However, at this level of organization the correlation did not persist to the end of the second growing season ($r_s = 0.393$; $p > 0.05$)(Figure 4.11). At the highest level of organization examined, the community level, there was no relationship between the magnitude of removal treatment effects and position of the site along the standing crop gradient in 1987 ($r_s = 0.320$; $p > 0.05$) or 1988 ($r_s = 0.091$; $p > 0.05$)(Figure 4.12).

DISCUSSION

Description of Standing Crop Gradient

There are several lines of evidence to suggest that disturbance was the primary factor controlling community structure and standing crop in the five wetland sites examined in this study. First, as indicated in figure 4.8, the dominant guild in site 1 was composed of facultative ruderal species, particularly *Leersia oryzoides*. *L. oryzoides* has been shown to have a high relative growth rate (Shipley and Keddy 1988), low competitive ability (Gaudet and Keddy 1988), and flowers during the first growing season (Boutin and Keddy, in press). According to Grime (1977; 1979), these characteristics are indicative of a ruderal species. At site 2, the dominant guild was composed of interstitial reed species, particularly *Eleocharis erythropoda*. This species also has a high growth rate (Shipley and Keddy 1988) and is a poor competitor (Gaudet and Keddy 1988), but devotes less resources to seed production during the first growing season than does *L. oryzoides*. If soil infertility was the primary factor reducing standing crop in these sites, one would instead expect to find a large proportion of 'isoetid' species which are small, evergreen rosette species with low growth rates and poor competitive ability (Boston 1986; Boston and Adams 1987; Moore *et al.* 1989). No isoetid species were found in any of the five experimental wetland sites.

Second, personal observations suggest that at sites 1, 2 and 3, ice scour and wave action during the spring high water period each had the potential to remove large patches of vegetation. Further, the observed sand deposition between growing seasons in sites 1 and 2 may be severe enough to eliminate all but ruderal species. The latter species can escape the effects of sand deposition by either recolonizing the site each growing season (the case at site 1) or by possessing sufficiently rapid growth rates to penetrate the layer of sand deposited each year (the case at site 2).

Third, the results from the transplant experiment indicated that no ramets of the three perennial species examined could overwinter and survive at site 1 even when the ramets were placed in fertile soil (Figure 4.5).

Further, while the two large, perennial species, *Lythrum salicaria* and *Scirpus fluviatilis*, both produced significantly less biomass when placed in sites of lower standing crop, increased soil fertility did not affect this response (Figure 4.6). Therefore, for these species the standing crop gradient is not the result of an underlying nutrient stress gradient and it is likely disturbance that prevents these species from dominating the low standing crop sites. The smaller reed species, *Eleocharis erythropoda*, was relatively unaffected by the transplant site except in the extreme situation at site 1. This species did not respond to increased soil fertility in sites 2 and 3, the two sites in which *E. erythropoda* was most abundant (Figure 4.6). Although, *E. erythropoda* produced significantly more biomass in site 4 when ramets were placed in fertile soil, it is likely that this species is normally excluded from this site because it is a poor competitor. Based on this preliminary experiment and the supporting evidence cited above, it can be concluded that the experimental standing crop gradient and the community composition patterns observed along this gradient were likely the result of a natural disturbance gradient.

Disturbance Effects Along the Standing Crop Gradient

The results of this study indicated that the low standing crop wetlands with a history of disturbance were less affected by a single disturbance event than were the high standing crop wetlands which did not have a history of disturbance (Figures 4.8, 4.9, 4.10, 4.11). This result is in agreement with the generally accepted notion amongst ecologists that systems that have been assembled in relatively unstable environments are more likely to resist new disturbances, especially those that mimic historical disturbance events (Denslow 1985; Rapport *et al.* 1985). Watt (1974) calls this the "Titanic effect", in which the less likely a disaster is to occur, the more disastrous will be the effects when it does. For example, Turner (1985) found that when surfgrass, *Phyllospadix scouleri*, was removed from an otherwise rarely disturbed surfgrass bed, recovery over the 3 year experiment was shown to be very slow with less than 1% recovery of space by *P. scouleri*. Similarly, tropical forests that are rarely subject to large-scale disturbances are highly susceptible to clear-cut logging and may require several hundred years to recover (Denslow 1985). Conversely, fire-adapted systems such as the garrigue vegetation in southern France (Malanson and Trabaud 1987) and grasslands in North America (Loucks *et al.* 1985) both recover quickly from imposed burns. Even coral reefs, which were previously thought to be highly stable systems, have shown rapid recovery times from severe disturbances (e.g., sea star predation, low tides) for which the system had a past history of exposure (Loya 1976; Colgan 1987).

The results indicated that wetland communities dominated by ruderal species or ruderal guilds were disturbance tolerant and that wetland communities dominated by matrix stress tolerators or matrix clonal dominants were disturbance intolerant. This result is not surprising and is consistent with the theory of r- and K selection (MacArthur and Wilson 1967) and Grime's (1979) C-S-R model. However, the expectation that ruderal species and guilds would also be the major benefactors from a disturbance in a disturbance intolerant community was not supported by the results of this study. For example, the two species at site 4 that demonstrated a significant increase in abundance after the removal treatment were *Agrostis stolonifera*, a matrix stress tolerator, and *Phalaris arundinacea*, a matrix clonal dominant. No ruderal species or guilds had a significant increase in abundance in sites 4 and 5 after the removal treatment. This apparent anomaly was probably because the effects of the disturbance were short-lived and not repeated. Therefore, the 'window of opportunity' was too narrow for ruderal species to disperse to and colonize these sites.

Prior to the complete removal treatment, each experimental site except site 3 was dominated by one species (Figure 4.9). Most of the observed short-term removal treatment effects at the community level of organization were consistent with the prediction that a temporary release from dominance produces conditions which favour an increase in species diversity (Grime 1979). In sites 1, 2 and 4, the complete removal treatment led to a significant short-term increase in richness and/or evenness (Figure 4.7). However, the removal treatment had the opposite effect in site 3 where richness and evenness were high prior to the complete removal treatment. Within one growing season, the dominant species had recovered in sites 1 and 2 and, as a consequence, no effects on richness or evenness were observed on this or subsequent sampling dates. At site 4 the dominant species, *Scirpus fluviatilis*, was significantly reduced by the removal treatment for the duration of the experiment and, as expected, richness remained elevated at this site for the 1987 growing season.

The Importance of Scale

This study considered three levels of biological organization in assessing the effects of a disturbance to wetland communities arranged along a standing crop gradient. The results indicated that the effects of the disturbance treatment were most strongly felt at the species level of organization, the finest-grained level of organization examined (Figures 4.10, 4.11, 4.12). At this level, the dominant species at each site were significantly affected by the disturbance treatment and the effects were longer lasting, particularly in high standing crop sites (Figure 4.9). However, at the highest level of organization examined, the community level, few disturbance effects that persisted to the next growing season were observed (Figure 4.7). This trend was evident in spite of a general decrease in the sensitivity of the data analyses at the lower levels of organization. For example, at the community level of organization, most control-treatment differences of greater than 20% ($Z > 1.2$) were detected as significant effects. However, at the species level of organization, control-treatment differences of 20 - 40% ($Z = 1.2 - 1.4$) were rarely detected as significant and in several cases differences of >100% ($Z > 2.0$) were not detected as significant. The decreased sensitivity of the analyses at the species level of organization was due to greater intra-treatment variability and reduced significance of the pre-treatment covariate at this level.

The experimental results indicated that the effects of the disturbance treatment evident at the lowest level of organization become incorporated in successively higher levels of organization (*sensu* O'Neill *et al.* 1986). For example, at the species level of organization, *Scirpus fluviatilis* was significantly reduced as a result of the removal treatment in site 4. *S. fluviatilis* belongs to the matrix stress tolerator guild. However, this guild was not affected by the removal treatment because another matrix stess tolerator species, *Agrostis stolonifera*, significantly increased as a result of the removal treatment (Figure 4.9). A similar trend was described by Kimmerer and Allen (1982) in their study of the bryophyte communities on the cliffs of the Kickapoo River. In this study it was observed that the factor determining patch composition within a given vegetation zone was the interval of time since the previous disturbance. However, this factor was incorporated at a higher level of organization, such that bryophyte zonation patterns were not affected by time since the most recent disturbance, but were instead controlled by a higher level process, disturbance frequency. In chapter 3, it was observed that microsite differences in water depth could account for within vegetation type variations in species richness but that these effects were incorporated at the among vegetation types level of organization. The results presented in this chapter indicated that microsite differences as a result of localized disturbance events could also account for variations in species richness at the community (or within vegetation type[1]) level of organization. However, these effects were not translated to predictable effects on species richness at the among vegetation types level of organization.

The general effects of disturbance can be measured as resilience and stability. Resilience is the degree to which a system's long-standing composition and structure can be disturbed and yet return to the normal operating range (*sensu* Gulati 1989) and function as before (Holling 1973, 1977, 1986). By this definition, it is apparent that at the species, guild and community levels of organization, the wetlands considered in this study were quite resilient to the effects of a single disturbance treatment in which the above-ground vegetation was removed. In order to compare the relative resilience of wetlands arranged along a disturbance gradient, a longer, more intense disturbance regime than was used in this study would be required. Stability can be defined as the propensity of a system to resist any departure from the normal operating range and, if disturbed, return rapidly to it with the least fluctuation (Holling 1973, 1977, 1986). In this study, the low standing crop wetlands with a history of disturbance were found to have a higher stability (higher resistance to disturbance, higher return rate following disturbance) than did the high standing crop wetlands which did not have a previous history of disturbance (lower resistance to disturbance, lower return rate following disturbance). However, this relationship was only evident at the finer-grained levels of organization and is thus scale dependent (Figure 4.13).

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[1] the within vegetation type level of organization includes all communities in a landscape with the same dominant species - when discussing a single homogeneous site, the use of these terms are synonymous.

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FIGURE CAPTIONS

Figure 4.1. Layout of quadrats in the field experiment showing borders, pathways and distance between quadrats.

Figure 4.2. Mean macronutrient levels (ug/g) in each of the five experimental wetland sites sampled on the Ottawa River near Luskville, Quebec. The sites were arranged along a standing crop gradient with site 1 having the lowest standing crop and site 5 having the highest standing crop.

Figure 4.3. Mean light intensity (microeinsteins/m^2/sec) at ground level in each of the five experimental wetland sites. Readings were taken between 1230 and 1400 hours on a clear day.

Figure 4.4. The intensity of disturbance from ice scour and wave action during the 1987 spring high water period at each of the five experimental wetland sites. Disturbance intensity was estimated by placing 50 pegs in the soil surface at each site in late autumn, 1986 and enumerating the number of removed and broken pegs in spring, 1987.

Figure 4.5. The number of survivors for each of three species from a one year transplant experiment in four of the five experimental wetland sites. At each site, six ramets of each species were placed in one of two soil types: (i) "native" soil from the transplant site, and (ii) "fertile" soil from site 5.

Figure 4.6. Mean total biomass of survivors for each of three species from the transplant experiment described in figure 4.5. There were no survivors in site 1. Significant differences ($p < 0.05$) in biomass are indicated for comparisons between sites 2, 3 and 4 for each species. Significant differences in biomass as a result of soil type treatment are indicated by a * symbol for each site and species ($p < 0.05$).

Figure 4.7. Mean total abundance of species (# contacts/m^2), richness (# species/m^2), and evenness in control and complete removal treatments at each of the five experimental wetland sites. The sampling dates were July, 1986

(#1, sites 1-5), October, 1986 (#2, sites 1-3), July, 1987 (#3, sites 1-5), September, 1987 (#4, site 1), and July, 1988 (#5, sites 1-4). The complete removal treatment was conducted after the first sampling date. Significant differences between control and removal treatments are indicated by a * symbol for each variable at each site on each sampling date ($p < 0.05$).

Figure 4.8. Mean relative abundance of seven functional guilds in control and complete removal treatments at each of the five experimental wetland sites. The sampling dates are the same as described in figure 4.7. Significant differences between control and removal treatments are indicated by a * symbol for each guild at each site on each sampling date ($p < 0.05$).

Figure 4.9. Mean relative abundance of individual species in control and complete removal treatments at each of the five wetland sites. Only those species which had at least 10% relative abundance on at least one sampling date and which had a signficant response ($p < 0.05$) to the removal treatment are shown. The sampling dates are the same as described in figure 4.7. Significant differences between control and removal treatments are indicated by a * symbol for each species at each site on each sampling date ($p < 0.05$).

Figure 4.10. The magnitude of effects as a result of the removal treatment (Z, see text for details) at the species level of organization for the experimental wetland sites. Sites 1-5 were sampled one growing season after the removal treatment (July, 1987) and sites 1-4 were sampled two growing seasons after the removal treatment (July, 1988). A Spearman rank correlation between Z and site standing crop was found to be significant for the 1987 ($r_s = 0.802$; $p < 0.01$) and 1988 ($r_s = 0.584$; $p < 0.05$) growing seasons.

Figure 4.11. The magnitude of effects as a result of the removal treatment (Z) at the guild level of organization for the experimental wetland sites. A Spearman rank correlation between Z and site standing crop was found to be significant for the 1987 growing season ($r_s = 0.477$; $p < 0.05$), but not the 1988 growing season ($r_s = 0.393$; $p > 0.05$).

Figure 4.12. The magnitude of effects as a result of the removal treatment (Z) at the community level of organization for the experimental wetland sites. The three community variables included were total number of contacts (triangles), richness (squares) and evenness (circles). When all three variables were considered together, the Spearman rank correlation was found to be not significant for both the 1987 ($r_s = 0.320$; $p > 0.05$) and 1988 ($r_s = 0.091$; $p > 0.05$) growing seasons.

Figure 4.13. A summary model describing the predicted level of effects for different levels of organization to a disturbance event in herbaceous communities arranged along a disturbance gradient. In general, plant communities which are regularly exposed to disturbance are expected to be much less affected by a single disturbance event than are communities not regularly exposed to disturbance. The effects of the disturbance event are predicted to be greater at finer levels of organization (species > guild > community). In addition, the effects of the disturbance event are expected to decrease as time from the disturbance event increases.

