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INTERSPECIFIC COMPETITION AND SPECIES DISTRIBUTIONS ALONG AN ENVIRONMENTAL GRADIENT:
FIELD EXPERIMENTS IN A LAKESHORE PLANT COMMUNITY

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ABSTRACT

The role of interspecific competition in controlling species distributions along a natural environmental gradient was examined. Both traditional methods, i.e. the comparison of ecological and physiological response curves, and new approaches, suggested by current models of species diversity, were used.

Vascular plant species were shown to be differentially distributed along a gradient of exposure to wave action in six small central Ontario lakes. The exposure gradient is characterized at one end by wave-washed, sparsely vegetated nutrient-poor beaches and at the other by sheltered, densely vegetated, nutrient-rich bays. Only the plant community within a narrow range of depth, the seasonally flooded zone, was considered. Species distributions along the exposure gradient were found to be similar regardless of the particular lake considered, suggesting that the mechanism producing species distributions along the exposure gradient is general to small lakes.

An experiment was conducted to test whether twelve species with different distributions along the exposure gradient also had different physiological response curves when grown without neighbours along a range of substrate types taken from the gradient. Species had significantly similar physiological response curves, suggesting that differential field distributions could not be attributed to different physiological responses alone.

A second experiment measured the physiological response curves of nine species grown singly along the natural exposure gradient at Axe Lake, Ontario. Species again had significantly similar physiological response curves, suggesting that differential field distributions are caused by interspecific competition. Both experiments indicate that shoreline species accumulate biomass most rapidly on sediments from sheltered bays.

The hypothesis that the importance of competition varied along the exposure gradient was tested by growing three species in cleared and uncleared plots at seven locations along the gradient at Axe Lake. The difference in biomass accumulated by ramets grown in cleared and uncleared plots was used as a measure of the intensity of diffuse competition at each location. Diffuse competition was found to be positively correlated with both standing crop and position along the exposure gradient. Diffuse competition was most intense in undisturbed, nutrient-rich habitats that support high standing crop values.

The last study tested for a correlation between species distributions along the gradient and their relative competititve abilities. Competitive abilities were measured in a diallel experiment, in which seven species were grown in all possible pairwise combinations at a starting density of two ramets per pot. The amount of biomass accumulated by

each species was found to vary according to the identity of its interspecific neighbours, indicating that species had significantly different competitive abilities. Competitive ability was found to be significantly correlated with mean position on the exposure gradient: dominant species occupied undisturbed, nutrient-rich shores while subordinates occurred in disturbed, nutrient-poor habitats.

In summary, shoreline plant species have different distributions but similar physiological response curves along the exposure gradient: species grown singly along the gradient accumulate biomass most rapidly on undisturbed nutrient-rich shores. The intensity of diffuse competition is greatest in such habitats, and the species found there tend to be those with relatively high competitive abilities. These results suggest that competition for space on sheltered shores may be an important force in producing species distributions along the exposure gradient.

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GENERAL INTRODUCTION

Ecology has been described as the study of the distribution and abundance of organisms in nature. The potential role of competition in regulating abundance and distribution has been recognized since the earliest writings in evolutionary ecology (Darwin 1859) and has generated considerable research, most recently reviewed by Schoener (1983) and Connell (1983).

A powerful tool for exploring how competition may determine species distributions is the experimental study of communities with zonation patterns along environmental gradients. One of the earliest examples of this approach is by Connell (1961), who used removal experiments to show that the distribution of one barnacle species was controlled by competition from a second species. Since then, many studies have tested for competition in controlling species distributions in the rocky intertidal. Lubchenco (1980) also used removal experiments to show how competition for space could determine algal distributions. Paine (reviewed in 1984) investigated the relationship between competition and predation in the rocky intertidal and suggested that competition could be reduced by the presence of a predator. Experiments in the rocky intertidal zone have shown the potential role of competition in controlling species distributions along an environmental gradient.

Some studies of terrestrial plant communities use purely descriptive data to infer that competition controls species distributions along gradients. Differential distributions have been taken as evidence of competitive displacement by Whittaker (1965) and Werner and Platt (1976). Without experimentation, however, it is difficult to attribute differential field distributions either to competitive displacement or to different physiological requirements.

A common method used to distinguish between physiological requirements and interspecific competition as causes of differential distributions is the measurement of the physiological response curves of component species. Ellenberg (1953) proposed the term physiological response curve to describe the growth of a species along a gradient in the absence of interspecific neighbours, and the term ecological response curve to describe either the growth of species along the gradient in the presence of neighbours or the species' distribution along the gradient in nature. The terms are similar to the fundamental and realized niches of Hutchinson (1959). The first is a measure of the species' physiological ability to exploit its environment in the absence of interspecific competition and the second is a measure of its exploitation pattern in the presence of competitors. A discrepency between a species' physiological response curve and ecological response curve is usually attributed to competition (Ernst 1978).

One of the first experimental studies that tested for the role of competition in controlling plant distriutions was that of Ellenberg (1954) who grew three grass species along a gradient of soil moisture in both monocultures and mixtures. He found that, grown singly, the species had similar patterns of biomass accumulation along the gradient, but that the same species grown in mixtures had different growth patterns, suggesting that interspecific competition controlled their distributions.

Several greenhouse studies have compared physiological response curves and ecological response curves and found evidence for competition. This was done by Pickett and Bazzaz (1978) using a soil moisture gradient and Parrish and Bazzaz (1982) for a gradient of soil nutrient concentration. Austin and Austin (1980) grew six grass species along a hydroponic nutrient gradient and demonstrated discrepencies between physiological response curves and ecological response curves. In an elegant analysis, Austin (1982) demonstrated that a species' performance at a particular location along the gradient in mixture was related to its relative performance at that location in monoculture. Austin _et al_. (1985) obtained similar results using thistle species. In contrast, Grace (1985) grew _Typha_ seedlings along a gradient of water-depth and found no evidence of displacement of optima.

A corresponding approach has been taken using field experiments along artificially formed gradients. Sharitz and McCormick (1973) investigated the partitioning of a soil depth gradient between two annual species by reconstructing the gradient under controlled conditions. They showed that competition sorted the two species into their respective habitats. Grace (1985) constructed a water-depth gradient to measure the physiological response curves and ecological response curves of the adults of two Typha species but found little evidence of competitive displacement.

Ernst (1978) cautioned that discrepencies between field distributions and physiological response curves measured along artificial gradients must be treated with caution, because discrepencies could result either from interspecific competition or from differences between the natural and experimental gradients. This problem can be overcome by measuring physiological response curves in the field along the actual gradient of interest. Such an approach has become more common in recent years. Grace and Wetzel (1981) compared the growth of two species of Typha along a water-depth gradient in a pond with their natural distributions and attributed the relatively narrow ecological response curves to interspecific competition. Snow and Vince (1984) grew saltmarsh species in different vegetation zones and concluded that competition limited the natural distribution of Puccinellia nutkaensis. Goldberg (1985) showed that the elimination of both competitors and seed predators was required in order for Quercus albocincta, an oak usually found in acidic, nutrient-poor habitats, to establish in a more nutrient-rich habitat.

Both field and greenhouse experiments conducted with a variety of species and gradients generally produce similar results: the physiological response curves of many species tend to be wider than their ecological response curves, and the optima of the two curves are often different, implying that competition plays a role in determining their distribution.

An entirely different approach to studying competition has been suggested by recent models of species diversity. These models are based on the observation that species diversity tends to be low where standing crop is high (Grime 1973, 1979) and disturbance, either from biotic (Lubchenco and Gaines 1981) or abiotic (Connell 1978, Huston 1979) factors, is low. The mechanism thought to cause this pattern is that the intensity of diffuse competition in nutrient-rich, undisturbed habitats is high and therefore only a few species with relatively high competitive ability can persist there. The assumption that competition intensity is related to standing crop and disturbance, however, has not been explicitly tested, although del Moral (1983) did relate the differential survival of transplants in natural vegetation to habitat productivity. Species-diversity models are relevant to the study of distribution because they predict that species of relatively high competitive ability should be found in undisturbed, nutrient-rich habitats while competitively subordinate species should occur in disturbed or nutrient-poor areas. This prediction remains untested.

This thesis uses both traditional and new approaches to study the role of competition in determining species distributions along an environmental gradient. This was accomplished by first testing whether competition controls species distributions and then testing for variation in the intensity of diffuse competition. The first chapter describes an experiment that compares the physiological and ecological response curves of twelve plant species using an experimental gradient. Chapter Two describes a similar experiment conducted on the natural gradient in the field. The third chapter explicitly tests for variation in the intensity of diffuse competition along the gradient while Chapter Four relates experimentally-measured competitive abilities of several species to their distributions in nature.

The environmental gradient

The environmental gradient chosen for study was the gradient of exposure to wave action that runs parallel to the waterline of small lakes. Horizontal variation in the abundance of plant species along the exposure gradient has been described by Pearsall (1920), Thunmark (1931), Keddy (1983), and Wilson and Keddy (1985). Exposure is a complex gradient that has both stress and disturbance (sensu Grime 1978) components. Disturbance is produced by the direct effect of wave action removing biomass more rapidly from exposed shores than from sheltered shores. Exposed shores are also stressful because relatively high levels of wave action there produce sediments with low organic matter content, low nutrient concentrations and coarse particle sizes (Keddy 1985). The exposure gradient is characterized at one end by wave-washed, sparsely vegetated, nutrient-poor beaches and at the other by sheltered, densely vegetated, nutrient-rich bays. In this study, position on the exposure gradient was quantified by measuring sediment organic matter content (Wilson and Keddy 1985): sediment organic matter content, nutrient concentration and the proportion of fine particles are all significantly negatively correlated with exposure (Keddy 1985). Field experiments were conducted at Axe Lake, Ontario (45° 23'N, 79° 30'W). The exposure gradient and associated plant communities at Axe Lake have been described by Keddy (1981, 1983).

CHAPTER 1

PLANT ZONATION ON A SHORELINE GRADIENT: PHYSIOLOGICAL RESPONSE CURVES OF COMPONENT SPECIES

Abstract

The distributions of twelve shoreline plant species were measured along a gradient of exposure to wave action in six central Ontario lakes. The frequencies of occurrence of eleven species varied significantly ($\underline{P} < 0.05$) along the exposure gradient. The same species were grown singly along an experimental gradient at ten organic matter content levels of shoreline sediment. Biomass accumulated after one growing season varied significantly ($\underline{P} < 0.05$) with sediment organic matter content for each of eleven species. The physiological response curves of the species along the gradient were similar ($\underline{P} < 0.01$). The experiment suggests that the differential distributions of the species along the organic content gradient are not entirely attributable to differential physiological responses to shoreline sediment.

INTRODUCTION

The distribution of freshwater plant species along gradients of depth and exposure has been subject to much study (reviewed by Hutchinson 1975; Spence 1982). The processes that produce zonation in shoreline vegetation, however, are not well understood; zonation is frequently assumed to result from the responses of species to changing abiotic factors (Snow and Vince 1984). In contrast, experiments in another zoned community, the rocky intertidal zone of coastlines, have shown that biological factors, such as competition and predation, are important in maintaining species distributions (e.g. Connell 1961; Lubchenco 1980). If abiotic factors alone determined species distributions, then species from different sections of a zoned community might be expected to have different physiological response curves (Mueller-Dombois and Ellenberg 1974; Ernst 1978; Austin and Austin 1980) when grown along the gradient in the absence of neighbours. If, <u>however,</u> between-species interactions, such as competition, also affect zonation, then species from different parts of a zoned community might have similar physiological response curves when grown singly along the gradient. In this case, zonation would result from biological interactions in the field. The purpose of this study was to describe the distributions of a set of species along a gradient of exposure to wave-action and then to experimentally test the similarity of their physiological response curves along the gradient. I therefore examined the distributions of twelve plant species of varying morphologies along the exposure gradient in order to test whether species are distributed differentially; this was done in several lakes to test whether distribution patterns are consistent at different locations. Secondly, I tested whether the twelve species had different or similar physiological responses to the gradient when grown singly in sediments representing the range of soil types found along the exposure gradient.

METHODS

Field distributions of shoreline species

The field distributions of twelve shoreline species (*Calamagrostis canadensis*, *Dulichium arundinaceum*, *Rhynchospora fusca*, *Cladium mariscoides*, *Eriocaulon septangulare*, *Juncus pelocarpus*, *Xyris difformis*, *Drosera intermedia*, *Hypericum ellipticum*, *Triadenum fraseri*, *Lysimachia terrestris* and *Lobelia dortmanna*) were measured along the exposure gradient. Nomenclature follows Gleason and Cronquist (1963) except for *Xyris difformis* Chapm. Species were chosen for their differing field distributions (Keddy 1981) and variety of growth forms. All twelve species are relatively common in the study area; one, *X. difformis*, is considered rare in Ontario (Randall and Keddy 1983). All species are capable of vigorous vegetative growth. Adult plants are dispersed within lakes during high water periods and are capable of establishment. Relative to vegetative growth, seedling establishment appears to be unimportant in determining species distributions.

Species distributions were determined during 7-31 August 1982 in the following central Ontario lakes (lake locations and number of vegetation samples taken from each lake are also given): Axe Lake (172 samples), Black Oak Lake (45°30' N, 86°13' W; 80), Burrows Lake (44°50' N, 79°40' W; 4), Hardy Lake (45°00' N, 79°29' W; 30), Matchedash Lake (44° 48' N, 79°30' W; 95) and Three Mile Lake (44° 54' N, 79°16' W; 91). Sampled lakes are underlain by Precambrian bedrock, predominantly granites and granite-gneiss, covered by shallow till. The till is partly covered by lacustrine and fluvial deposits; all sampling lakes were once part of glacial Lake Algonquin (Chapman 1975). The aquatic flora of the lakes in this region has been described by Miller and Dale (1979), Keddy (1981) and Keddy and Reznicek (1982). Each sampled lake contained most of the study species; lakes with human dwellings were avoided. Within a lake, all shoreline, except bedrock, peat bog and shrub (e.g. _Myrica gale_ L.) communities, was sampled at regular spatial intervals. The spacing of samples in each lake depended on the abundance of appropriate habitat: Axe Lake had nearly 2 km of sandy shore and was sampled every 20 m, while Black Oak Lake, which is dominated by exposed bedrock, was sampled at 2 m intervals. Two metres was the minimum spacing. The presence or absence of all study species within a 0.25 m^2 wire hoop was recorded for each sample unit. The location of each sample unit along the exposure gradient was determined by measuring sediment organic matter content. Sediment was sampled from the centre of the hoop by taking a trowel-full of soil 5 cm thick, the average maximum rooting depth. Because it was not possible to freeze soil samples at the study lakes, samples were sealed in polyethylene bags and stored in the shade for about three weeks after which they were frozen for 1-2 months until analysis for sediment organic matter content. Organic matter content was determined for each sediment sample according to Dean (1974). Substratum organic content is expressed as the percentage loss of dry sample mass upon ignition.

The range of organic matter content found along the shorelines was divided into eight classes (Table 1) and the frequency of occurrence for each species in each class was computed. To test whether the abundance of each species varied along the gradient, the presence and absence values for the classes were tested with a χ^2 test for _k_ independent samples (Siegel 1956). Also, for every species, the ranks of relative frequency of occurrence across the classes were determined so that the class with the highest relative frequency was ranked first, the class with the next highest frequency was ranked second, etc. The rankings produced a numerical expression of each species' abundance along the gradient. The agreement of different species' distributions along the gradient was tested using Kendall's coefficient of concordance (_W_) (Siegel 1956).

Agreement of field distributions between lakes

To test whether particular species were always found at the same relative position along the exposure gradient in different lakes, the range of organic matter content found was divided into five broad classes so that the four lakes from which more than fifty samples had been taken had large numbers of samples within each class. Six common species occurred in the four most frequently sampled lakes to the extent that they were found at least ten times in one or more organic content classes in three out of four lakes. For each lake, the organic content class in which each species had its highest abundance was noted. The species were then ranked within the lake from those occurring most frequently in high organic matter content classes to those occurring most frequently in low organic content classes. The agreement of species ranking along the gradient between lakes was tested using Kendall's W.

Measurement of physiological response curves

Highly organic sediment was collected from five lakes in the study area: Black Oak Lake, Cardwell Lake (45° 20'N, 79° 30'W), Coldwater Lake (45° 00'N, 79° 48'W), Deer Lake (44° 57'N, 79° 27'W) and Horseshoe Lake (44° 50'N,79° 38'W). These lakes were similar in bedrock, size, and human history. Sediment was gathered in equal portions from three sites within each lake, for a total of fifteen sources. Collection sites were highly organic shorelines in sheltered bays.

The sediments were pooled and mixed by hand for 2 h. This produced one end of the experimental gradient that was typical of organic shorelines in the study lakes. The other end of the gradient was represented by sand obtained from a quarry 2 km from Coldwater Lake. Eight intermediate levels of organic content were formed by mixing a known volume of sand and organic sediment for each level. Each was mixed for 1 h by hand and then put into water-tight pots (15.5 cm diameter). Five samples of each treatment level were frozen for later determination of organic matter content.

Approximately seventy-five ramets (White 1979) of each study species were collected at Axe Lake on 25 May 1982. Plants were carefully removed from the substrate, washed, and stored in lake water for up to 4 days, until planted. For each species, I attempted to select individuals of equal size and stage of development.

Five ramets of each species were planted in individual pots at each level of the gradient. In spite of care taken to standardize ramet size, there was still variation among those selected. To ensure that this variation was spread over the entire gradient, ramets were sorted into three classes (small, medium and large) and the ten largest and ten smallest plants were randomly assigned over the entire gradient. The pots were distributed in a completely randomized design within an outdoor exclosure at the University of Guelph, 300 km southwest of the study area.

Soil in the pots was saturated by daily watering with deionized water.

Plants were harvested over five days beginning 1 September 1982. Whole plants were washed to remove soil and dried to constant weight. Plants were allowed to cool for 1 h before being weighed.

Biomass values were log-transformed to meet the assumptions of analysis of variance and the significance of treatment effects were tested for each species. To test for similarity of physiological responses, the ranks of mean dry weights of each species along the gradient were determined so that the gradient level with the greatest dry weight was ranked first, the level with the next highest dry weight ranked second ,etc. The agreement of ranks among species along the gradient levels was tested using Kendall's W.

RESULTS

Field distributions of shoreline plants

Abundance varied significantly ($P < 0.05$) along the exposure gradient for all species but *Rhynchospora fusca* and species had different patterns of distribution (Kendall's W, $s = 581$, $k = 7$, $N = 12$, $P > 0.05$). Fig. 1 shows that some species have peak abundances at the more sheltered, organic end of the gradient (*Dulichium arundinaceum*, *Triadenum fraseri*) , some at intermediate levels (*Xyris difformis*, *Cladium mariscoides*) , and others were found most frequently at the exposed, sandy end (*Jancus pelocarpus*, *Eriocaulon septangulare*).

To make the results from the field and experimental gradients comparable, the field gradient was divided into eight classes: seven classes were scaled to the experimental gradient while the eighth class includes all samples with organic content greater than the highest level of the experimental gradient (Table 1). As well, the first three levels of the experimental gradient were pooled into one class and the next two levels were pooled into a second class; the dry weights of plants grown at these levels were pooled into the new classes for statistical analysis. The upper five levels of the experimental gradient were not changed. This manipulation produced seven organic matter content classes that were comparable between the field and experimental data (Table 1). The same species, and organic content classes, were necessary to test for concordance among species within both the field and experimental studies. Therefore, some field samples were not considered in this set of analyses, including samples with organic content between 6.00 and 7.99% and samples with organic content greater than 24.0%.

Agreement of field distributions between lakes

Six species (*D. arundinaceum*, *E. septangulare*, *J. pelocarpus*, *Drosera intermedia*, *L. terrestris*, and *Triadenum fraseri*) occurred frequently enough in four lakes (Axe, Black Oak, Matchedash, and Three Mile) for their distributions along the organic content gradient to be compared (Appendix 1). These common species agreed in their rankings along the gradient among lakes (Kendall's W, $s = 216$, $k = 4$, $N = 6$, $P < 0.01$) suggesting that the zonation pattern is similar regardless of the lake considered.

Measurement of physiological response curves

Biomass varied significantly ($P < 0.05$) with position on the gradient for all species but *Drosera intermedia* (data are summarized in Appendix 2). The physiological response curves of the species along the gradient were similar (Kendall's W, $s = 1{,}914$, $k = 7$, $N = 12$, $P < 0.01$). Most species achieved maximum dry weight at the same end of the gradient (Figure 2). One species, *Hypericum ellipticum* , achieved maximum biomass at an intermediate level of organic content. No species performed best at the sandy end of the gradient.

FIG. 1. The field distributions of twelve shoreline species along the exposure gradient in six Canadian lakes. Classes formed as in Table 1. Relative abundance along the gradient varied significantly (P <0.05) for all species but *Rhynchospora fusca*. Species were distributed differentially along the gradient (Kendall's W, P > 0.05).

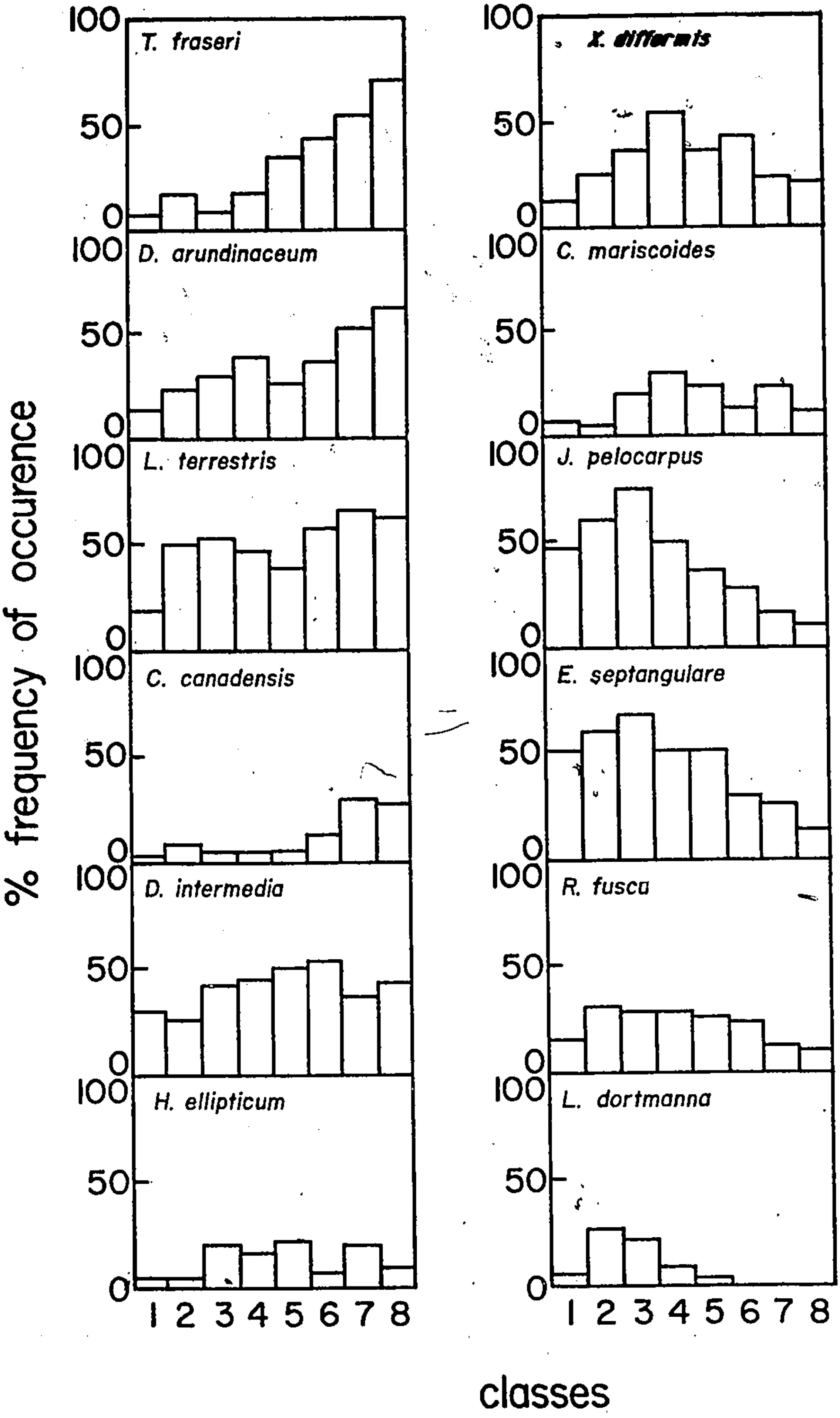

% frequency of occurence
T. fraseri
X. difformis
D. arundinaceum
C. mariscoides
L. terrestris
J. pelocarpus
C. canadensis
E. septangulare
D. intermedia
R. fusca
H. ellipticum
L. dortmanna
100
50
0
1 2 3 4 5 6 7 8
classes