FIGURE 4.1

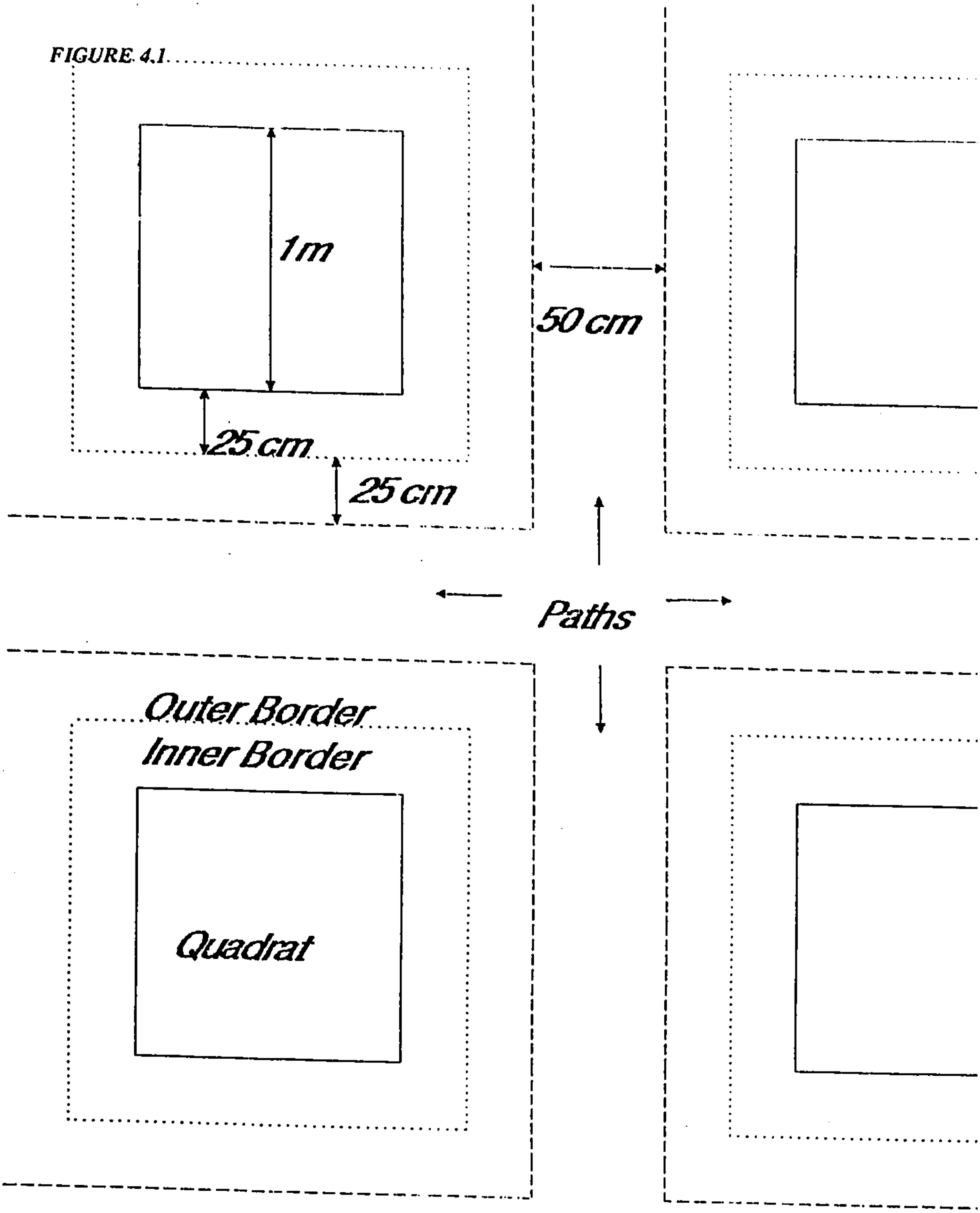


FIGURE 4.2

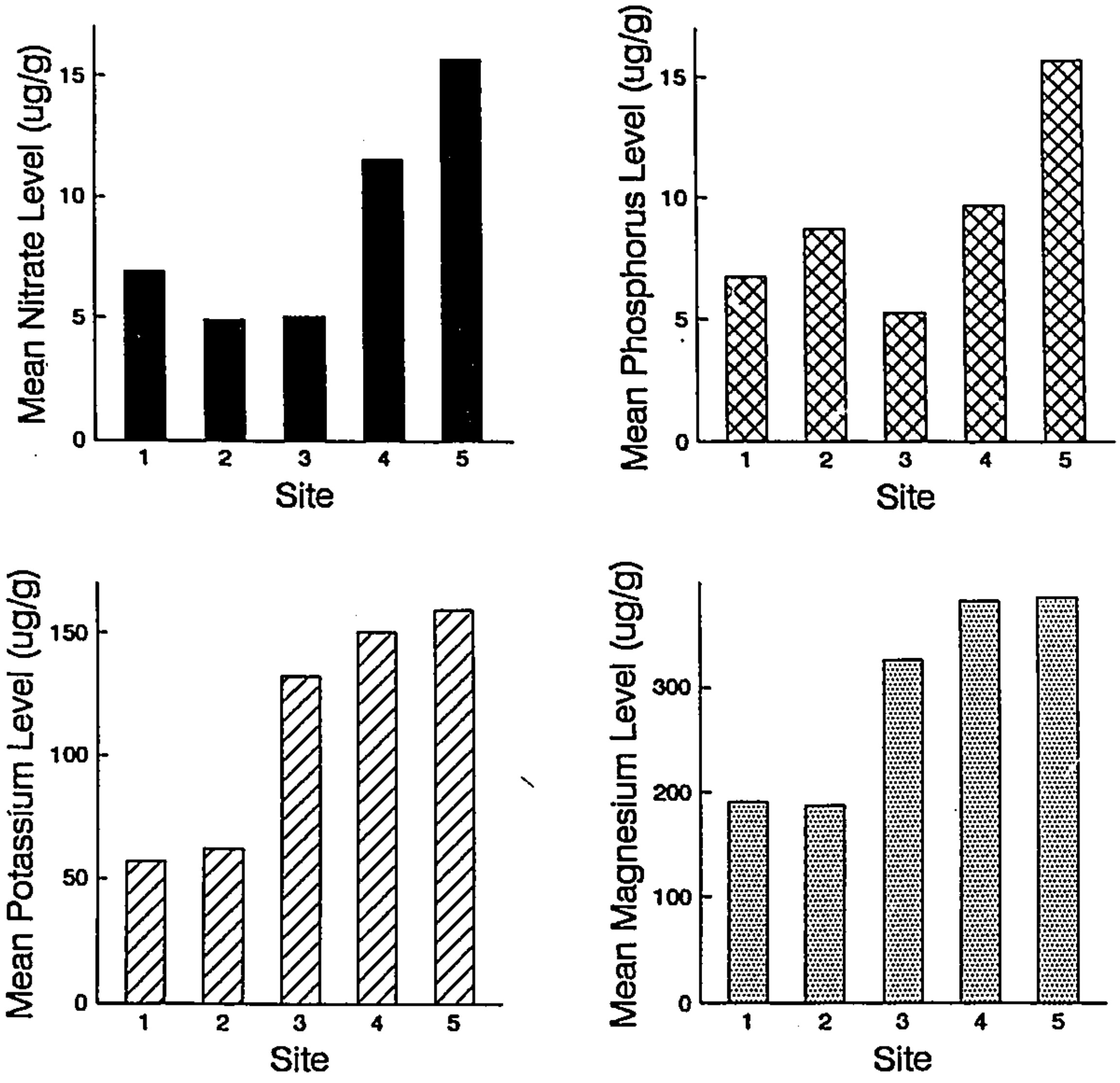

Mean Nitrate Level (ug/g)
0
5
10
15
1
2
3
4
5
Site
Mean Phosphorus Level (ug/g)
0
5
10
15
1
2
3
4
5
Site
Mean Potassium Level (ug/g)
0
50
100
150
1
2
3
4
5
Site
Mean Magnesium Level (ug/g)
0
100
200
300
1
2
3
4
5
Site

FIGURE 4.3

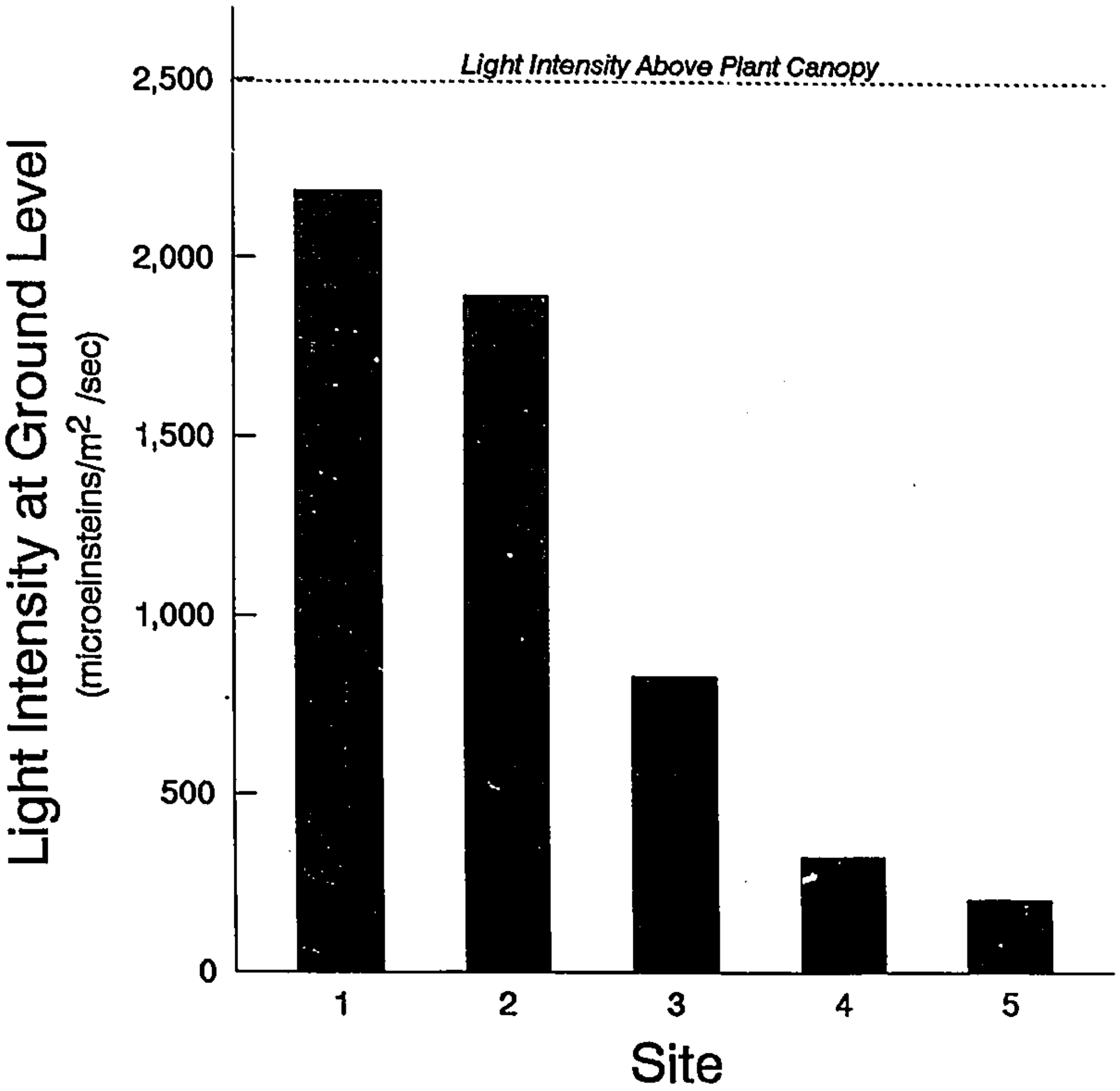

Light Intensity Above Plant Canopy
Light Intensity at Ground Level
(microeinsteins/m2 /sec)
2,500
2,000
1,500
1,000
500
0
1
2
3
4
5
Site