FIG. 2. Biomass as a function of sediment organic matter content in an experiment with twelve shoreline species grown singly. Levels as defined in Table 1. Biomass varied significantly among treatments for all species but *D. intermedia*. Species responses to the sediment organic content were similar (Kendall's W, $P < 0.01$).

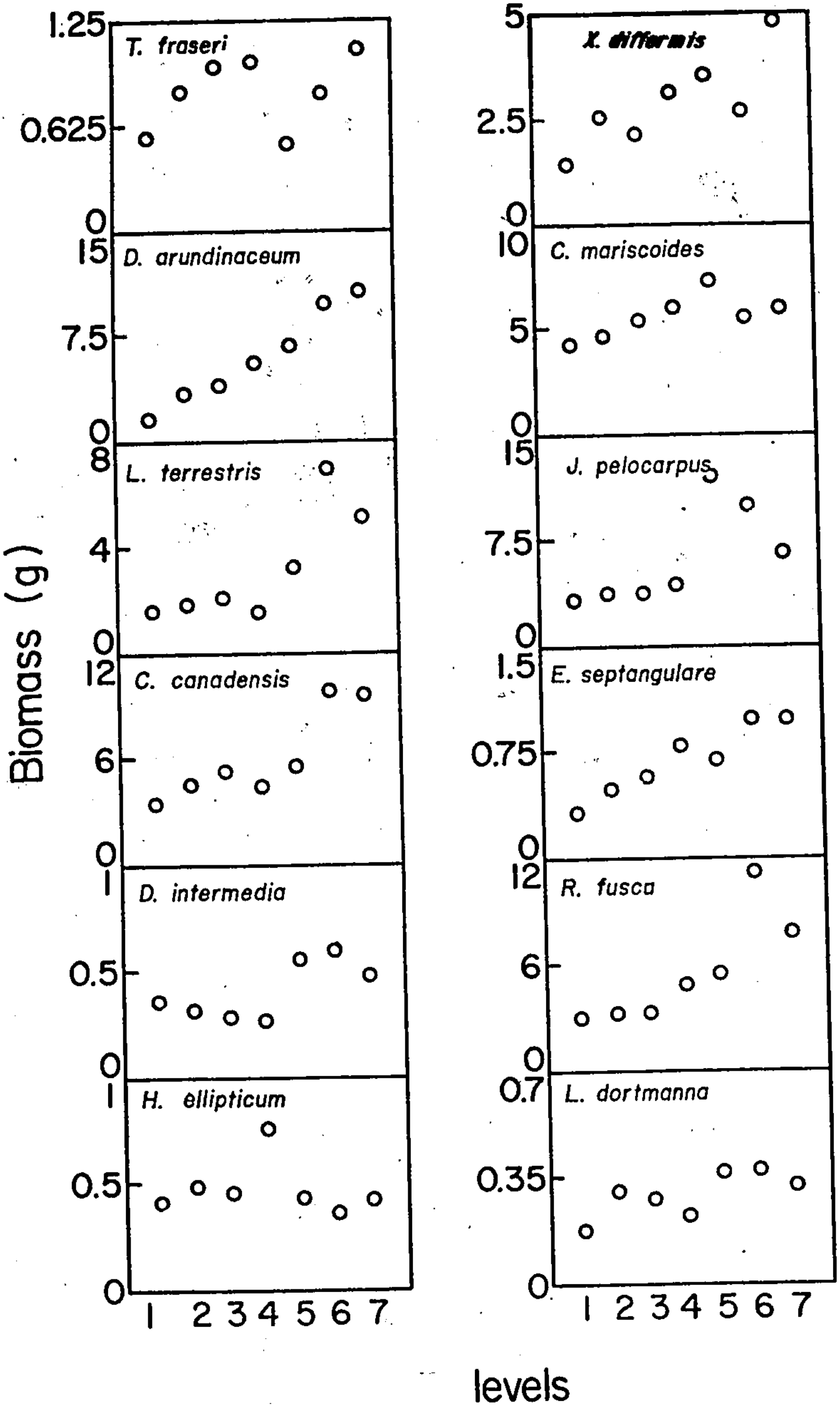

Biomass (g)
levels
T. fraseri
1.25
0.625
0
D. arundinaceum
15
7.5
0
L. terrestris
8
4
0
C. canadensis
12
6
0
D. intermedia
1
0.5
0
H. ellipticum
1
0.5
0
X. difformis
5
2.5
0
C. mariscoides
10
5
0
J. pelocarpus
15
7.5
0
E. septangulare
1.5
0.75
0
R. fusca
12
6
0
L. dortmanna
0.7
0.35
0
1 2 3 4 5 6 7
1 2 3 4 5 6 7

Table 1. Data manipulations used to make the substrate organic content levels used in the experiment comparable to the range of substrate organic content over which species distributions were measured in the field.

Experimental substrates			Field substrates	
Original Level*	Organic Content (%) x̄±S.D.	Pooled Level†	Class§	Organic Content Range (%)
1	0.88±0.04	1	1	0.00 - 0.99
2	0.80±0.03			
3	0.81±0.05			
4	1.13±0.08	2	2	1.00 - 1.49
5	1.22±0.08			
6	1.72±0.39	3	3	1.50 - 1.99
7	2.70±0.26	4	4	2.00 - 3.99
8	5.29±0.20	5	5	4.00 - 5.99
9	12.60±0.37	6	6	8.00 -15.99
10	20.69±0.58	7	7	16.00 -23.99

* Levels 1 to 3 and 4 to 5 were combined for analysis of biomass to make the experimental treatments correspond with the range of organic content found in the field.

† These levels were used to test the significance of treatment effects and concordance of responses.

§ These levels were used to test for concordance of species distributions.

DISCUSSION

The exposure gradient is strongly correlated with other variables important to plant growth, including nutrient concentrations and particle sizes (Keddy 1985). It is a multivariate gradient; sediment organic matter content is one variable that is relatively easy to measure and it may be used as a marker of position along the complex environmental gradient.

Plant distributions vary significantly along the organic content gradient and the pattern is similar among different lakes, suggesting that the mechanism sorting species along the gradient is present independent of the particular lake considered.

The most striking feature of the results, in light of the species' differential field distributions, is the similarity of their physiological response curves. This suggests that zonation may not be entirely attributable to individual species' physiological responses to changing physical factors: interactions with other plants may also be important in determining a species' distribution along the exposure gradient.

Two assumptions have been made in interpreting the experimental results. The first is that the organic content gradient used in the experiment is similar to that in the field. An attempt was made to account for variability in the gradient by sampling in several lakes and by combining sediments from several lakes for the experiment. One factor that was not accounted for by the experiment was the direct effect of wave action. Wave action may affect biomass accumulation (Jupp and Spence 1977) , but the species considered here occur just above the water-line during the growing season and their growth in the field may not be directly influenced by waves. Secondly, it is assumed that plants were allowed to grow long enough for differences among them to be shown; the 90-day time-span of the experiment includes the period of highest growth rates (Auclair, Bouchard and Pajackzowski 1976).

A feature common to recent reviews concerning the mechanisms that produce shoreline zonation is the limited consideration of the possible importance of between-species competition among aquatic plants (Hutchinson 1975; Spence 1982). The results of this experiment suggest that the physiological responses of species to a physical gradient alone are insufficient to account for zonation. These results are consistent with those of Misra (1938) who found that <u>Potamogeton</u> <u>pectinatus</u> grew best on the organic sediment upon which it was most commonly found, but that <u>Isoetes</u> <u>lacustris</u> , which is most abundant on sandy sediments, also grew best on sediment with high organic content; Misra speculated that between-species competition might affect the distribution of some aquatic plants. When considering vertical zonation, Buttery and Lambert (1965) proposed that competition produced the zonation of <u>Phragmites communis</u> and <u>Glyceria maxima</u>. Similarily, Grace and Wetzel (1981) suggested that between-species competition determined the vertical distributions of two species of <u>Typha</u>.

Because physiological response curves alone seem to be unable to account for lakeshore zonation patterns, the role of biological interactions in determining species distributions in this community requires further examination.

CHAPTER 2

PLANT ZONATION AND THE PHYSIOLOGICAL RESPONSE CURVES OF COMPONENT SPECIES: A FIELD EXPERIMENT

Abstract

The distributions of nine shoreline plant species were measured along a gradient of exposure to wave action at Axe Lake, Ontario. The frequencies of occurrence of six species varied significantly along the gradient. Species were distributed differentially along the gradient. The same species were then grown singly along the exposure gradient at Axe Lake for 14 months. Physiological response curves of component species were significantly concordant. The results suggest that the differential distributions of species along the gradient are produced by the effects of neighbours.

INTRODUCTION

A common method of testing for the role of interspecific competition in producing zonation patterns along environmental gradients is to compare the ecological and physiological response curves of the component species. In this method, the physiological response curve of a species, measured as its pattern of biomass accumulation when grown along the gradient in the absence of interspecific neighbours, is compared with its ecological response curve, measured either as its distribution along the gradient in nature or its growth along the gradient in the presence of neighbours (Mueller-Dombois and Ellenberg 1974, Pickett and Bazzaz 1978, Austin and Austin 1980, Austin _et al._ 1985, Wilson and Keddy 1985). A discrepency between the physiological response curve and ecological response curve of a species is often attributed to competition (Ellenberg 1953). Ernst (1978), however, cautions that such discrepencies may also be produced by differences between the experimental gradient used to measure the physiological response curve and the environmental gradient underlying the species' distribution in nature. This problem can be overcome by measuring physiological response curves in the field along the natural environmental gradient (Grace and Wetzel 1981, Snow and Vince 1984, Wilson and Keddy 1985). The objective of this research was to use a field experiment to test whether competition is partly responsible for controlling the distributions of members of a multispecies community along a natural gradient. This was done by describing the differential distributions of the species along the gradient and then testing whether their physiological response curves were also different. Different physiological response curves would indicate that physiological responses to abiotic factors varying along the gradient are of primary importance in determining species distributions, whereas similar physiological response curves would suggest that interspecific competition is influencing the distributions of at least some species.

METHODS

Ecological Response Curves

The distributuions of nine shoreline plant species (*Dulichium arundinaceum*, *Triadenum fraseri*, *Lysimachia terrestris*, *Cladium mariscoides*, *Rhynchospora fusca*, *Xyris difformis*, *Juncus pelocarpus*, *Eriocaulon septangulare* and *Lobelia dortmanna* nomenclature follows Gleason and Cronquist 1963, except *X. difformis* Chapm.) were measured along the exposure gradient at Axe Lake during 19-21 August 1984. Quadrats (0.5 x 0.5 m, *N*=243) were placed at 10 m intervals along the waterline and the presence of all species recorded. The location of each quadrat along the exposure gradient was determined by measuring the organic matter content (Dean 1974) of a sediment sample (3.5 cm diameter, 5 cm deep) from the centre of each quadrat. Samples were frozen at -10° C within one week of collection until analysis one month later.

Species distributions along the exposure gradient were described by breaking down the range of sediment organic ~~matter~~ content found into three classes (class 1: 0.0-2.9%, class 2: 3.0-8.0%, class 3: 10.0-30.0%) corresponding to the exposed, intermediate and sheltered shores described by Keddy (1981). The frequency of occurrence of each species in each class was calculated. The presence and absence values for the species in the three classes were examined using a χ^2 test for k independent samples (Siegel 1956) to test whether the abundance of each species varied significantly along the exposure gradient. For each species, the ranks of frequency of occurrence of each class along the gradient were then determined so that the class with the lowest relative frequency was ranked first, the class with the intermediate frequency was ranked second and the class with the highest frequency of occurrence was ranked third. Rankings produced a numerical expression of each species' abundance along the gradient. The agreement of distributions among species along the exposure gradient was tested using Kendalls coefficient of concordance (Siegel 1956).

Physiological Response Curves

Seven experimental stations were chosen to represent the range of the exposure gradient at Axe Lake. In August 1983 plastic pots (each 15 cm diameter, 9.5 cm deep with four 1 cm^2 drainage holes) were installed at each station by removing a core of soil the size of the pot, putting it into the pot and replacing the potted soil in the shoreline. Pots were arranged in four adjacent rows parallel to the shore, 10 cm vertically above the 16 August 1983 waterline. All aboveground vegetation was removed from the pots and a surrounding border 15 cm wide.

Ramets of study species were collected at Axe Lake on 15 June 1984. Seventy ramets of approximately equal size within each species were chosen for transplanting. Ten ramets of each species were planted (1 ramet per pot) in a randomized design at each station on 16 June 1984. Pots were weeded monthly during the growing season until the experiment was harvested during 19-22 August 1985. Ramets were washed, dried to constant weight and total biomass was measured.

The effect of treatment location on the growth of each species was tested using a general linear model of analysis of variance (Ray 1982), which takes into account the unbalanced design produced by varying ramet survival among treatments.

The positions of the experimental stations on the exposure gradient were determined by sampling sediment organic matter content ($\underline{N}$ = 10 replicates) at each station.

In order to produce comparable physiological and ecological response curves, the results from the three most exposed stations were pooled into one class and those from the three intermediate stations were pooled into a second class. The results from the most sheltered station were not combined. This manipulation produced three data classes (mean sediment organic matter content associated with class 1: 1.54%, class 2: 4.13%, class 3: 19.21%) that were comparable to the classes used to describe the species' field distributions. These pooled classes were then ranked for each species such that the class with the lowest mean biomass was ranked first and the class with the highest mean biomass was ranked third. The agreement among species' physiological response curves along the exposure gradient was then tested using Kendall's coefficient of concordance.

RESULTS

Ecological Response Curves

Abundance varied significantly ($P < 0.05$) along the exposure gradient for all species except *Dulichium arundinaceum*, *Rhynchospora fusca* and *Lobelia dortmanna*. Species had differential patterns of distribution along the gradient (Kendall's W, $s = 6$, $P > 0.05$). Fig. 3a shows that some species (e.g. *Triadenum fraseri*, *Lysimachia terrestris*) are most abundant on sheltered, organic shores while others (e.g. *Juncus pelocarpus*, *Eriocaulon septangulare*) are more common on sandy, exposed shores.

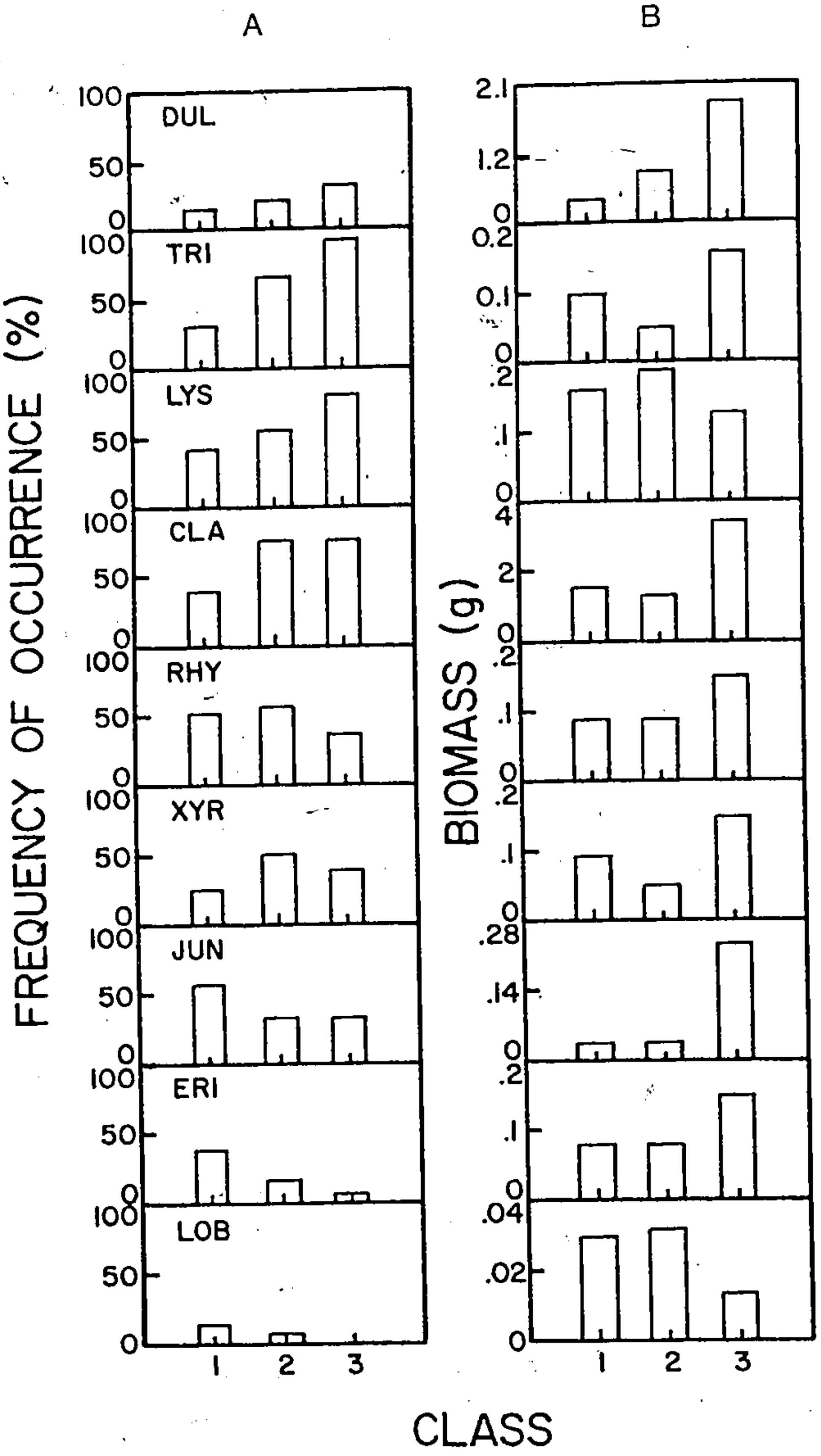
Physiological Response Curves

Biomass accumulation varied significantly ($P < 0.05$) with position on the exposure gradient for Dulichium, Lobelia and Cladium mariscoides (data are summarized in Appendix 3). When all species were considered simultaneously, their physiological response curves along the gradient were significantly similar (Kendall's W, $s = 56$, $P < 0.05$). Figure 3b shows that species accumulated most biomass in sheltered, organic bays, except for Lobelia, which accumulated significantly less biomass in this habitat.

FIG.3a. The distributions of nine plant species along the exposure gradient at Axe Lake. Species such as Dulichium arundinaceum and Triadenum fraseri are most common on sheltered organic shores while others, such as Eriocaulon septangulare and Lobelia dortmanna are restricted to disturbed, sandy shores.

FIG. 3b. The physiological response curves of the same species grown singly along the exposure gradient at Axe Lake for 14 months. Species have significantly concordant physiological response curves along the gradient.

Species names are abbreviated as follows: DUL: Dulichium arundinaceum, TRI: Triadenum fraseri, LYS: Lysimachia terrestris, CLA: Cladium mariscoides, RHY: Rhynchospora fusca, XYR: Xyris difformis, JUN: Juncus pelocarpus, ERI: Eriocaulon septangulare, and LOB: Lobelia dortmanna.


A
B
FREQUENCY OF OCCURRENCE (%)
BIOMASS (g)
DUL
TRI
LYS
CLA
RHY
XYR
JUN
ERI
LOB
100
50
0
2.1
1.2
0
0.2
0.1
0
.2
.1
0
4
2
0
.28
.14
.04
.02
1
2
3
CLASS

DISCUSSION

The distributions of species along the exposure gradient at Axe Lake (Fig. 3a) are similar to those described by Wilson and Keddy (1985) for six Ontario Lakes (Fig.1, this thesis). They showed that species distributions along the exposure gradient in four separate lakes were in the same rank order, suggesting that the mechanism determining species distributions along the gradient is present regardless of the particular lake considered.

In contrast to the species' different distributions, their physiological response curves along the gradient are significantly similar (Fig. 3b). The fact that position on the exposure gradient affected biomass accumulation in the case of only three species may be attributable to low survivorship at some stations increasing variance and obscuring treatment effects. In spite of this, Fig. 3b shows that species generally accumulated more biomass on sheltered shores with high sediment organic matter content. An exception is Lobelia, which accumulated significantly less biomass in sheltered habitats. This contrasts with the physiological response curves of two other species common on exposed shores, Juncus and Eriocaulon, which accumulate more dry weight on organic shores. The complete absence of Lobelia from sheltered shores (Fig. 3a) is correlated with its low growth rate there (Fig. 3b), indicating that the physiological response curve of this species along the exposure gradient may be of primary importance in determining its distribution.

This interpretation is based on patterns of biomass accumulation; mortality may also vary along the gradient (App. 3). However, missing values in Appendix 3 represent both ramet death and the removal of living transplanted ramets by wave action, making the interpretation of missing values difficult.

The overall similarity of the physiological response curves shown in Fig.3b suggests that the zonation pattern in the field cannot be attributed only to different physiological responses to the exposure gradient. Because the physiological response curves were produced by the measurement of biomass of individuals grown in the absence of neighbours, the zonation pattern along the gradient may result partly from the effects of neighbours.

A number of studies have shown that interspecific competition may influence the distribution of plant species along environmental gradients (Sharitz and McCormick 1973, Pickett and Bazzaz 1978, Austin and Austin 1980, Austin _et al_. 1985, Goldberg 1985), including gradients in aquatic environments (Misra 1938, Seddon 1965, Buttery and Lambert 1965, Grace and Wetzel 1981, Snow and Vince 1984, Wilson and Keddy 1985). In contrast, other studies have found no evidence that competition influences the distribution of wetland plants (Moyle 1945, McCreary, Carpenter and Chaney

1983).