FIGURE 4.4

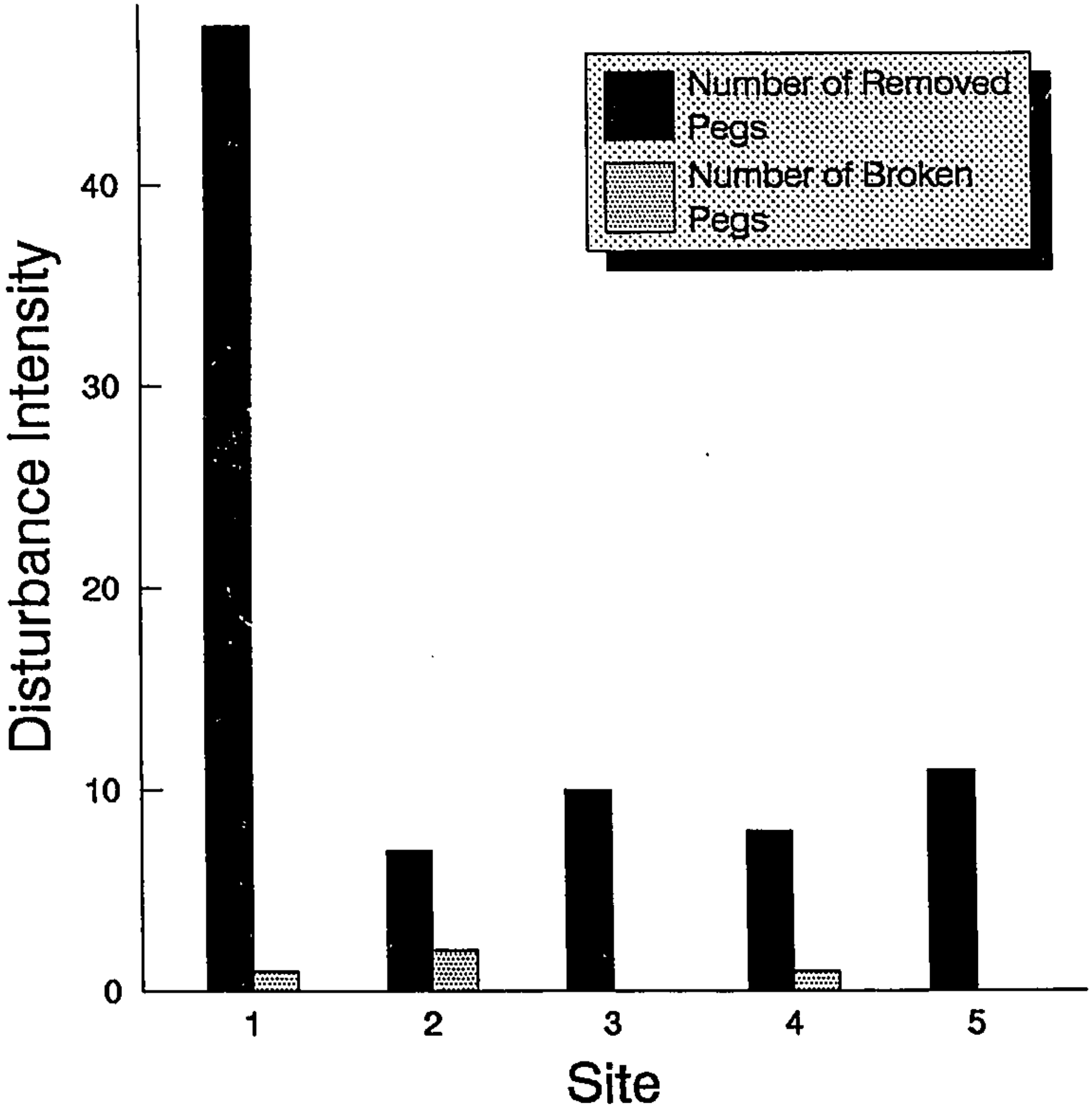

Number of Removed Pegs
Number of Broken Pegs
Disturbance Intensity
0
10
20
30
40
1
2
3
4
5
Site

FIGURE 4.5

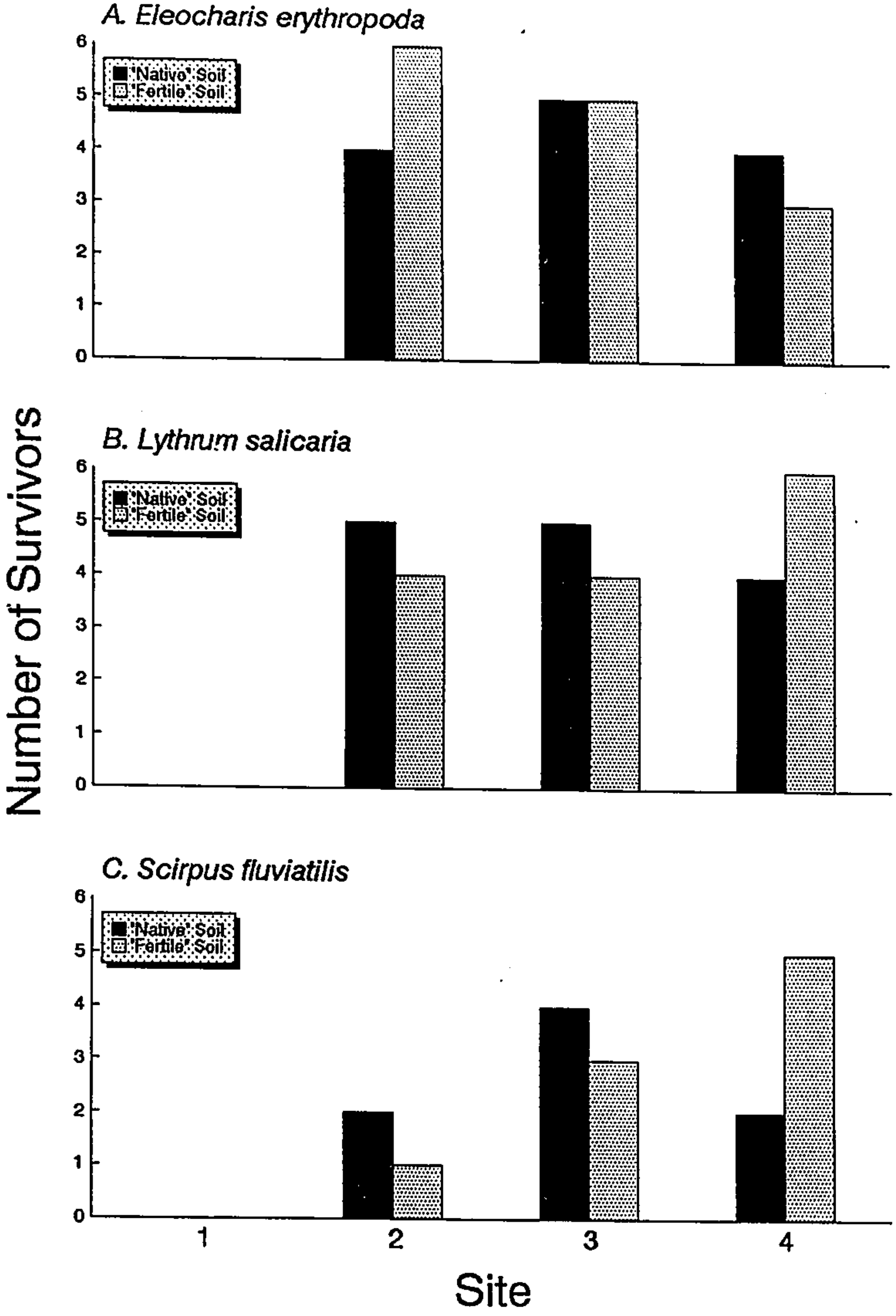
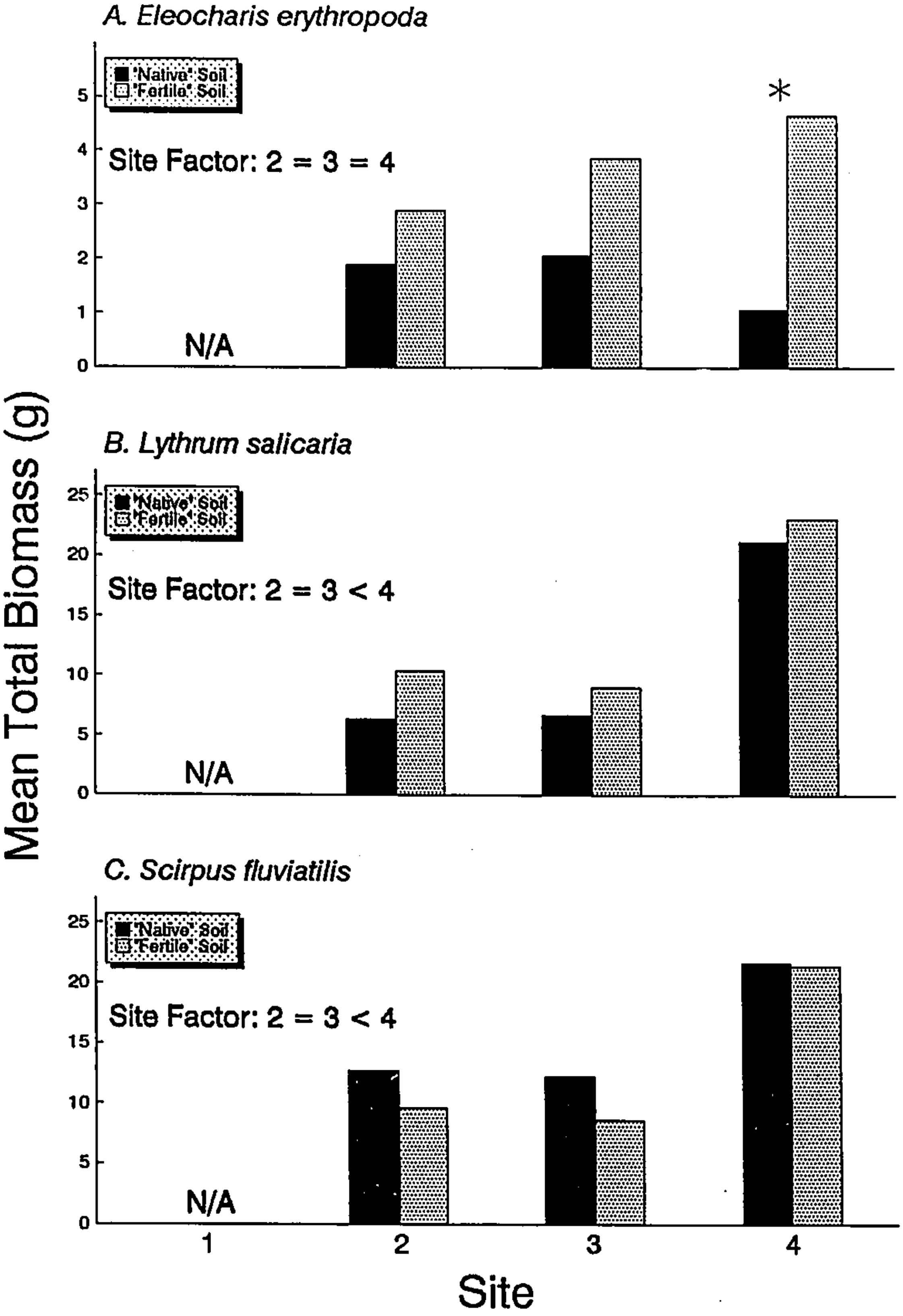
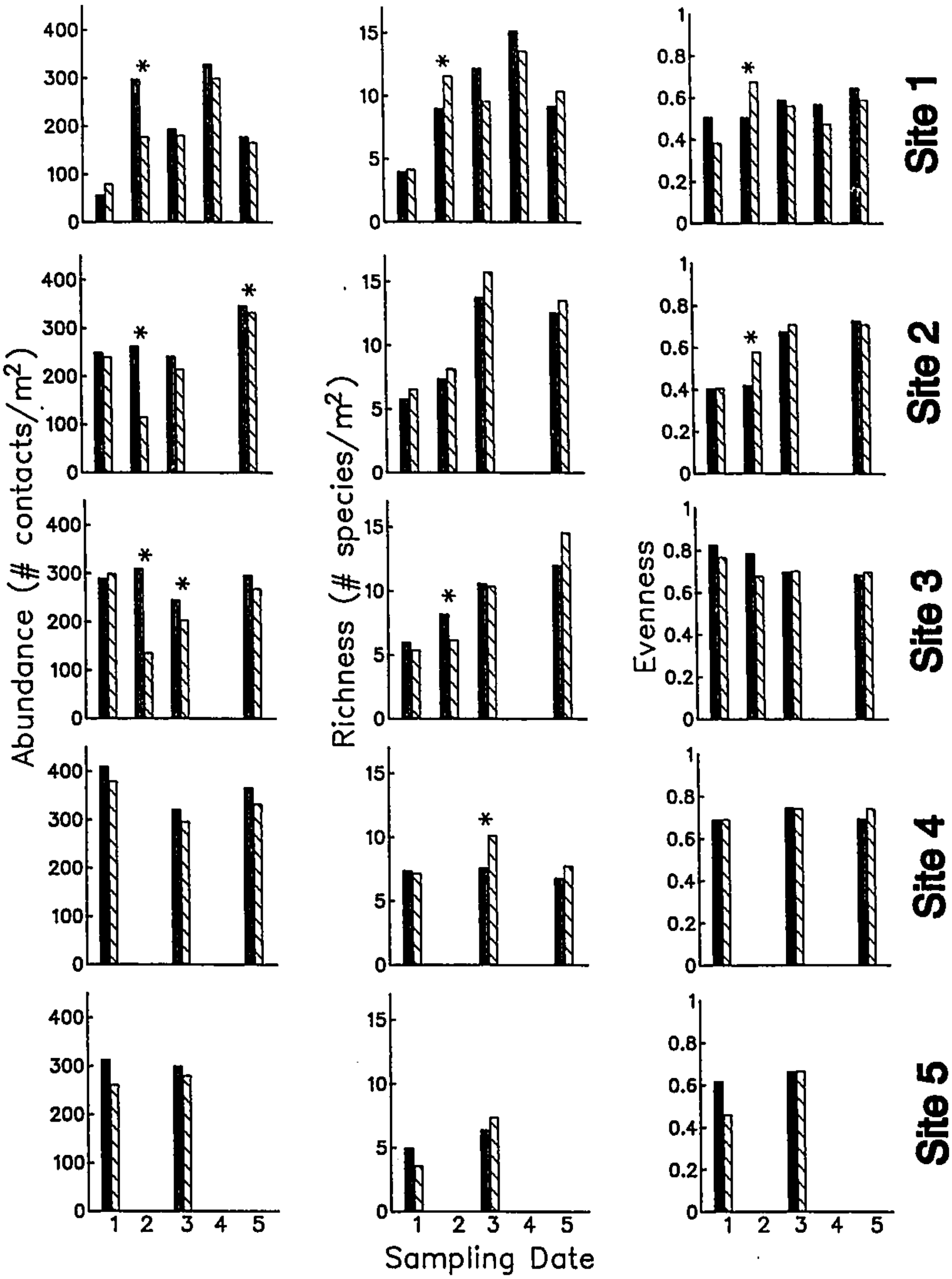

A. Eleocharis erythropoda
B. Lythrum salicaria
C. Scirpus fluviatilis
■ 'Native' Soil
▨ 'Fertile' Soil
Number of Survivors
0
1
2
3
4
5
6
1
2
3
4
Site

FIGURE 4.6



A. Eleocharis erythropoda
'Native' Soil
'Fertile' Soil
Site Factor: 2 = 3 = 4
*
N/A
0
1
2
3
4
5
B. Lythrum salicaria
'Native' Soil
'Fertile' Soil
Site Factor: 2 = 3 < 4
N/A
0
5
10
15
20
25
C. Scirpus fluviatilis
'Native' Soil
'Fertile' Soil
Site Factor: 2 = 3 < 4
N/A
0
5
10
15
20
25
Mean Total Biomass (g)
1
2
3
4
Site

FIGURE 4.7



Abundance (# contacts/m²)
Richness (# species/m²)
Evenness
Site 1
Site 2
Site 3
Site 4
Site 5
0
100
200
300
400
5
10
15
0.2
0.4
0.6
0.8
1
*
1
2
3
4
5
Sampling Date

FIGURE 4.8

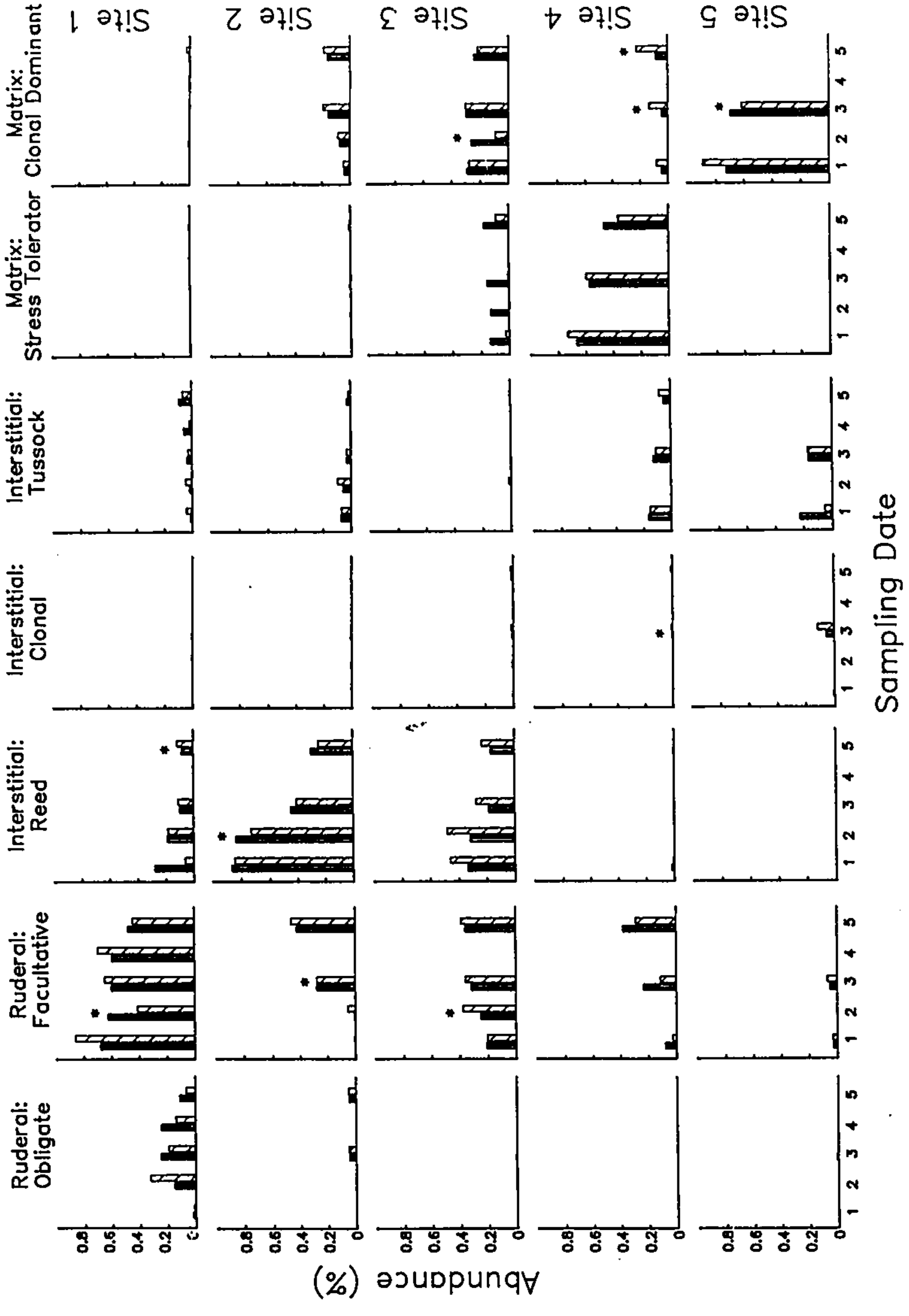

Ruderal: Obligate
Ruderal: Facultative
Interstitial: Reed
Interstitial: Clonal
Interstitial: Tussock
Matrix: Stress Tolerator
Matrix: Clonal Dominant
Site 1
Site 2
Site 3
Site 4
Site 5
Abundance (%)
0
0.2
0.4
0.6
0.8
Sampling Date
1
2
3
4
5
*

FIGURE 4.9

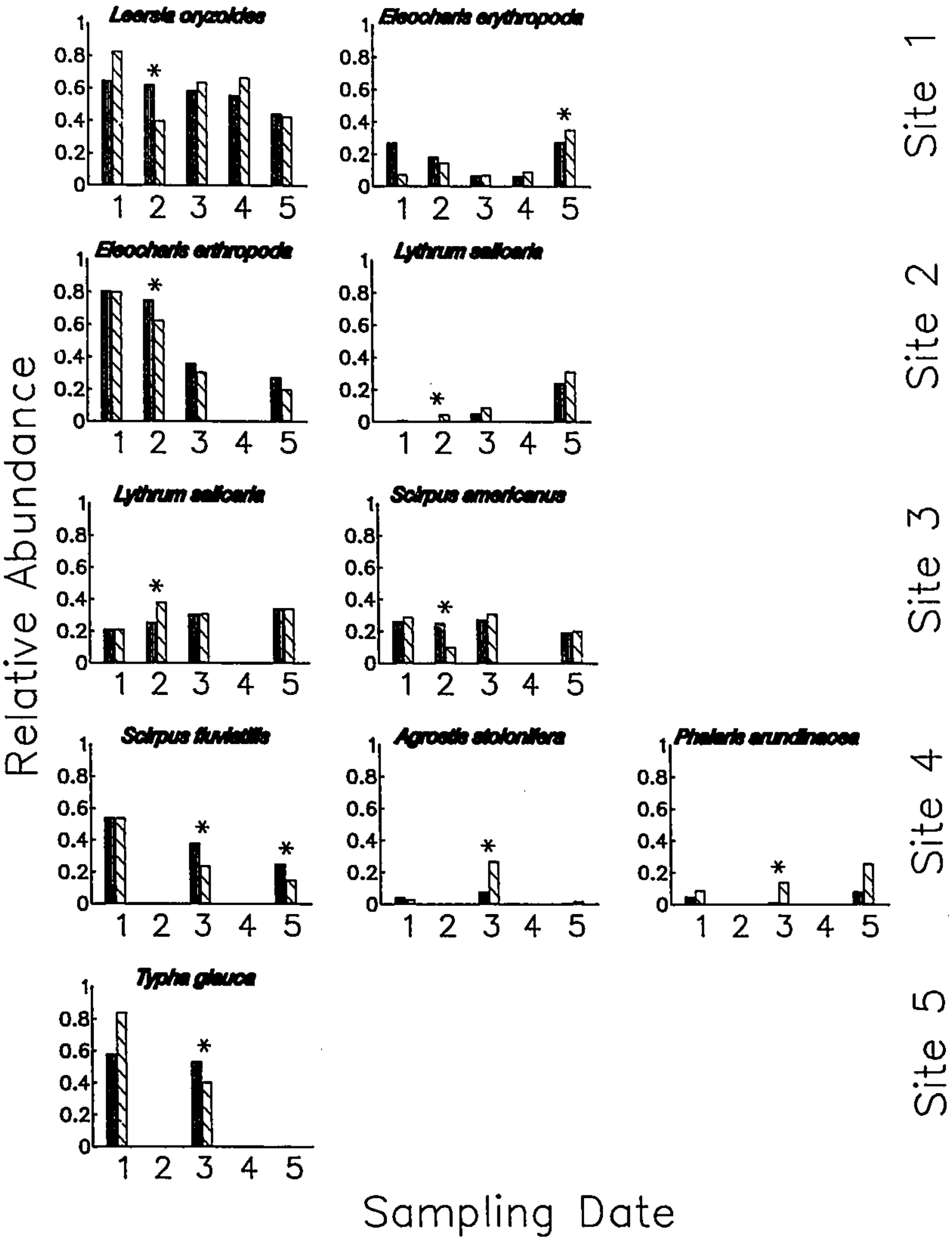

Leersia oryzoides
Eleocharis erythropoda
Site 1
Eleocharis erthropoda
Lythrum salicaria
Site 2
Lythrum salicaria
Scirpus americanus
Site 3
Scirpus fluviatilis
Agrostis stolonifera
Phalaris arundinacea
Site 4
Typha glauca
Site 5
Relative Abundance
Sampling Date
0
0.2
0.4
0.6
0.8
1
1 2 3 4 5
*

FIGURE 4.10

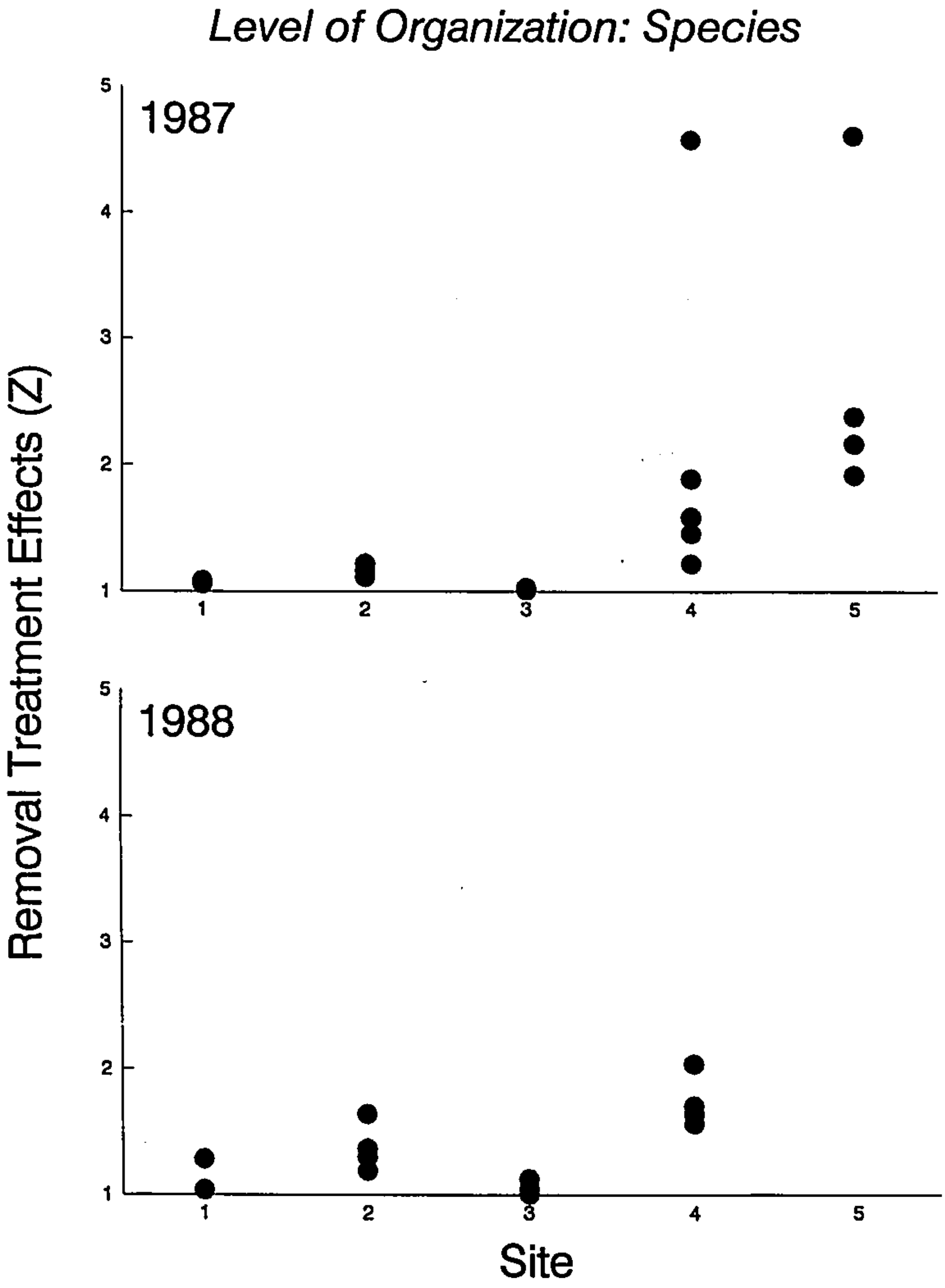

Level of Organization: Species
1987
1988
Removal Treatment Effects (Z)
Site
1
2
3
4
5
1
2
3
4
5