Other field experiments have indicated that the distribution of plant species along the exposure gradient at Axe Lake may result at least partly from competition. Wilson and Keddy (in press) have shown that the distributions of seven species along the gradient are related to their competitive abilities. Competitive dominants such as Dulichium occupy sheltered, nutrient-rich shores where standing crop is high and diffuse competition is most intense (Wilson and Keddy 1986), whereas subordinate species such as Eriocaulon are restricted to sandy, exposed shores.

In summary, plant species are distributed differentially along the exposure gradient but have significantly similar physiological response curves along the gradient, indicating that interspecific competition may be partially responsible for the observed zonation pattern. Species of both sheltered habitats (e.g. Lysimachia terrestris) and exposed beaches (e.g. Eriocaulon septangulare) accumulate more biomass on undisturbed, nutrient shores than on sandy shores subject to high levels of wave action; small, slow-growing species are presumably displaced from the nutrient-rich habitats by competitive exclusion.

CHAPTER 3

MEASURING DIFFUSE COMPETITION ALONG AN ENVIRONMENTAL GRADIENT: RESULTS FROM A SHORELINE PLANT COMMUNITY

Abstract

I propose a method for measuring variation in diffuse competition along an environmental gradient. This approach has two advantages over pair-wise competition experiments conducted in homogeneous environments. First, it may be more realistic, since individuals in nature are usually confronted with a variety of neighbours, i.e. diffuse competition. Secondly, this approach allows us to test whether variation in diffuse competition is correlated with gradients in environmental factors. I used a field experiment to test whether diffuse competition is correlated with standing crop and sediment organic matter content in a lakeshore plant community. Diffuse competition was significantly positively correlated with both of these factors. Further, standing crop was found to be positively correlated with sediment organic matter content, suggesting that a general measure of habitat productivity may be indirectly related to the intensity of diffuse competition. These results support models of species diversity and adaptive strategies which assume that the importance of competition within a community varies predictably.

INTRODUCTION

Ecological literature is rich with studies of competition in plant communities. Most experimental studies are limited by necessity to the examination of pairwise interactions within a small group of species (e.g. Putwain and Harper 1970, Sharitz and McCormick 1973, Grace and Wetzel 1981, Fowler 1982, Silander and Antonovics 1982, Rabinowitz et al. 1984). In nature, however, an individual may compete with a constellation of species in various combinations and densities, i.e. an individual is often faced with diffuse competition (MacArthur 1972). In spite of its importance in natural communities, diffuse competition has received almost no experimental attention (Davidson 1985). I define diffuse competition as the effect of all neighbours in limiting the biomass accumulation of an individual.

Current ecological models describing life-history traits and species diversity are based on the untested assumption that the intensity of diffuse competition varies with standing crop (Grime 1979), disturbance (Connell 1978, Huston 1979) or grazing (Lubchenco and Gaines 1981). Measuring diffuse competition at several locations along an environmental gradient simultaneously would allow explicit testing of this assumption and its associated models.

This study had three objectives: i) to present a method for measuring diffuse competition along an environmental gradient; ii) to use this method to test whether diffuse competition is correlated with standing crop in a natural plant community; and iii) to test whether diffuse competition was correlated with an important environmental gradient underlying the community.

METHODS

Measuring diffuse competition along a gradient

A general method is presented for measuring variation in diffuse competition. Several locations are chosen along an environmental gradient. Each location is divided in half, one half cleared of all above-ground biomass, and ramets of several species are planted in each half. The density of transplanted ramets should be so low that shoots do not shade each other and below-ground parts do not come into contact. Ramets are allowed to grow for one or more growing seasons before harvest of above and below-ground biomass. The biomass accumulated by transplanted ramets in cleared and uncleared treatments is compared in order to calculate diffuse competition at each location:

$$1) \qquad DC = \left[\sum_{i=1}^{n} \left(\frac{C_i - U_i}{C_i} \right) \right] n^{-1}$$

where DC is a measure of diffuse competition, C_i is equal to the mean dry weight of species i in the cleared treatment. U_i is equal to the mean dry weight of the species in the uncleared control, and n is equal to the number of transplanted species. The difference between the dry weight of ramets in cleared and uncleared treatments is divided by the mean dry weight of the species in the cleared plots to account for the relative size of each species. The correlation between diffuse competition and some measure of the environmental gradient is then calculated.

Diffuse competition

Diffuse competition was measured at eight locations chosen to represent the range of standing crop on the shore of Axe Lake, Ontario (Keddy 1983). Each location consisted of a cleared treatment plot and an adjacent uncleared control plot. Each plot comprised 30 pots (each 15 cm diameter, 12 cm deep, with eight 1 cm^2 drainage holes) in six rows of five pots each, installed by removing a sediment core the size of the pot, putting it into a pot and replacing the potted soil in the sediment. Pots excluded invading rhizomes and allowed harvesting of below-ground biomass. All above-ground vegetation was removed from the treatment plots and from a 15 cm border surrounding the cluster of pots. Any emerging shoots were removed over the course of the experiment.

Ten ramets of three shoreline species (*Juncus pelocarpus*, *Rhynchospora fusca*, *Lysimachia terrestris*) were transplanted into each plot. All species are found over the entire range of the exposure gradient (Wilson and Keddy 1985). *Juncus*, a small (5 - 15 cm tall, Gleason and Cronquist 1963) graminid that grows in dense mats, is most often found on sandy, exposed shores (Wilson and Keddy 1985); Rhynchospora is a rhizomatously spreading graminid (15 - 40 cm tall) distributed evenly along the exposure gradient, while Lysimachia is a tall (40 - 80 cm), leafy rhizomatous herb most often found on sheltered shores with high sediment organic matter content. Species were chosen for their different morphologies. Ramets were collected on 3 July, planted during 3-6 July and harvested 6 September 1984. The experiment was harvested after a single growing season because it would not have been possible to identify shoots arising from transplanted rhizomes in the following year.

The position of each experimental location on the exposure gradient was measured by determining the mean organic matter content (Dean 1974) of six sediment samples (each 3.5 cm diameter, 5 cm deep) taken from each location.

Standing crop was harvested from a 0.2 x 0.2 m quadrat adjacent to each of the two plots at each location on 25 August 1984. Standing crop samples were dried to constant weight and the mean standing crop was determined for each location.

The correlation between DC and standing crop for all locations was calculated using Pearson's r after arcsine transformation of DC. DC was transformed because it was a proportion. Although DC calculated for three species together gives a general measure of diffuse competition, DC can also be calculated for each species individually to test for among-species differences in responses. This can be done by calculating DC as in Equation 1 for each species and then testing for a correlation between DC and standing crop.

Standing crop

I tested the hypothesis that standing crop is related to the exposure gradient in order to interpret the experimental results with reference to abiotic factors. The shoreline of Axe Lake was sampled at 20 m intervals at the waterline during 17-21 August 1984 (N=83). At each interval, standing crop was harvested from a 0.2 x 0.2 m quadrat and a sediment sample was taken for organic matter content analysis. The correlation between standing crop and sediment organic matter content was tested using Pearson's r.

RESULTS

Diffuse competition was significantly correlated with standing crop (r =0.76, P =0.02) for all transplanted species considered together (data are summarized in Appendix 4). Figure 4 shows that diffuse competition increases with community standing crop.

The relationship between diffuse competition and standing crop varied when the transplanted species were considered separately. Lysimachia terrestris showed no correlation between DC and standing crop (r ±0.04, P =0.46), Juncus pelocarpus showed a weak correlation (r =0.57, P =0.07) and

Rhynchospora fusca showed a strong correlation (*r* =0.80, *P* =0.01).

Diffuse competition is also significantly correlated with sediment organic matter content (*r* =0.76, *P* =0.02) for the three transplanted species considered together. Figure 5 shows that diffuse competition is most intense in relatively undisturbed habitats with high sediment nutrient concentrations. Sandy shorelines, exposed to wave-action and with nutrient-poor sediments, had relatively low levels of diffuse competition.

Standing crop is significantly correlated with sediment organic matter content (*r* =0.79, *P* <0.01). Figure 6 shows that standing crop is highest on sheltered shores with high sediment organic matter content.

FIG.4. The relationship between diffuse competition, as calculated in Eq.1, and standing crop on the shoreline of Axe Lake. Diffuse competition is significantly correlated with standing crop.

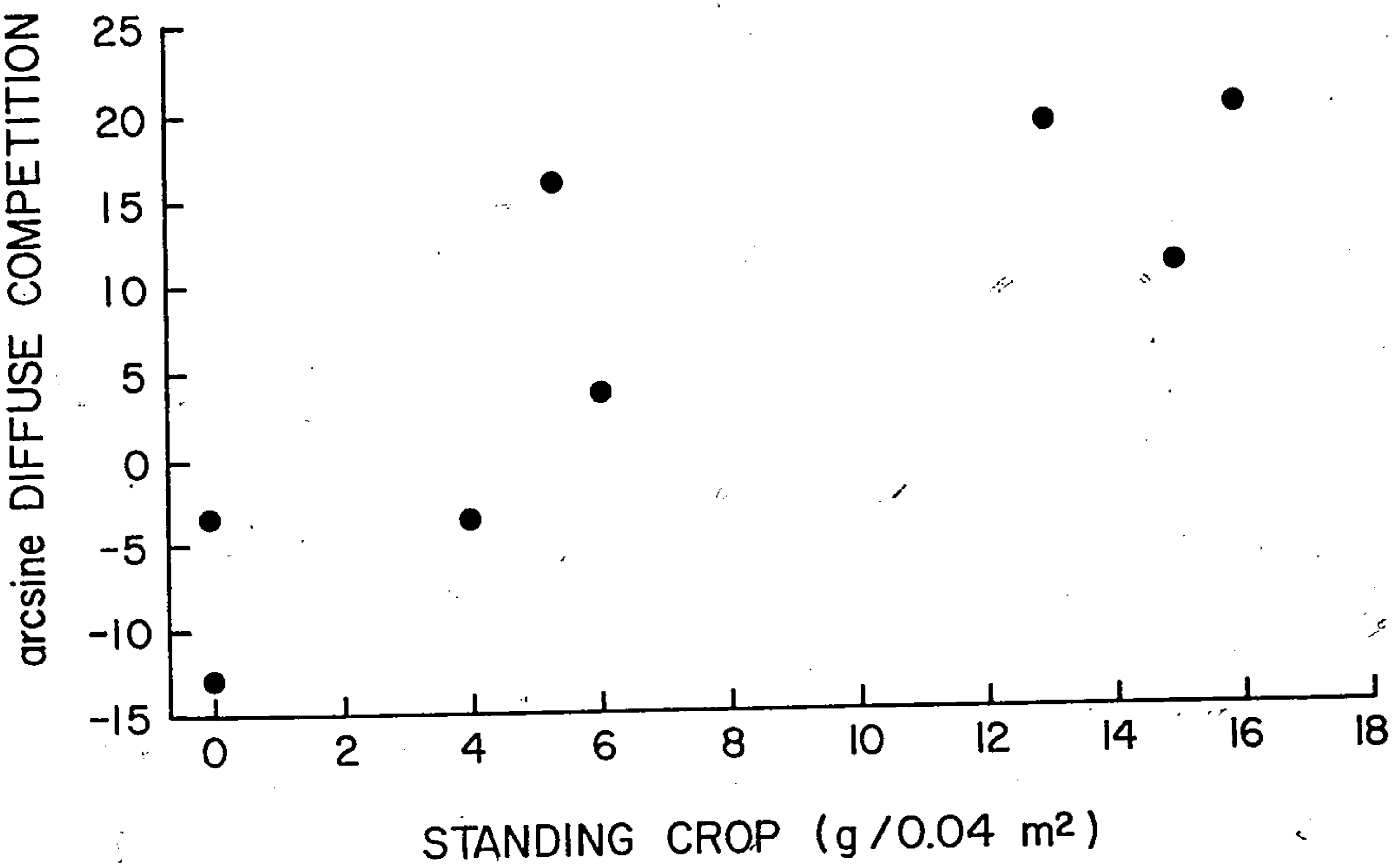

arcsine DIFFUSE COMPETITION
25
20
15
10
5
0
-5
-10
-15
0
2
4
6
8
10
12
14
16
18
STANDING CROP (g /0.04 m²)

FIG.5. The relationship between diffuse competition and sediment organic matter content on the shore of Axe Lake. Organic content is low on exposed shores (left) and high on sheltered shores (right). Diffuse competition is significantly correlated with sediment organic content.