FIGURE 4.11

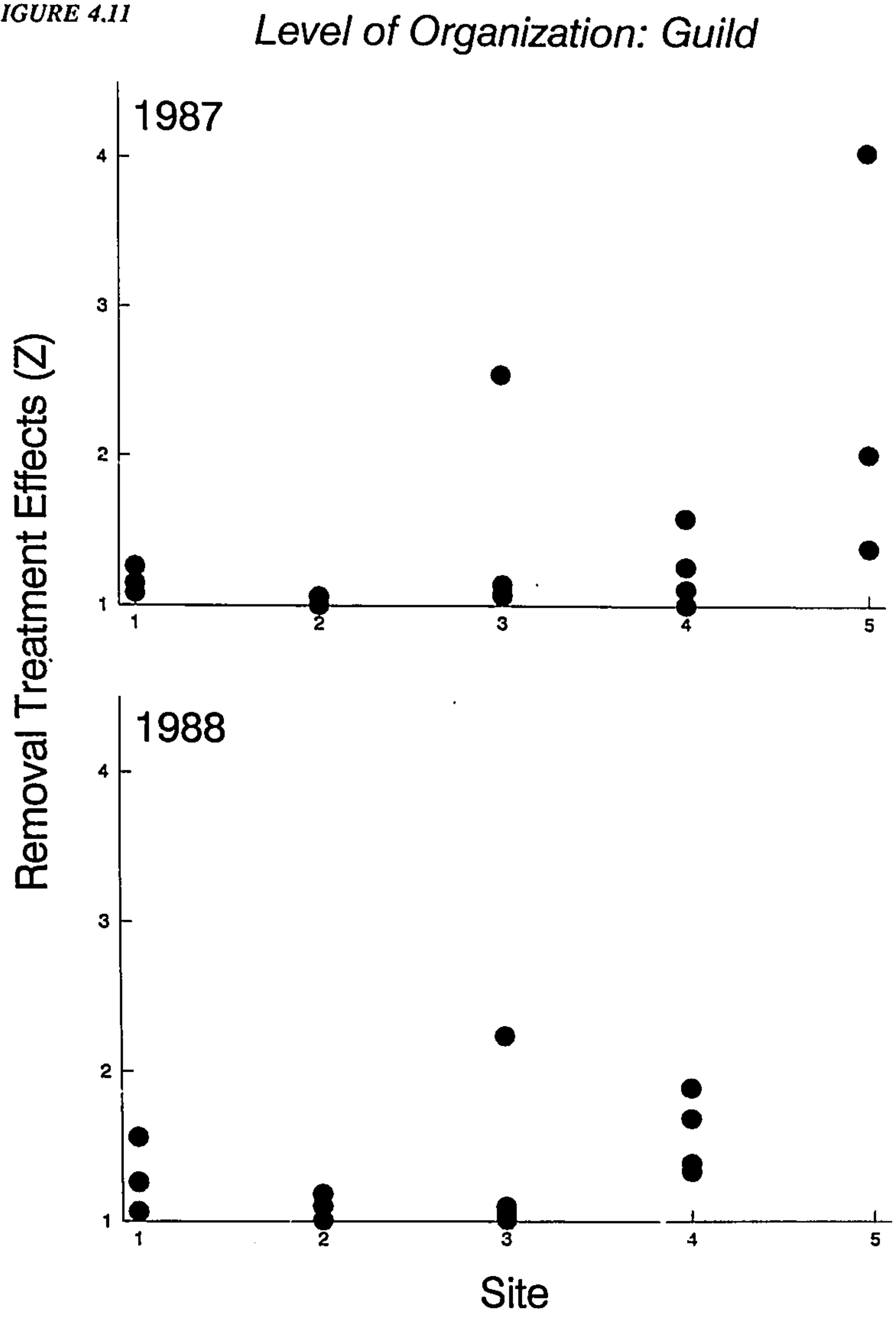

Level of Organization: Guild
1987
1988
Removal Treatment Effects (Z)
1
2
3
4
1
2
3
4
5
Site

FIGURE 4.12

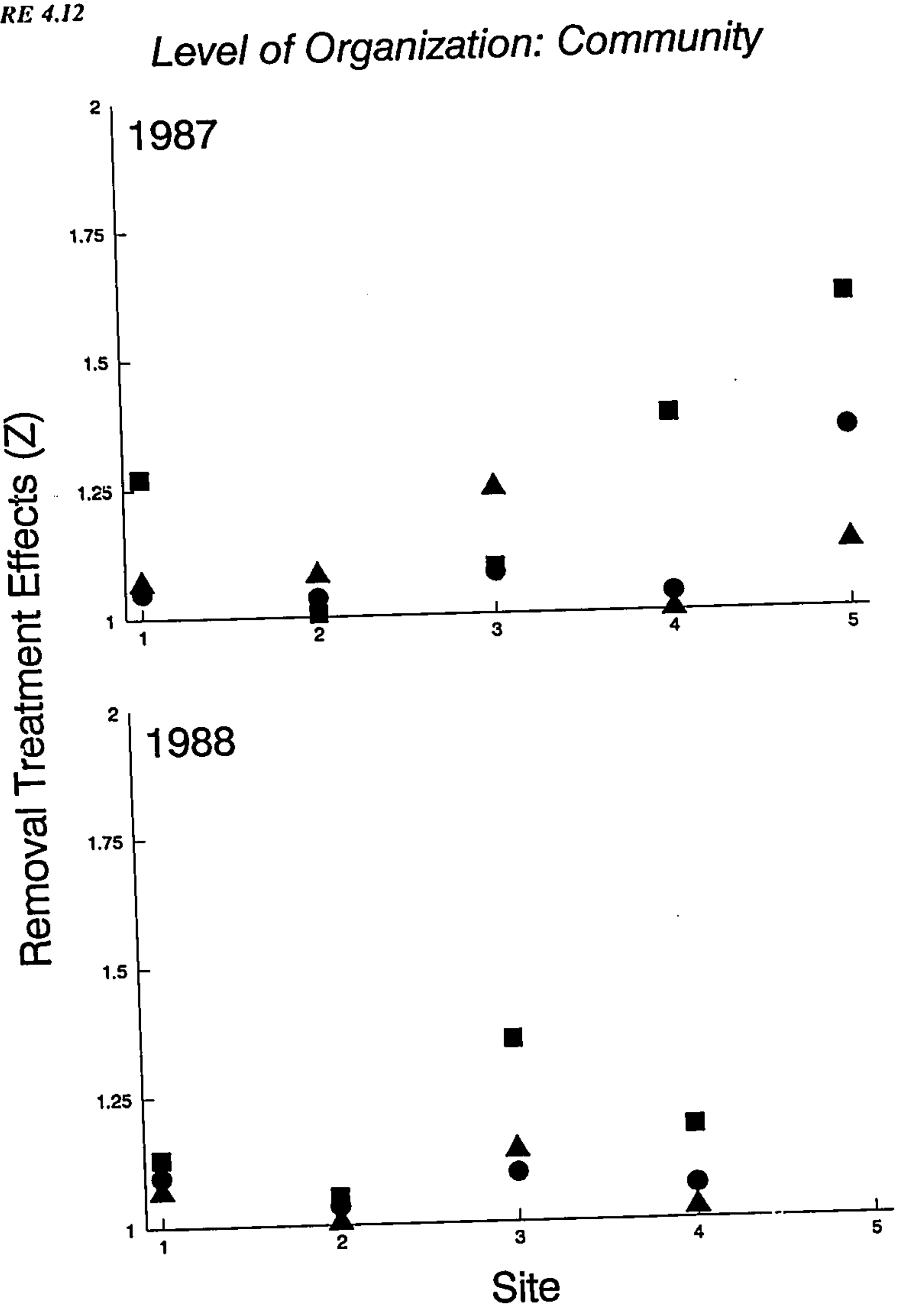
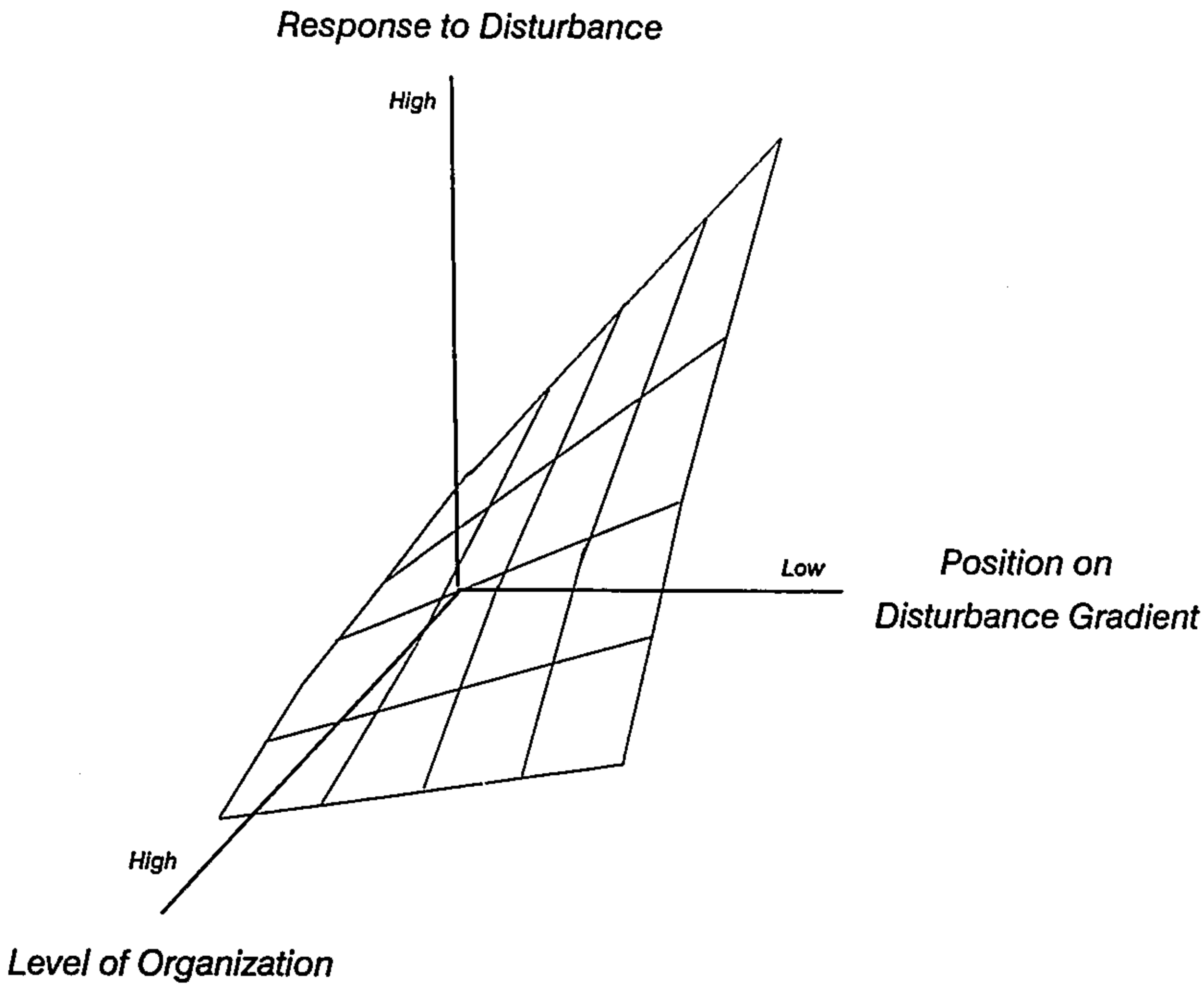

Level of Organization: Community
Removal Treatment Effects (Z)
1987
1988
2
1.75
1.5
1.25
1
1
2
3
4
5
Site

FIGURE 4.13


Response to Disturbance
High
Low
Position on
Disturbance Gradient
High
Level of Organization

CHAPTER 5

IMPLICATIONS FOR THE CONSERVATION AND MANAGEMENT OF WETLANDS

"The first rule of intelligent tinkering is to save all the parts."

Thomas Lovejoy

INTRODUCTION

Wetland losses due to human exploitation have been extensive in the last century. In spite of their many ecological, economic and social values, more than 50% of original wetland areas have been lost in the United States (Frayer *et al.* 1983) and Southern Canada (Lynch-Stewart 1983; Bardecki 1984; van Patter and Hilts 1985). Though attitudes have shifted to conservation rather than exploitation of wetlands, conflicts with agriculture, industry, cottage development and urban sprawl are inevitable. Therefore it is of primary importance that clear scientific criteria be utilized for setting priorities in selecting wetlands for conservation (McCormick 1978).

Much research into the functioning of wetlands has focussed on cyclically disturbed wetlands (e.g., van der Valk and Davis 1976, 1978; van der Valk 1981; Pederson and van der Valk 1984; Keddy and Reznicek 1982, 1986). Such wetlands require cyclical disturbance to permit regeneration from buried seeds. Much of this research has been done in prairie potholes (Pederson and van der Valk 1984). As a consequence, current wetland evaluation and management practices are often based on principles derived from this rather narrow range of wetland systems (e.g., Weller 1978; Pederson and van der Valk 1984). However, there is another class of wetlands typified by chronically low standing crop. The low standing crop of these wetlands may be the result of any number of factors (e.g., soil infertility, exposure to waves or ice scour, sand deposition) but, in general, these wetlands are characterized by plants of small stature (e.g., Keddy 1981, 1983, 1985; Boston and Adams 1987; Day et al. 1988; see examples in Table 5.1).

Low standing crop wetlands have been found to contain a wide array of species morphologies (e.g., reeds, isoetids, insectivorous species) and life history types (annuals and perennials)(Table 5.1). Table 5.1 shows that many low standing crop wetlands in eastern Canada contain isoetid and insectivorous plant species, both of which may be an indicator of poor soil fertility (Givnish *et al.* 1984; Boston and Adams 1987). Other low standing crop wetlands, such as those found at sites 1 and 2 at Luskville (see chapter 4), are dominated by ruderal plant species characteristic of highly disturbed sites. At present, we lack the necessary information to make appropriate conservation and management decisions concerning low standing crop wetlands.

If the ultimate goal of nature conservation is to preserve genetic diversity as stated in the World Conservation Strategy (International Union for the Conservation of Nature and Natural Resources 1980), then the most efficient means of reaching this goal is to conserve systems with high species richness and numerous rare species. In fact, traditional methods of ecological site evaluations have included species richness and number of rare species as important selection criteria (Margules and Usher 1981). More recent studies have emphasized community species composition as an important selection criterion, the goal being to preserve the maximum range of vegetation types (Nilsson 1986). The purpose of this chapter is to compare a large number of wetlands in eastern Canada which vary in standing crop and represent much of the variation in Temperate zone wetlands. The dependent variables of species richness, number of rare species, and number of vegetation types will be used to determine the relative value of low standing crop wetlands in wetland conservation. The management implications of the experimental microcosm (Chapter 3) and field (Chapter 4) studies will also be discussed for low standing crop wetlands.

CONSERVATION VALUE OF LOW STANDING CROP WETLANDS

Study Locations and Descriptive Surveys

The three primary study locations at Presqu'ile, Westmeath, and Luskville were described in chapter 1. Additional wetlands were also surveyed at Wilsons Lake in the Tusket River valley of Nova Scotia (43°55'N, 65° 53'W)(Wisheu 1987) and in 22 sites on the Canadian Shield in the Georgian Bay area of Ontario. These wetlands were found on lake shorelines and were also characterized by low standing crop. Corresponding high standing crop wetlands were not surveyed at these locations as was done at the three primary study locations. The descriptive surveys conducted at Presqu'ile, Westmeath and Luskville were described in chapter 1. At Wilsons Lake, the species present in each of 119 quadrats (0.25 m x 1.0 m) arranged along a standing crop gradient were determined during 1-26 August, 1984. In the Georgian Bay area a total of 57 0.5 m x 0.5 m quadrats were randomly located and sampled from 22 lakes during 19 - 27 August, 1987. In each quadrat, the species present within each of nine equivalent subdivisions were recorded. Quadrat standing crop at both of these additional locations was then determined as previously described in chapter 1. All voucher specimans were deposited at the DAO herbarium except those from the Georgian Bay locations which were deposited at the University of Toronto herbarium.

Species richness was calculated as the number of species per 0.25 m^2 quadrat and the results plotted against quadrat standing crop for all 401 quadrats. Nationally rare plant species were determined by reference to The Rare Vascular Plants of Canada (Argus and Pryer, unpubl.). The number of rare plant species per 0.25m^2 quadrat was then calculated and the results plotted against quadrat standing crop for all 401 quadrats. The methods used to determine the relationship between number of vegetation types and standing crop were previously described in chapter 1.

Species Richness, Number of Rare Species and Number of Vegetation Types

At very low standing crop (1 - 25 g/m^2) species richness varied from 2 - 12 species (Figure 5.1). As standing crop increased, species richness rapidly increased to a maximum of 12 - 20 species between 60 to 400 g/m^2. Above 400 g/m^2 species richness gradually declined to 2 - 6 species at high standing crop (>600 g/m^2). Figure 5.2 indicates that the low standing crop wetlands surveyed often had many nationally rare species while high standing crop wetlands did not (>600 g/m^2). Further, several of the rare species encountered are not only nationally rare but are threatened (e.g., *Sabatia kennedyana* Fernald) or endangered (e.g., *Coreopsis rosea* Nutt.) in Canada (Argus and Pryer, unpubl.). The rare species encountered in this study are listed in table 5.2 along with their current national status. In low standing crop wetlands, almost every wetland observed had a unique vegetation type as was described in chapter 1 (Figure 1.1).

These results clearly indicate that low standing crop wetlands have a much higher conservation value than do high standing crop wetlands. Therefore, if the goal of preserving genetic diversity (International Union for the Conservation of Nature and Natural Resources, 1980) is to be realized, then low standing crop wetlands must be given high conservation priority.

MANAGEMENT OF LOW STANDING CROP WETLANDS

There are three major threats to the low standing crop wetlands described in this thesis other than from direct habitat losses (e.g., to infilling, drainage, etc.). These are: (1) human disturbances (e.g., trampling, all-terrain vehicles), (2) eutrophication, and (3) invasion by *Lythrum salicaria*. Each of these will be discussed in turn with data included from the microcosm and field experiments where appropriate.

Human Disturbances

The low standing crop wetlands examined in this thesis can be divided into two classes to describe their predicted response to human disturbances: infertile and disturbed wetlands. Plant species of infertile wetlands share a number of characteristics important in their response to human disturbances. For instance, infertile wetland species are often evergreen (Boston 1986; Boston and Adams 1987; Keddy and Wisheu 1989; Wisheu and Keddy 1989), have relatively low growth rates (Shipley and Keddy 1988) and are small (Wisheu 1987). Therefore, these species can be classified as stress-tolerators (*sensu* Grime 1977; Boston and Adams 1987). In general, habitats dominated by stress-tolerators are sensitive to and recover very slowly from disturbance events (Thorhaug 1980), in part because of the inherently slow growth rates of stress tolerators (Grime 1979). For example, Hylgaard and Liddle (1981) demonstrated that a Danish sand dune plant community experienced a 50% reduction in plant cover and a 75% reduction in number of species with a relatively light trampling regime of 200 passages by one person spread over 3-4 months. Keddy and Wisheu (1989) found that all-terrain vehicles eliminated 90% of one of the largest remaining stands of a threatened infertile wetland species, *Sabatia kennedyana*. Further, Keddy *et al.* (1989) found that infertile wetland seed banks were reduced in sites damaged by all-terrain vehicles (550 seeds/m^2 in damaged sites versus 10,000 seeds/m^2 in intact sites). Together, these studies demonstrate that infertile wetlands are very sensitive to the effects of human disturbances both in the initial damage phase and in the slow recovery period afterwards.

Low standing crop sites may also occur in relatively fertile conditions in highly disturbed areas. Sites 1 and 2 at the Luskville study location are examples of these types of wetlands. Typically, these wetlands are dominated by annual species with rapid growth rates and large seed banks. The results from chapter 4 indicate that low standing crop wetlands dominated by annual species are tolerant of disturbances such as the removal of above ground vegetation. Thus, the sensitivity of low standing crop wetlands to disturbance is variable. This variability emphasizes the point raised earlier - wetland management based on the principles of a narrow range of wetlands (i.e., cyclically disturbed wetlands) are not appropriate for all wetlands.

Eutrophication

Many low standing crop wetlands are also being subjected to increasing eutrophication pressures as a result of agricultural runoff, sewage and, in some cases, by direct fertilizer applications by wetland managers. The negative effects of nutrient loading on aquatic communities have been well documented (e.g., IJC 1980), but the effects of eutrophication on wetlands have received less attention. Previous studies have indicated that nutrient loading in previously infertile systems has the effect of reducing species richness (Silvertown 1980; Tilman 1987) and converting unique vegetation types to types which are more commonly observed (Ehrenfeld 1983; Morgan and Phillip 1986; Tilman 1987). Many rare species which are usually of small stature will also be competitively eliminated by large, rapidly growing species such as *Typha spp.* (Wilson and Keddy 1986; Gaudet and Keddy 1988). The 'centrifugal organization' model of wetlands shown in Figure 1.1 illustrates these points. As fertility and standing crop increase, vegetation types converge on the central region of *Typha* dominance. Because *Typha* is a large clonal perennial, it competitively eliminates the smaller, less aggressive low standing crop wetland species including those species which are rare, threatened or endangered (Table 5.3). Therefore, species typical of infertile wetlands will progressively disappear from the landscape as eutrophication continues.

The effects of fertility level on species richness in a wetland microcosm experiment was described in chapter 3. The results indicated that by the end of the second growing season, species richness was much lower in the 'fertile' treatments for all twelve habitat treatments (Figure 3.3). Qualitative observations suggest that it was the smaller plant species which were being eliminated from the 'fertile' treatments by larger, more aggresive species. Therefore, this study demonstrated the potential negative effects of eutrophication on low standing crop wetlands.

Lythrum salicaria

Lythrum salicaria is a tall, perennial European species that is rapidly invading native wetlands and forming dense, self-perpetuating stands. At present, approximately 190,000 hectares of wetlands are lost to *L. salicaria* per year in the United States alone (Keddy 1988). Further, it appears that not only is species richness being reduced in native wetlands by invasion of *L. salicaria*, but many rare species are also being eliminated. Personal observations indicates that *L. salicaria* can invade a wide range of wetland habitats including wet ditches, riverine shorelines and cattail marshes. However, it is not known what impacts, if any, *L. salicaria* is likely to have on low standing crop wetlands.

In the microcosm experiment described in chapter 3, *L. salicaria* was included in all treatments. In the first growing season (1987), *L. salicaria* became established in most treatments but, in general, was not a major component of the vegetation. However, by the second growing season (1988), *L. salicaria* had dramatically increased in abundance in all treatments except those that were flooded for all or part of the growing season (Figure 5.3). In terms of absolute abundance, *L. salicaria* produced more biomass in 'fertile' treatments. However, relative to the other species present, *L. salicaria* experienced the same dramatic increases in abundance in both the 'fertile' and 'infertile' treatments. Given that mature *L. salicaria* plants can survive for up to 20 years and produce >2,000,000 seeds per year (Keddy 1988), it seems certain that these trends are likely to continue until most other species have been eliminated.

Further evidence from field experiments confirms the threat posed by *L. salicaria* to low standing crop (and high standing crop) wetlands. Figure 5.4 shows that in a wide range of wetland habitats along the Ottawa River; *L. salicaria* seedlings were far more abundant than seedlings of native species. Only in the deeper water, *Sparganium* dominated habitats were *L. salicaria* seedlings occurring in relatively low numbers. Figure 5.5 shows that *L. salicaria* has been increasing in abundance in a wide range of native wetland habitats over the last three growing seasons. These increases occurred in both low standing crop (e.g., *Eleocharis erythropoda* site) and high standing crop (e.g., *Scirpus fluviatilis* site) wetlands and in both disturbed and control treatments. Together, the results of the microcosm and field experiments demonstrate that *L. salicaria* poses a major threat to low standing crop wetlands.

IMPLICATIONS

Most wetland evaluations tend to favour fertile, high standing crop wetlands particularly in cases where low standing crop wetlands do not have rare species (e.g., Ontario Ministry of Natural Resources 1983). Similarly, management strategies are often designed to produce high standing crop wetlands (e.g., by fertilization) as a means of maximizing wildlife productivity (e.g., Weller 1978). However, the results presented in this chapter clearly demonstrate that low standing crop wetlands have high conservation value and therefore conservation priorities and management strategies need to adjusted to better reflect this value and to better reflect the priorities of the World Conservation Strategy.

The three major threats to low standing crop wetlands outlined in this chapter are not easily eliminated. However, several measures are possible. (1) In areas where significant low standing crop wetlands occur, particularly infertile wetlands, human traffic must be kept at a low level and the use of all-terrain vehicles eliminated altogether. In provincial and federal parks, this measure can best be achieved by declaring infertile, low standing crop wetlands as nature reserves and providing adequate buffer zones. (2) To preserve low standing crop wetlands in their present state requires dealing with the indirect eutrophication effects from agricultural runoff and sewage. This is a difficult problem for the wetland manager. Purchasing buffer zones around low standing crop wetlands is one possible measure which could prevent unwanted nutrient enrichment. Managing watersheds to minimize eutrophication is discussed in IJC (1980). (3) Perhaps the most difficult problem with regards to low standing crop wetlands is how to prevent the invasion and establishment of *Lythrum salicaria*. No reliable means of eliminating *L. salicaria*, once present, has yet been demonstrated, although prolonged flooding may be an effective measure in certain habitats. However, flooding and other drastic treatments (e.g., chemical spraying) are likely to have severe negative impacts on the native vegetation and thus are probably unsuitable. With possible biological control of *L. salicaria* years away, it seems that preventative measures are the only measures likely to be effective. These include: (i) regular surveys of low standing crop wetlands to find *L. salicaria* before it becomes established and (ii) immediate elimination of *L. salicaria* when found (e.g., by handpulling or contact herbicides).

Figure 5.2 speaks louder than any words could on the essential importance of conserving low standing crop wetlands to protect rare and endangered species. This function of wetlands, one of the three pillars of the World Conservation Strategy, needs greater emphasis. Changing public attitudes about the value of low standing crop wetlands, and reducing the threats to them are high priorities to enable us to develop a truly representative system of protected wetland habitats in Canada.

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Table 5.1. Variation in life form and life history type in various wetlands with low standing crop. Species nomenclature follows Gleason and Cronquist (1963) except where authorities are given.

Low standing crop wetlands	*Annual species*	*Reeds*[g]	*Isoetids*[h]	*Insectivorous species*[i]
Nova Scotia Gillfillan L.[b]		*Eleocharis smallii* Britt. *E. tenuis* *Equisetum arvense* *E. fluviatile* *Juncus filiformis*	*Eleocharis acicularis* *Eriocaulon septangulare* *Gratiola aurea* *Isoetes acadiensis* Kott. *Juncus pelocarpus* *Lobelia dortmanna* *Lycopodium inundatum*° *Ranunculus reptans* L. *Sabatia kennedyana* *Xyris difformis* Chapm.°	*Drosera intermedia* *D. rotundifolia* *Sarracenia purpurea* *Utricularia cornuta* *U. geminiscapa* *U. subulata* *U. vulgaris*
Wilsons L.[c]	*Elatine minima*	*Eleocharis robbinsii* *E. smallii* Britt. *E. tenuis* *Equisetum fluviatile* *Juncus filiformis* *Scirpus validus*	*Eleocharis acicularis* *Eriocaulon septangulare* *Isoetes tuckermani* A. Br. *Juncus pelocarpus* *Lobelia dortmanna* *Lycopodium inundatum*° *Myriophyllum tenellum* *Ranunculus reptans* L. *Sabatia kennedyana* *Xyris difformis* Chapm.°	*Drosera intermedia* *D. rotundifolia** *Utricularia cornuta* *U. purpurea** *U. resupinata* *U. vulgaris**
Ontario Axe L.[d]	*Bidens* sp.	*Eleocharis smallii* Britt. *Juncus filiformis* *Scirpus torreyi*	*Eriocaulon septangulare* *Juncus pelocarpus* *Lobelia dortmanna* *Lycopodium inundatum*° *Myriophyllum tenellum* *Xyris difformis* Chapm.°	*Drosera intermedia* *D. rotundifolia** *Utricularia cornuta* *U. gibba* *U. intermedia* *U. purpurea* *U. resupinata* *U. vulgaris*
Ottawa R[e]		*Eleocharis erythropoda* *E. smallii* Britt. *Equisetum fluviatile* *Scirpus acutus* *S. americanus*	*Eleocharis acicularis* *Eriocaulon septangulare* *Isoetes echinospora* *Juncus pelocarpus* *Myriophyllum tenellum* *Potamogeton gramineus* *Ranunculus reptans* L. *Sagittaria graminea*	
Presqu'ile[f]	*Aristida longespica* *Bidens cernua* *B. frondosa* *Panicum flexile* *Scleria verticillata* *Sporobolus vaginiflorus*	*Eleocharis elliptica* Kunth. *Equisetum fluviatile* *E. variegatum* *Juncus alpinoarticulatus* Choix. ex. Vill. *J. balticus* *Rhynchospora capillacea* *Scirpus americanus*	*Carex aurea*° *Parnassia glauca*°	*Utricularia minor*
Westmeath[f]	*Bidens cernua* *B. frondosa* *Fimbristylis autumnalis* *Gratiola neglecta* *Impatiens capensis* Meerb. *Ludwigia palustris* *Polygonum lapathifolium* *P. neglectum* Bess. *P. persicaria* *Sporobolus vaginiflorus*	*Eleocharis elliptica* Kunth. *E. smallii* Britt. *Equisetum fluviatile* *Scirpus acutus* *S. americanus*	*Eleocharis acicularis* *Eriocaulon septangulare* *Juncus pelocarpus* *Ranunculus reptans* L.	*Drosera intermedia*** *Utricularia cornuta*** *U. vulgaris***