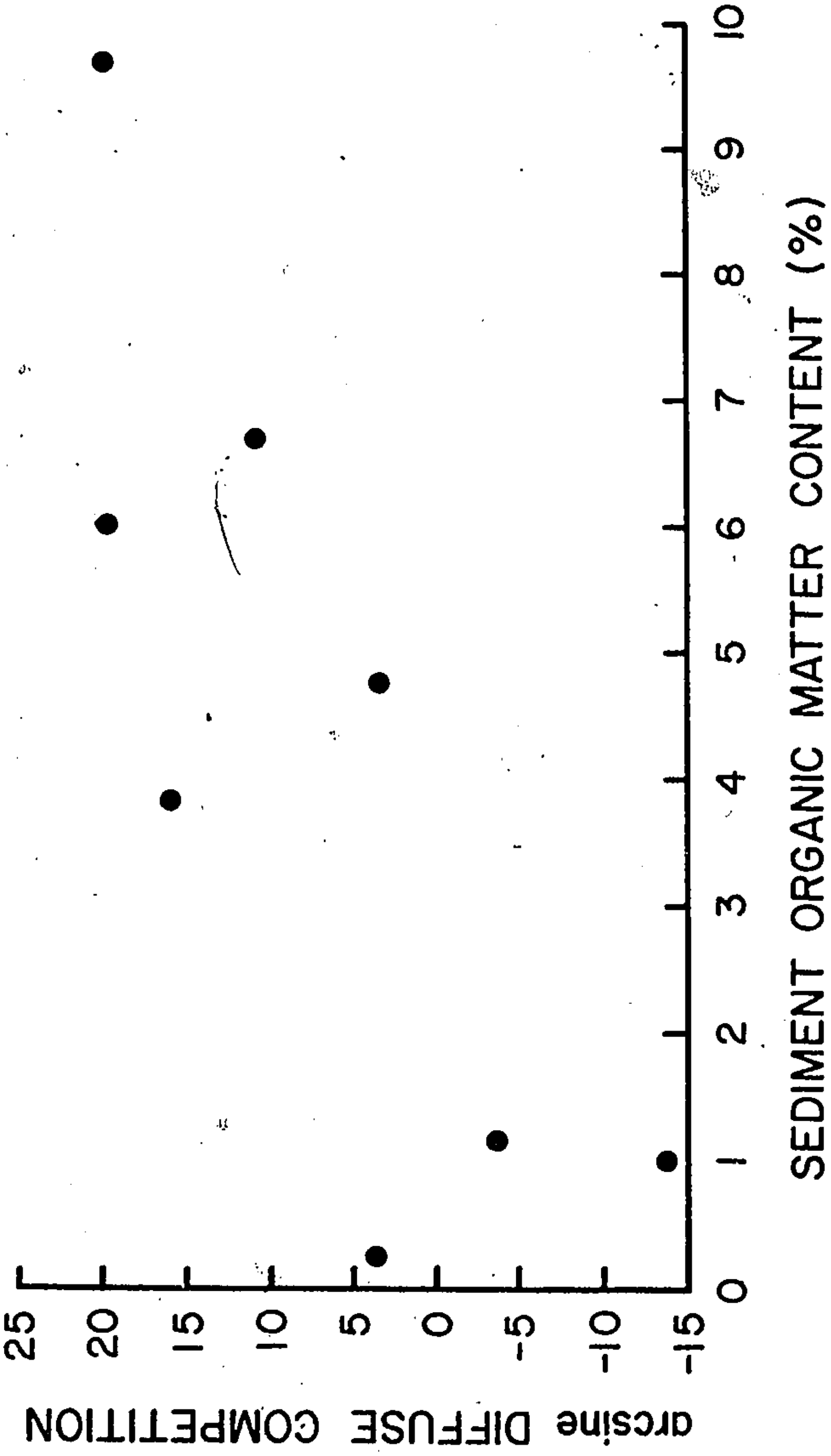
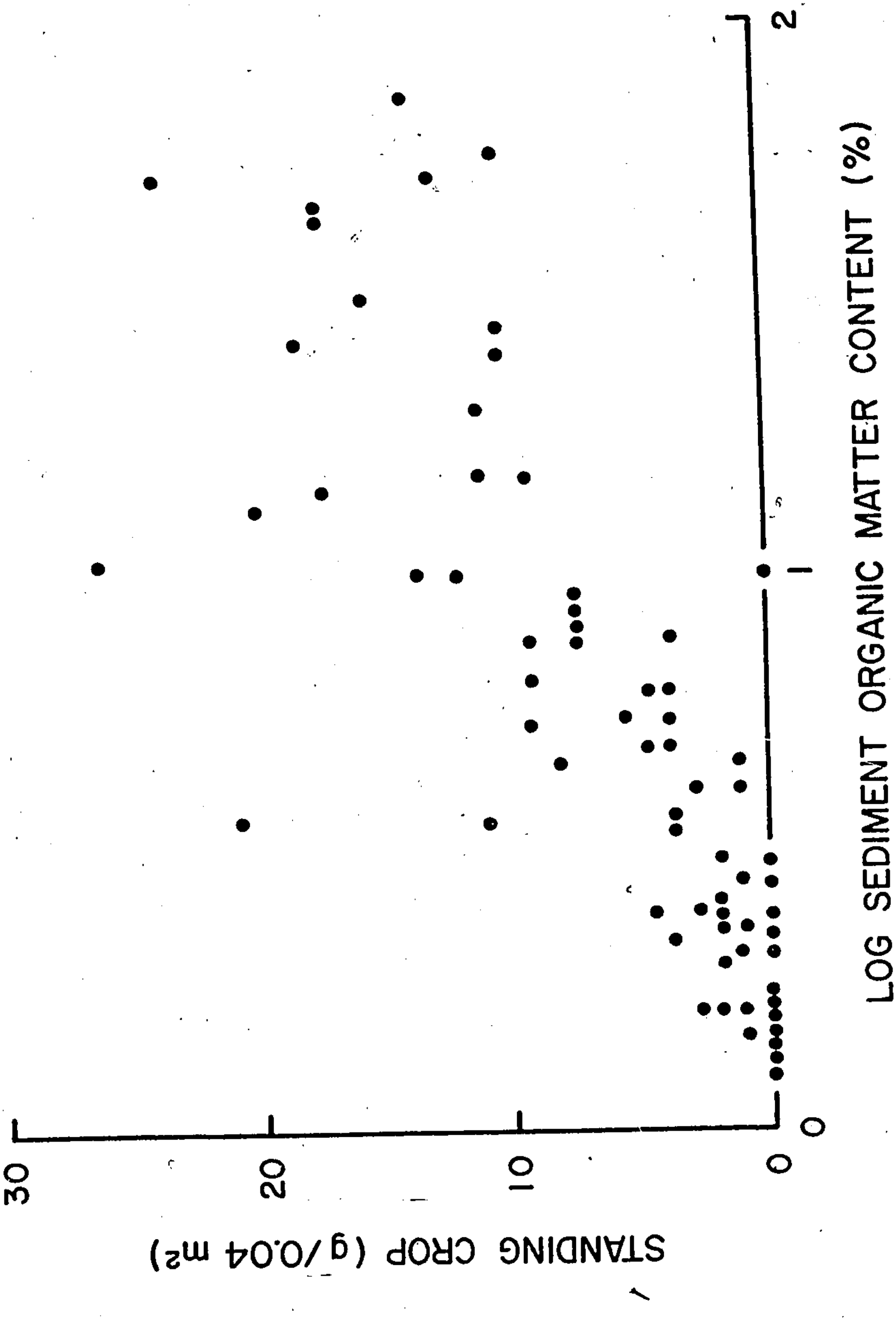

arcsine DIFFUSE COMPETITION
25
20
15
10
5
0
-5
-10
-15
SEDIMENT ORGANIC MATTER CONTENT (%)
0
1
2
3
4
5
6
7
8
9
10

FIG.6. The relationship between community standing crop and sediment organic matter content at Axe Lake. Standing crop is lowest on exposed, sandy shores and highest on sheltered shores with organic sediments.


STANDING CROP (g/0.04 m²)
30
20
10
0
0
1
2
LOG SEDIMENT ORGANIC MATTER CONTENT (%)

DISCUSSION

These results suggest that diffuse competition in a shoreline plant community is most intense where infrequent disturbance and nutrient-rich soils result in high standing crop.

I have assumed that the experiment ran long enough to detect variation in diffuse competition. Transplant shock resulting from desication was presumably unimportant because the ramets were transplanted under water. The experiment was conducted over 65 days during the season of warmest temperatures and greatest productivity for southern Canadian wetlands (Auclair _et_ _al_. 1976). Allowing the experiment to run for a second summer would likely increase the difference between plants grown in cleared and uncleared plots, producing a stronger relationship between diffuse competition and standing crop than is shown ~~in Figure~~ 4. I have also assumed that removing only above-ground biomass from cleared plots actually decreases competition. Below-ground biomass in the plots may continue to compete with transplanted ramets (Newman 1973). Below-ground competition, if present, would cause diffuse competition to be underestimated. Although the length of the experiment and below-ground competition may affect the measurement of competition, both of these factors should have resulted in an underestimation of diffuse competition in this study. Alternatively, below-ground biomass in cleared plots might have died, releasing nutrients and stimulating growth, resulting in an overestimation of diffuse competition. The production of new shoots from rhizomes and tubers in the cleared plots over the course of the experiment, however, makes this unlikely.

The relationship shown in Figure 4 varies with the species used to measure diffuse competition. A species may be insensitive to variation in diffuse competition if it is a strong competitor and seldom affected by competition. For example, the large and leafy Lysimachia terrestris showed no correlation between diffuse competition and standing crop. The use of different species in the experiment produces not only a general measure of diffuse competition, but can also provide information on the differential responses of several species to a gradient of of diffuse competition.

Mutualism among individuals is suggested where the values of DC in Figures 4 and 5 are negative. In these cases, plants grown with neighbours accumulated more biomass than those grown singly. On lakeshores mutualism might be expected at highly exposed sites where neighbours could provide shelter from wave action and stabilization of sediments. Mutualism may be tested for by determining whether the y-intercept of a regression line describing the relationship between diffuse competition and standing crop (Fig.4) is significantly less than 0. In this case, it was not (t =1.89, P =N.S.) (Zar 1974). Using more experimental locations than were employed in this experiment might allow better tests of hypotheses concerning intercepts and curvilinearity.

A mechanism common to several current models of species diversity is that there is variation in the intensity of competition within a community (Grime 1973, 1979, Connell 1979, Huston 1979, Lubchenco and Gaines 1981). Connell (1983) has discussed how the importance of competition may vary spatially, but no field experiment has explicitly tested for variation in diffuse competition along an environmental gradient. The results reported here corroborate the assumption that diffuse competition is inversely related to disturbance and environmental stress.

The role of exposure to wave-action as an underlying control of diffuse competition is suggested by the correlation between standing crop and sediment organic matter content (Fig.6). Shores exposed to high amounts of wave action have low sediment organic matter content and low standing crop, which may result in low intensities of diffuse competition.