Low standing crop wetlands	*Annual species*	*Reeds*[g]	*Isoetids*[h]	*Insectivorous species*[i]
Quebec Luskville[f]	*Bidens cernua* *B. frondosa* *Callitriche deflexa* *Cyperus aristatus* *C. diandrus* *C. rivularis* *Eleocharis obtusa* Sch. *Gnaphalium uliginosum* *Juncus bufonius* *Lindernia dubia* *Panicum capillare* *Xanthium strumarium*	*Eleocharis acicularis* *E. erythropoda* *E. smallii* Britt. *Equisetum fluviatile* *Juncus bufonius* *J. effusus* *J. nodosus* *Scirpus acutus* *S. americanus*	*Eleocharis acicularis*	

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[a] Species nomenclature follows Gleason & Cronquist (1963) except where authorities are given.

[b] Unpublished data analysed in Keddy (1984).

[c] Wisheu (1987); see also Keddy (1985).

[d] Keddy (1981); see also Keddy (1983).

[e] Day *et al.* (1988).

[f] C. Gaudet, D. Moore & P. Keddy (unpublished data).

[g] As defined in Day *et al.* (1988); 'leafless' shoots.'

[h] From Table 1 in Boston & Adams (1987); ° similar species.

[i] * personal observations; ** unpublished reports.

Table 5.2. Mean macronutrient levels (ppm) and mean above ground standing crop (g/0.25 m^2)(n=15) in each of five wetland sites sampled at each of three study locations (Presqu'ile, Westmeath and Luskville)[1].

Location	Standing Crop	NO_3	P	K	Mg
Presqu'ile					
1	17.8	7.33	1.13	17.3	43.3
2	67.0	9.07	1.33	34.5	69.9
3	86.8	7.80	1.00	35.2	53.9
4	173.1	8.93	1.00	52.7	63.1
5	421.6	9.20	4.20	15.5	32.9
Westmeath					
1	4.0	18.00	3.27	36.7	74.3
2	54.5	7.07	5.27	38.3	130.5
3	131.9	7.87	19.40	62.5	243.7
4	163.0	16.40	10.93	59.0	345.0
5	315.8	27.33	25.73	93.4	236.9
Luskville					
1	32.7	6.93	6.80	56.9	191.2
2	40.0	4.93	8.73	62.0	187.3
3	92.3	5.07	5.27	132.3	326.6
4	124.6	11.60	9.67	150.3	383.0
5	277.7	15.73	15.67	159.4	386.9

[1] the data from the three study locations were collected at different points in the growing season and in different years and therefore caution should be exercised when comparing between Presqu'ile, Westmeath and Luskville.

Table 5.3. The current status of rare species from over twenty wetlands sampled in Ontario, Quebec and Nova Scotia. Species nomenclature follows Gleason & Cronquist (1963) except where authorities are given.

Location	Species	Status
Nova Scotia		
Wilsons Lake	*Coreopsis rosea*	***
	Solidago galetorum	*
	Habenaria flava	*
	Hydrocotyle umbellata	***
	Panicum longifolium	*
	Rhexia virginica	*
	Sabatia kennedyana	**
	Xyris difformis Chapm.	*
Ontario		
Georgian Bay area	*Panicum rigidulum* Nees. var. *rigidulum*	*
	Rhexia virginica	*
	Xyris difformis Chapm.	*
Presqu'ile	*Aristida longespica*	*
	Scleria verticillata	*
Westmeath	---	--
Quebec		
Luskville	*Lindernia dubia*	*

* Nationally rare
** Nationally threatened
*** Nationally endangered

FIGURE CAPTIONS

Figure 5.1. Species richness versus standing crop in 401 0.25 m^2 quadrats from wetlands located in Ontario (Presqu'ile Provincial Park, Westmeath and near Georgian Bay), in Quebec (Luskville marshes) and in Nova Scotia (Wilsons Lake).

Figure 5.2. Number of nationally rare species versus standing crop in each of 401 quadrats from wetlands located in Ontario, Quebec and Nova Scotia.

Figure 5.3. Percent *Lythrum salicaria* cover changes over a two year period in twelve wetland habitat treatments each duplicated at two fertility levels ('infertile', 'fertile')(n = 5). See the text of chapter 3 for a more complete description of the wetland habitat treatments and the experimental design.

Figure 5.4. Densities (No./0.25 m^2) of the three most common species of seedlings in eight vegetation types found along the Ottawa River (data from Day *et al.* 1988). Dominant genera in each of the vegetation types are indicated.

Figure 5.5. Percent *Lythrum salicaria* cover changes over a three year period in each of five vegetation types along the Ottawa River. The arrow indicates the timing of a complete removal of above-ground vegetation in the disturbed treatments (n = 5). The dominant species in each vegetation type are indicated. Standing crop and soil fertility are lowest at the top left of the figure and increase to the highest levels at the bottom right of the figure.

FIGURE 5.1

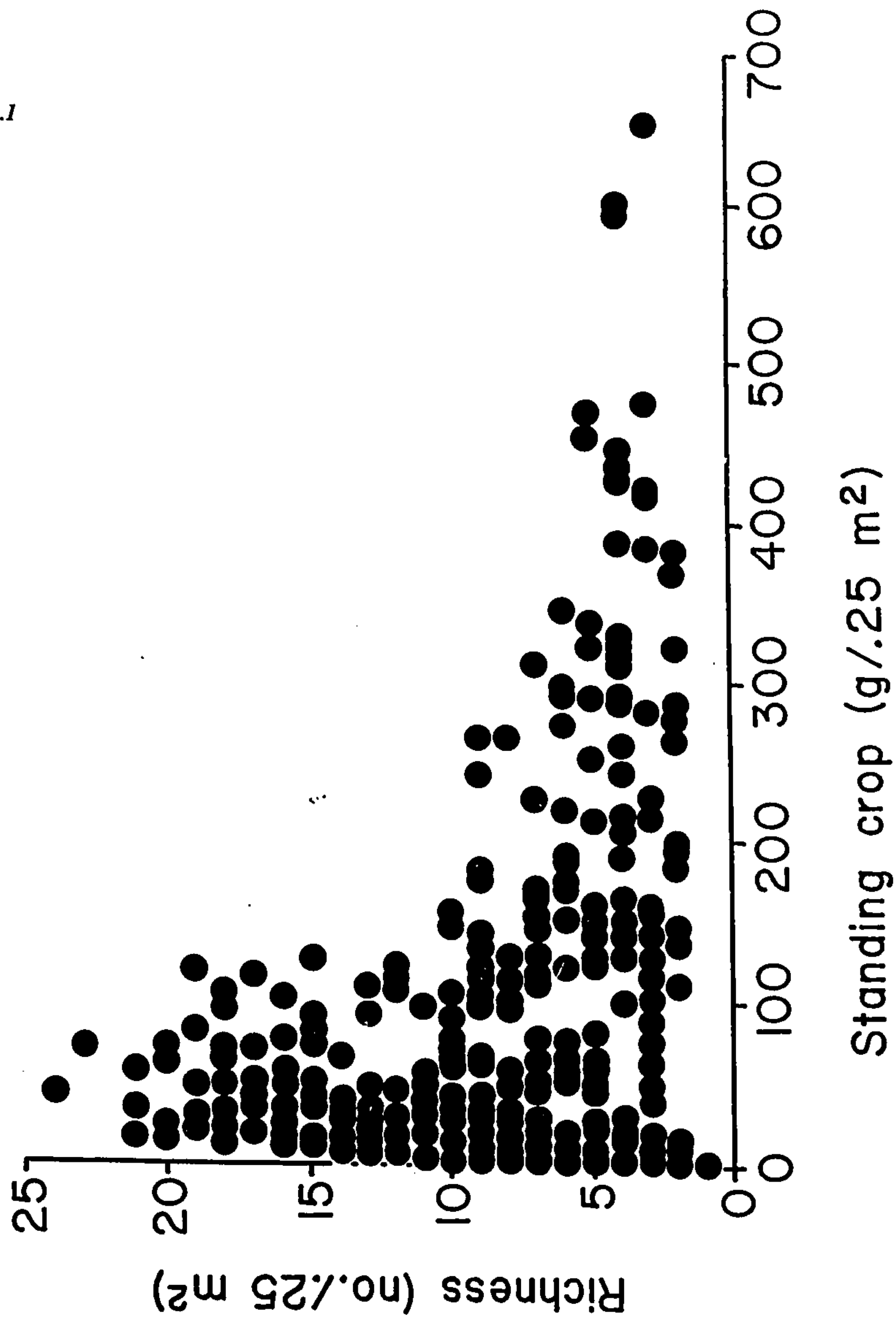

Richness (no./.25 m²)
0
5
10
15
20
25
Standing crop (g/.25 m²)
0
100
200
300
400
500
600
700

FIGURE 5.2

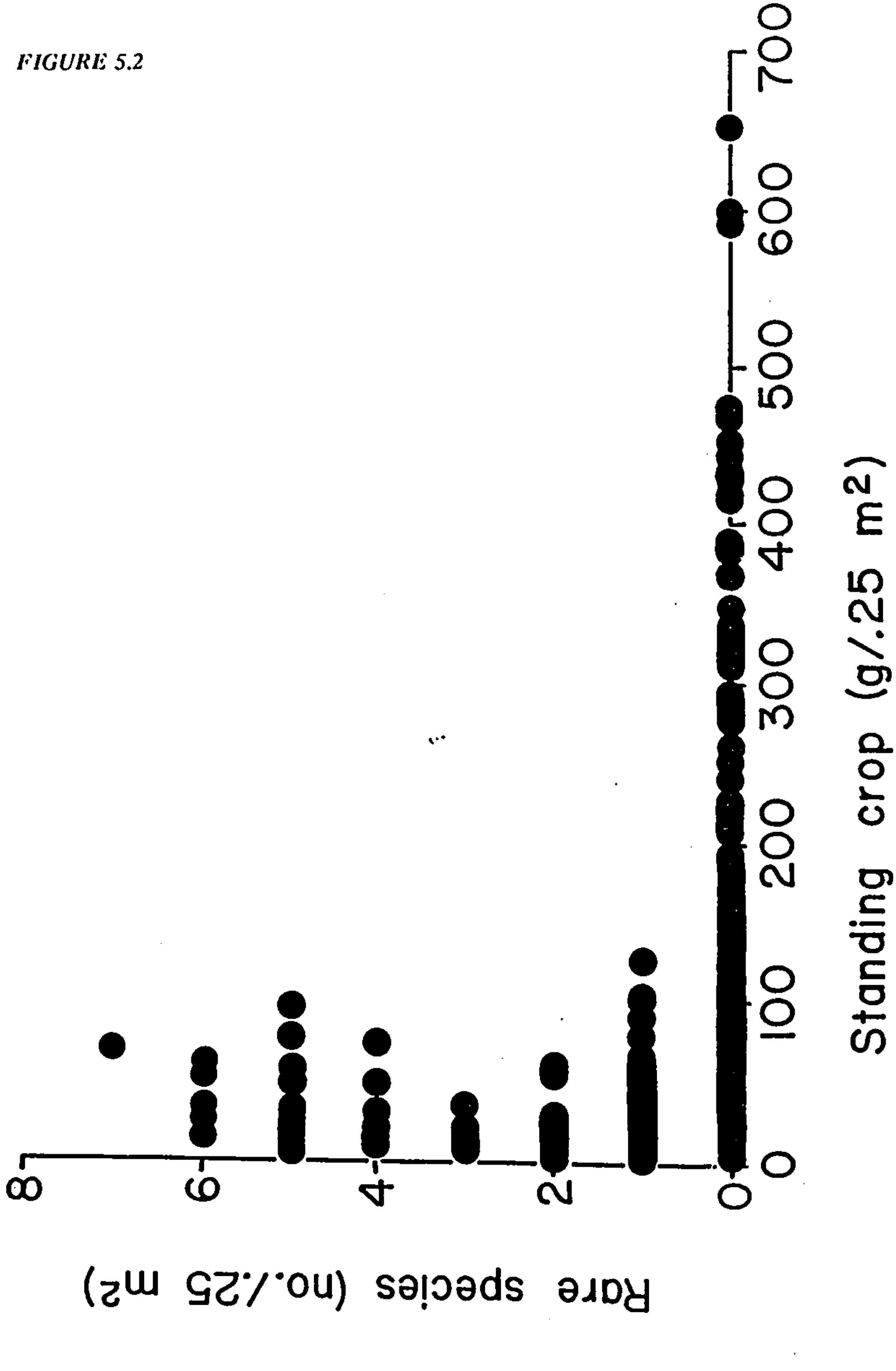
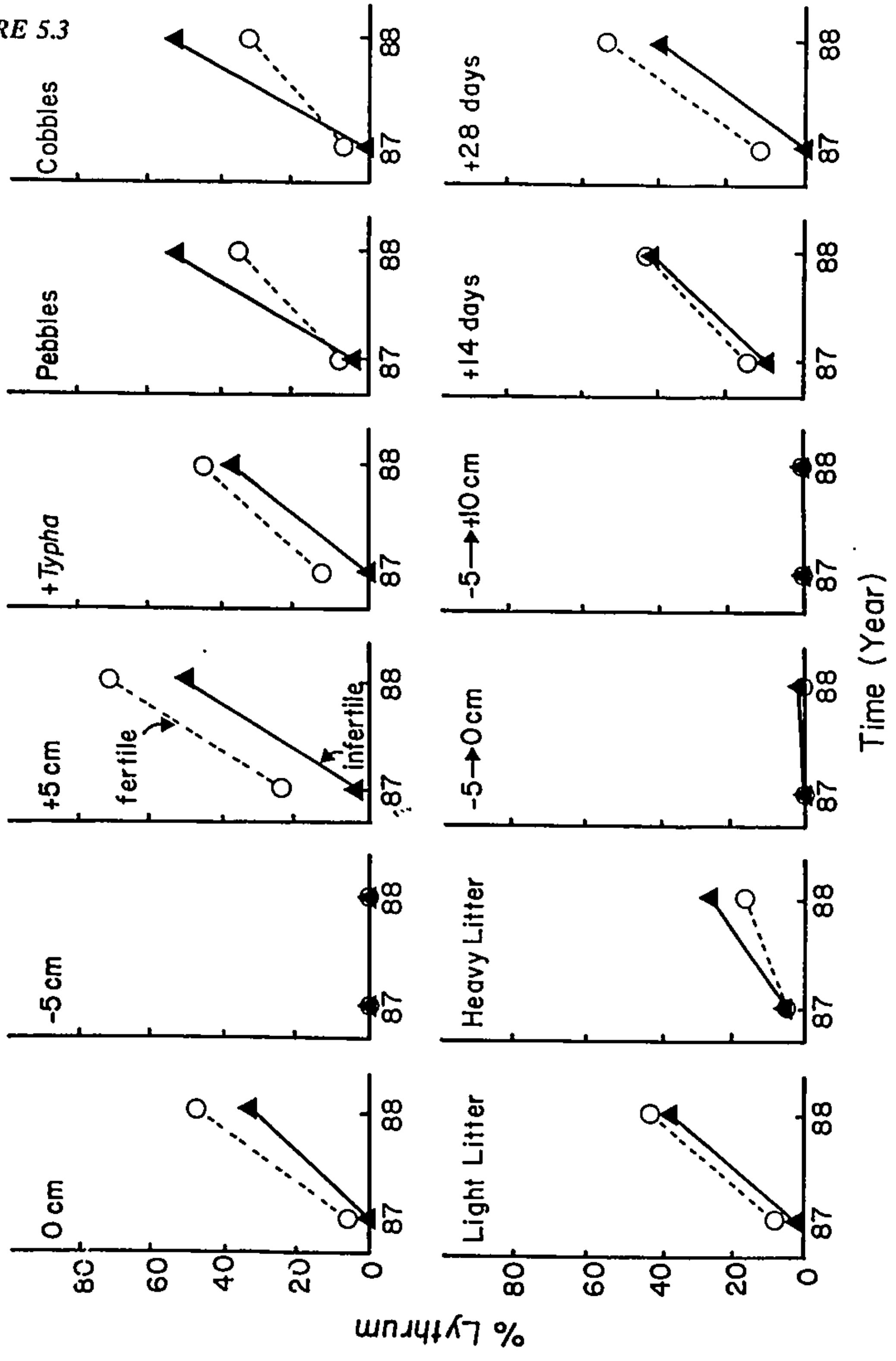