These results agree with those of del Moral (1983) who related the differential survival of transplants in natural vegetation to habitat productivity and competition intensity. In a greenhouse experiment, Bazzaz and Harper (1976) grew a mixture of two species in soils of high and low fertility. They found that survival declined more rapidly and that one species was eliminated entirely on fertile soil, suggesting that competition was more intense under productive conditions. Experimental evidence shows that competition may be more intense in productive habitats than in unproductive environments (c.f. Newman 1973, Chapin and Shaver 1985).

Although controversy has surrounded the study of competition in ecological communities (Salt 1983), these results indicate that diffuse competition may vary predictably in nature. Moreover, Figures 4 and 5 suggest that the success of any particular experiment at measuring competition can depend on the environment considered. For example, field experiments with lakeshore plants have found no evidence that competition is at work in relatively disturbed or nutrient-poor habitats (McCreary _et_ _al_. 1983, Titus and Stephens 1983). In contrast, experiments in undisturbed and nutrient-rich field sites have suggested an important role for competition (Buttery and Lambert 1965, Grace and Wetzel 1981). Testing for variation in diffuse competition along environmental gradients in other plant communities may provide a more general understanding of the role of competition in nature.

CHAPTER 4

THE RELATIONSHIP BETWEEN PLANT COMPETITIVE ABILITY AND POSITION ALONG A NATURAL GRADIENT OF STRESS AND DISTURBANCE: A FIELD EXPERIMENT

Abstract

I tested the prediction that plant species growing in undisturbed, nutrient-rich habitats tend to have higher competitive abilities than those found in disturbed or nutrient-poor habitats. The distributions of seven species (Eriocaulon septangulare, Rhynchospora fusca, Hypericum ellipticum, Juncus pelocarpus, Lysimachia terrestris, Dulichium arundinaceum and Drosera intermedia) were measured along a gradient of exposure to wave action on the shore of Axe Lake, Ontario. Species distributions on the exposure gradient were quantified by determining the mean sediment organic matter content of the quadrats containing each species. Competitive abilities were measured in a field experiment in which species were grown together in all pair-wise combinations (N=10 replicates). Species had significantly different competitive abilities (P <0.01). Species found on exposed, nutrient-poor shores (e.g. E. septangulare) had low competitive abilities while those growing on sheltered, nutrient-rich shores (e.g. D. arundinaceum) had high competitive abilities. Competitive ability was significantly correlated with mean position on the exposure gradient.

INTRODUCTION

Grime (1973, 1977) predicted that species found in undisturbed, nutrient-rich habitats should have high competitive abilities relative to species found in more disturbed or stressful habitats. Models of species diversity proposed by Connell (1978) and Huston (1979) also imply that species occurring in infrequently disturbed habitats should have high competitive abilities. While the role of interspecific competition in determining species distributions along environmental gradients has received experimental attention (e.g. Sharitz and McCormick 1973, Mueller-Dombois and Ellenberg 1974:354, Pickett and Bazzaz 1979, Austin and Austin 1980, Grace and Wetzel 1981, Austin 1982, Parrish and Bazzaz 1982, Silander and Antonovics 1982, del Moral 1983, Snow and Vince 1984, Austin et al. 1985, Goldberg 1985) no test of this proposed relationship between species competitive abilities and distributions has been performed for a multi-species community. I examined the prediction that species' distributions along an environmental gradient are related to their competitive abilities. I first described the field distributions of seven plant species along the lakeshore exposure gradient, a natural environmental gradient that incorporates both stress and disturbance (*sensu* Grime 1979). I then measured the competitive abilities of the same species in a nutrient-rich, undisturbed habitat using a diallel experiment (Harper 1977). Lastly, I tested for a correlation between competitive ability and mean position on the environmental gradient. Competitive ability is defined as the ability of an individual to accumulate biomass in the presence of neighbours.

METHODS

Field distributions

The distributions of seven vascular plant species, Eriocaulon septangulare, Rhynchospora fusca, Hypericum ellipticum, Juncus pelocarpus, Lysimachia terrestris, Dulichium arundinaceum and Drosera intermedia (nomenclature follows Gleason and Cronquist 1963) were measured along the exposure gradient on the shoreline of Axe Lake, Ontario. Species distributions along the exposure gradient were described by breaking down the range of sediment organic matter content found into seven classes (class 1: 0.0-0.9%, class 2: 1.0-1.9%, class 3: 2.0-3.9%, class 4: 4.0-7.9%, class 5: 8.0-15.9%, class 6:16.0-31.9%, class 7: >32.0%) and calculating the relative frequency of occurrence of the seven study species in each class. Quadrats (0.5 x 0.5 m, N=243) were placed at 10 m intervals along the waterline of Axe Lake during 17-21 August 1984 and the presence of all species in each quadrat was recorded. Organic matter content of a sediment sample from the centre of each quadrat was determined and the sample categorized by the classes described above. Sediment samples (3.5 cm diameter, 5 cm deep) were frozen at -10° C within one week of collection and analyzed for organic content one month later (Dean 1974). Organic content is expressed as a percentage of sample dry weight. The mean position of each species on the exposure gradient was determined by calculating the mean sediment organic content value for the set of quadrats containing each species.

Competitive abilities

Competitive abilities were measured in a diallel experiment (Harper 1977) on the shore ~~of Axe~~ Lake. Polypropylene beakers (400 ml, diameter=8.5 cm) were filled with a bottom layer of 200 ml of sand and a top layer of 200 ml of organic shoreline sediment obtained from a sheltered shore of Axe Lake. This potting medium simulated the natural stratification of sediments on sheltered shores. Plants were collected during 18-20 May 1984. Ramets of each species of approximately equal size were selected and a subset of ten were randomly chosen for initial dry weight determination. Ramets were randomly assigned to beakers to produce ten replicates of all possible pair-wise combinations with two ramets per beaker during 21-22 May. Beakers were placed on flats just above the waterline on the shoreline in a sheltered bay and watered daily with lake water. A cylinder of fiberglass window screen 15 cm high was installed in each beaker on 28 June to ensure that ramets interacted only with the neighbour in their own beaker and did not influence the growth of plants in other beakers. The experiment was harvested during 1-4 September 1984. Plants were dried to constant weight and the total biomass of each species in each beaker was measured.

Results from competition experiments are often transformed as relative yield per plant (Harper 1977:260, Fowler 1982) in order to compare the yields of species of different sizes. Because I used vegetatively reproducing ramets, however, the relative increase of dry weight per plant (RIP) was of greater interest than relative yield. Relative increase per plant was calculated as

$$RIP_{ij}=(HDW_{ij}-SDW_{i})/(HDW_{ii}-SDW_{i})$$

where RIP_{ij} is the relative increase per plant of species i when grown with species j, HDW_{ij} is the harvested dry weight of one ramet of species i when grown with one ramet of species j, SDW_{i} is the mean starting dry weight of one ramet of species i, and HDW_{ii} is the mean harvested dry weight of one ramet of species i when grown with a conspecific neighbour. Thus, the RIP of a ramet grown with another of the same species is 1. A ramet may have RIP less than or greater than 1 when grown with a ramet of another species. An RIP value of less than 1 suggests that a species accumulates less biomass in the presence of an interspecific neighbour than with a conspecific neighbour. An RIP value greater than 1 suggests that the species accumulates more biomass when grown with an interspecific neighbour than with a conspecific neighbour.

Diallel experiments provide two measures of competitive ability. The first is the mean RIP of each species when grown with all species of neighbours. This mean RIP may be termed the target score because it is a measure of the mean effect of all species of neighbours on the single species acting as a target. A species has a high target score if, on average, it grows better with all other species than with itself. A species has a low target score if, on average, the species grows less well with all other species than with itself. The species can be ranked in order of competitive ability using target scores such that strong interspecific competitors have high target scores and subordinate competitors have lower scores.

The second measure of competitive ability produced by this analysis is the mean RIP associated with each species acting as a neighbour on all target species. The mean RIP of all target species with which a particular neighbour species was grown is called the neighbour score for that species. A species has a high neighbour score if, on average, other species tend to grow better with that interspecific neighbour than with themselves. A species has a low neighbour score if other species tend to grow less well with the interspecific neighbour than with themselves. Thus, species can be ranked in order of their competitive abilities using their neighbour scores such that strong competitors have low neighbour scores (because they suppress target species) and subordinate competitors have higher neighbour scores (because they release target species). Target and neighbour scores may be negatively correlated (Jacquard 1968).

A two-factor analysis of variance was used to test for significant target and neighbour effects. No transformation was found to produce homoscedasticity of variances. The results of the analysis should therefore be interpreted with caution, although Ito (1980) states that ANOVA is extremely robust under heteroscedastic conditions when sample sizes are large and equal, and dimensionality is low. Tukey's studentized range test was used to identify groups of species not significantly different in competitive ability.

Competitive abilities and field distributions

Correlations were calculated between mean position on the exposure gradient and both measures of competitive ability (target and neighbour scores) using 1-tailed Pearson's r. To test the significance of the correlation between mean position and overall competitive ability, the probabilities associated with the correlations between position and both target and neighbour scores were combined (Sokal and Rohlf 1969). Correlations were then calculated for the complete set of seven species and for the set with one insectivorous species, *Drosera intermedia* , excluded.

RESULTS

Field distributions

Fig.7 shows the distribution along the exposure gradient of each species. Eriocaulon septangulare occurred most frequently on exposed shores with low sediment organic matter content while Lysimachia terrestris and Dulichium arundinaceum were most common on sheltered shores with high organic content. Others, such as Rhynchospora fusca and Juncus pelocarpus, had intermediate distributions.

Competitive abilities

Table 2 shows the RIP of each species grown in all possible pairwise combinations. ANOVA (Table 3) showed significant effects ($P < 0.01$) for both target scores (rows in Table 2) and neighbour scores (columns). Groups of species not significantly different in competitive ability are given in Table 2.

Competitive abilities and field distributions

A significant correlation was found between competitive ability and mean position on the exposure gradient for the set of species excluding the insectivorous Drosera intermedia (correlation between competitive ability measured as target scores and position: $r = 0.77$, $P = 0.035$; correlation between competitive ability measured as neighbour scores and position: $r = -0.68$, $P = 0.068$; combined probability: χ^2

=12.07, 0.01< P <0.025)(Fig.8). A weaker relationship was found when *D.intermedia* was included in the analysis (target scores: r =0.61, P =0.071; neighbour scores: r =-0.36, P =0.211).

FIG.7. The distributions of seven plant species along the exposure gradient at Axe Lake, Ontario. Exposure is measured as sediment organic matter content (Wilson and Keddy 1985). The mean sediment organic content associated with each species is indicated by an arrow. Species' names are abbreviated as follows: Eri: Eriocaulon septangulare, Rhy: Rhynchospora fusca, Jun: Juncus pelocarpus, Hyp: Hypericum ellipticum, Dro: Drosera intermedia, Lys: Lysimachia terrestris, Dul: Dulichium arundinaceum.