Rare species (no./.25 m²)
0
2
4
6
8
Standing crop (g/.25 m²)
0
100
200
300
400
500
600
700

FIGURE 5.3



0 cm
-5 cm
+5 cm
fertile
infertile
+*Typha*
Pebbles
Cobbles
Light Litter
Heavy Litter
-5→0 cm
-5→+10 cm
+14 days
+28 days
% Lythrum
0
20
40
60
80
87
88
Time (Year)

FIGURE 5.4

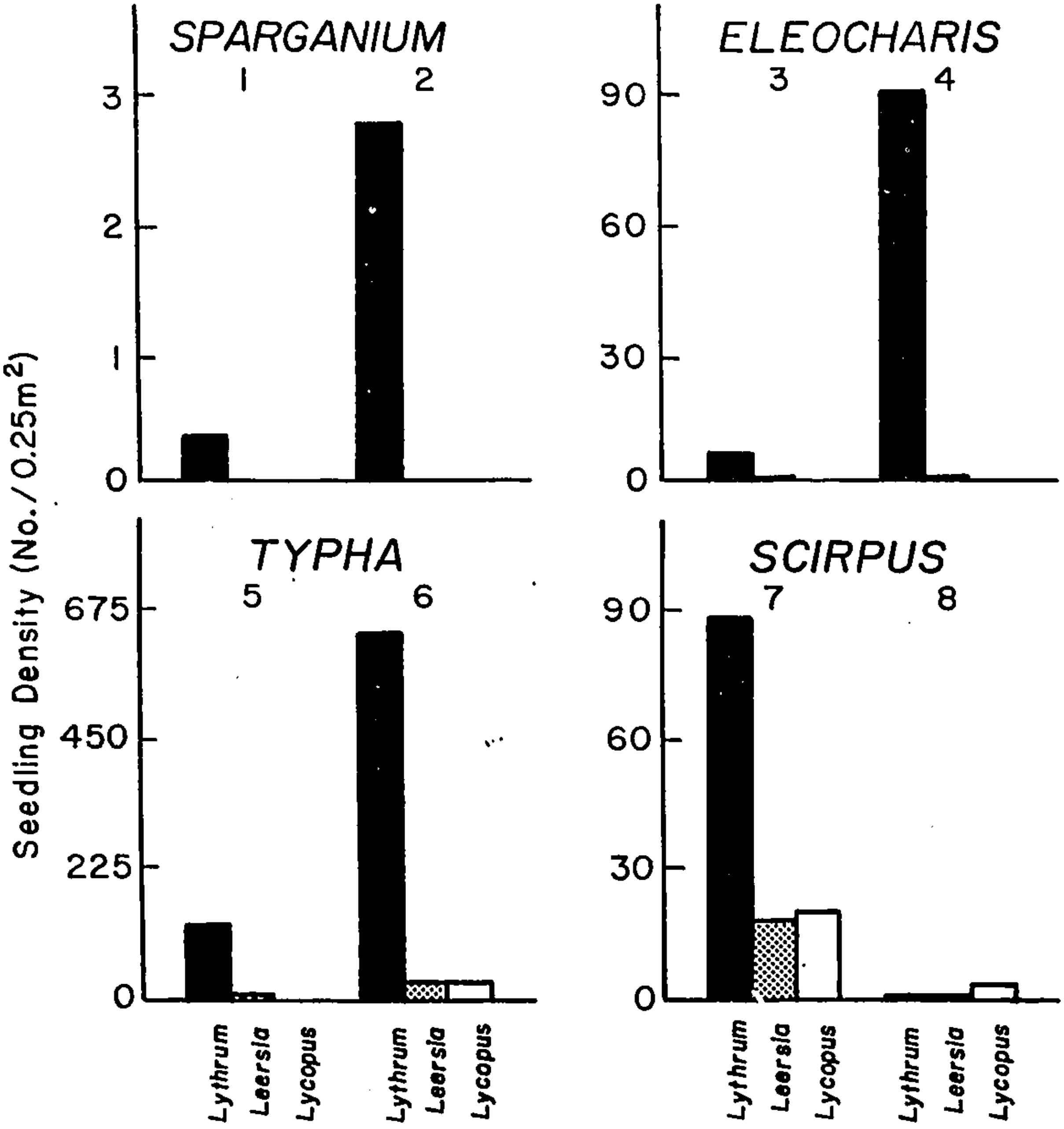
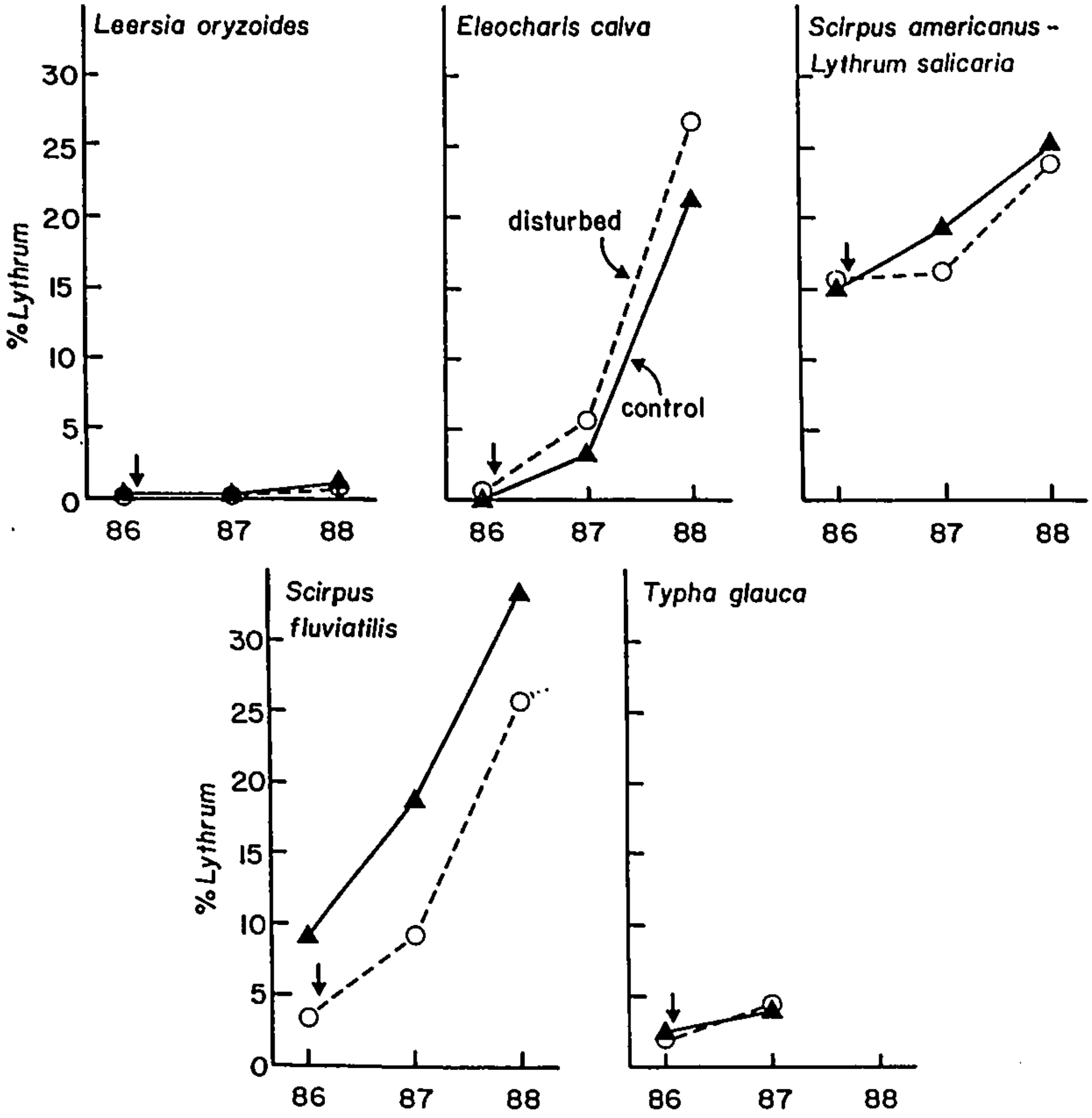

SPARGANIUM
1
2
ELEOCHARIS
3
4
TYPHA
5
6
SCIRPUS
7
8
Seedling Density (No./0.25m²)
3
2
1
0
90
60
30
0
675
450
225
0
90
60
30
0
Lythrum
Leersia
Lycopus
Lythrum
Leersia
Lycopus
Lythrum
Leersia
Lycopus
Lythrum
Leersia
Lycopus

FIGURE 5.5



Leersia oryzoides
Eleocharis calva
Scirpus americanus - Lythrum salicaria
Scirpus fluviatilis
Typha glauca
% Lythrum
0
5
10
15
20
25
30
86
87
88
disturbed
control

GENERAL SUMMARY

The first major conclusion from this thesis is that models of pattern and process in plant communities have limitations defined by the level of organization for which they are applicable. Grime's species richness/standing crop model has received much support in studies which considered a broad range of vegetation types, that is, at the among vegetation types level of organization. However, the model was found to have no predictive power when a single vegetation type was considered. At this finer-grained level of organization, other features of the local environment such as microsite differences or time since the most recent disturbance were shown to be more useful variables for predicting species richness. Similarly, at a much coarser-grained level of organization, the global level, the independent variables which have been shown to best predict species richness and number of vegetation types were climatic variables such as evapotranspiration and geographical variables such as degree of isolation.

The second major conclusion from this thesis is that processes acting at one level of organization are not likely to be transmitted to higher levels of organization. For example, a single disturbance event in wetlands was shown to have large effects on the abundance of individual species, particularly in high standing crop wetlands. However, the effects of the disturbance treatment were reduced at the next highest level of organization, the guild level. The disturbance treatment had little effect on community level variables such as species richness and evenness. In essence, increases in the abundance of one species were "balanced" by decreases in the abundance of another species from the same guild. Thus, the effects of the disturbance treatment were not transmitted to higher levels of organization.

The two conclusions reached above are two of the major principles embodied by hierarchy theory. Many of the past sterile debates in ecology occurred because groups studying different scales interacted without first specifying the level of organization which they were exploring. Future progress in ecology hinges on the willingness of ecologists to accept the principles of hierarchy theory, and to use these principles in developing models of pattern and process.