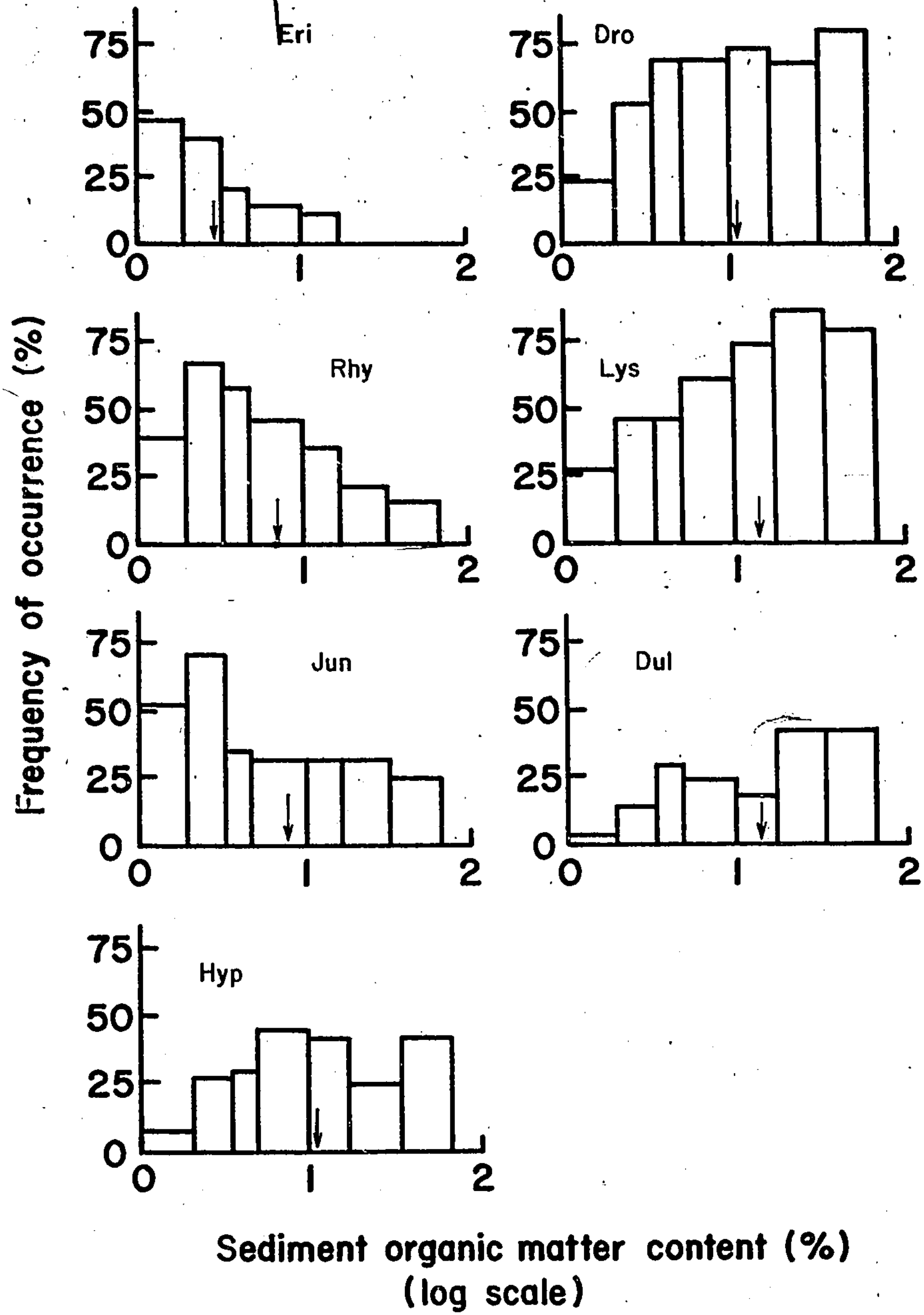

Eri
Dro
Rhy
Lys
Jun
Dul
Hyp
0
25
50
75
0
1
2
Frequency of occurrence (%)
Sediment organic matter content (%)
(log scale)

TABLE 2. Relative increase per plant (RIP) of seven species grown in all pairwise combinations.

Target species*	Neighbour Species							Target scores‡
	Dul	Jun	Lys	Hyp	Rhy	Dro	Eri	
Dul	1.00	1.33	1.18	1.17	1.25	1.18	1.34	1.20^{ab}
Jun	0.63	1.00	1.34	1.46	1.46	1.52	1.49	1.28^{a}
Lys	0.88	0.87	1.00	1.63	1.63	1.78	1.57	1.31^{a}
Hyp	1.09	0.99	0.91	1.00	1.22	1.29	1.23	1.11^{abc}
Rhy	1.05	0.73	0.93	0.91	1.00	1.21	1.36	1.03^{bc}
Dro	0.98	0.91	0.93	1.02	1.02	1.00	1.11	0.98^{bc}
Eri	0.65	0.71	0.88	0.89	0.87	1.48	1.00	0.93^{c}
Neighbour scores‡	0.89^{a}	0.93^{ab}	1.03^{abc}	1.15^{bcd}	1.21^{cd}	1.35^{d}	1.30^{d}	

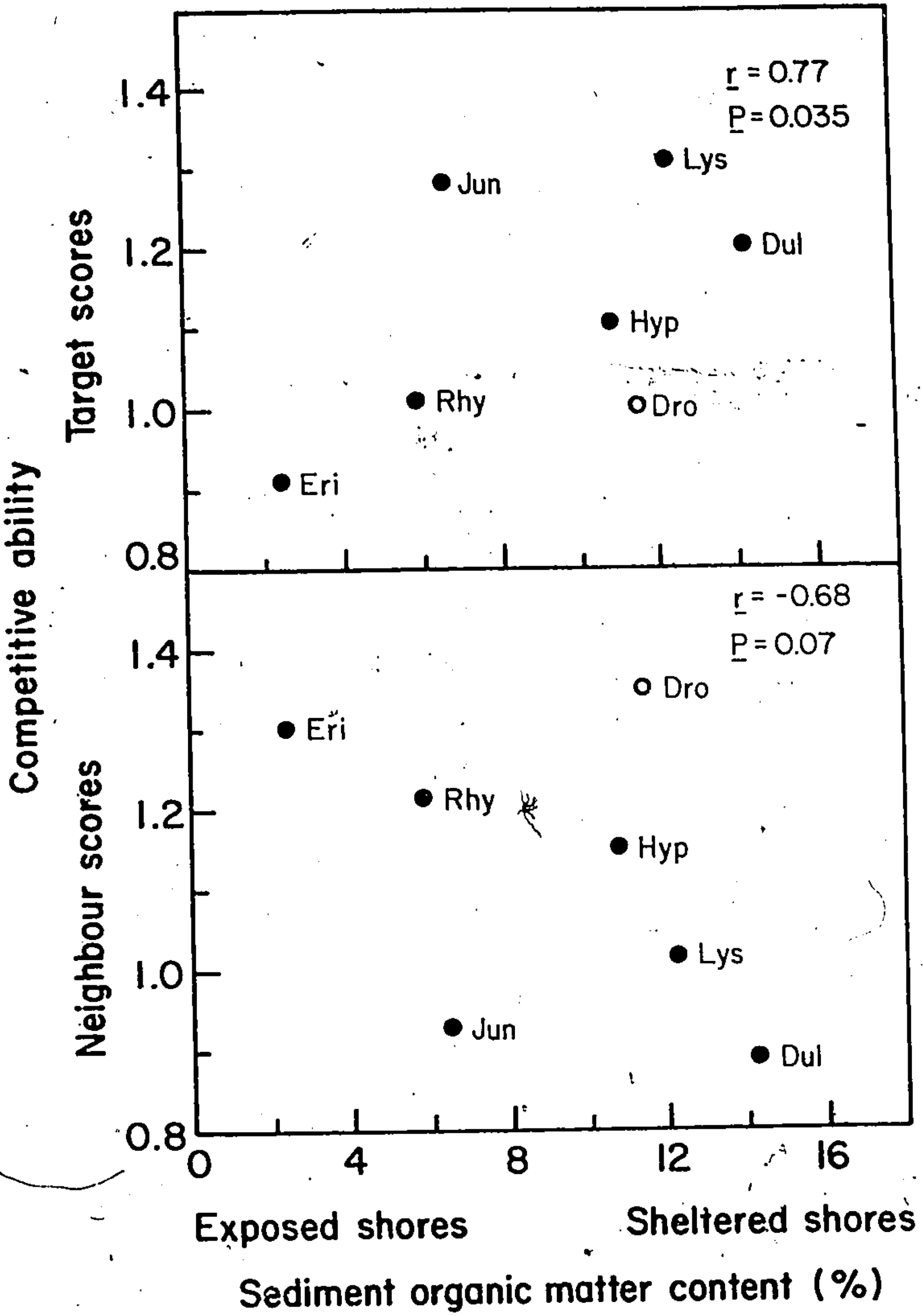
* Species names abbreviated as in Fig.7 .

‡ Target and neighbour scores not significantly different from one another (Tukey's studentized range test, $P < 0.05$) are denoted by superscripts.

TABLE 3. Two-factor analysis of variance of diallel experiment.

Source	D.F.	SS	MS	F	P
Targets	6	9.37	1.56	7.79	0.01
Neighbours	6	13.37	2.23	11.11	0.01
Error	461	92.47	0.20		
Total	473	115.22			

FIG.8. The relationship between the competitive abilities and mean positions on the exposure gradient of seven plant species: Competitive abilities were measured as target scores (the mean relative increase in dry weight of a species grown in the presence of all species of neighbours) and as neighbour scores (the mean relative increase in dry weight of all species in the presence of a particular target species). Correlations are given for the set of species excluding the insectivorous Drosera intermedia. Species names are abbreviated as in Fig.7.


r = 0.77
P = 0.035
Lys
Jun
Dul
Hyp
Rhy
Dro
Eri
Target scores
1.4
1.2
1.0
0.8
r = -0.68
P = 0.07
Dro
Eri
Rhy
Hyp
Lys
Jun
Dul
Neighbour scores
Competitive ability
1.4
1.2
1.0
0.8
0
4
8
12
16
Exposed shores
Sheltered shores
Sediment organic matter content (%)

DISCUSSION

The diallel experiment demonstrates that the study species have significantly different competitive abilities. There are many factors, however, that may influence species ranking within a competitive hierarchy produced by an experiment. Probably the most important of these is the environment in which the experiment is conducted (Harper 1977). Fowler (1982) found that the dominance hierarchy described by diallel experiments varied with water availability and time of year. Moore and Williams (1983) showed that the competitive hierarchy within a group of weedy species varied with soil nutrients. I used an experimental environment representing sheltered bays, that portion of the exposure gradient where plants accumulate biomass most rapidly (Wilson and Keddy 1985) and disturbance is minimal (Keddy 1985). Community standing crop and diffuse competition are also highest in this habitat (Wilson and Keddy 1986) and competitive ability is presumably most important for success in this type of environment. The results do not exclude the possibility that competitive dominance varies with position on the exposure gradient (Tilman 1985).

Competitive hierarchies may also vary seasonally: the experiment was performed during the only time of the year the plants are capable of growth, since the shoreline is covered by deep water, ice and snow from October to May. Further, this experiment considered only pair-wise species interactions and may not provide information about the species' relative aggressiveness in multi-species mixtures. Lastly, Inouye and Schaffer (1981) note that the outcome of any replacement series experiment (many of which comprise a diallel experiment) may vary with total density. Aarssen (1985) has also warned against comparing the suppression of two species when the carrying capacities for the species in the experiment are unknown. The competitive hierarchy described by this experiment is likely unique to the particular starting density used. In summary, while diallel experiments have clearly-recognized limitations, they do allow among-species comparisons of competitive ability while controlling for density, abiotic factors and neighbours (McGilchrist 1965, Norrington-Davies 1967, Harper 1977, Fowler 1982).

The use of mean RIP values (target and neighbour scores) as a measure of competitive ability should be interpreted with caution, because RIP may be > 1 for two distinct reasons. RIP > 1 may indicate i) that one species has outcompeted the other; or ii) that the species of interest exploits a different array of resources than its interspecific neighbour. In the second case, RIP is attributable to niche differentiation (Aarssen pers. comm.). Niche differeniation is suggested where RIP > 2. In contrast, RIP values < 1 (suppression) can only be attributed to interspecific competition. An alternative analysis of competitive ability that avoids confusion between competitive ability and niche differentiation is to consider only RIP values that are attributable to competitive suppression, i.e. cases where RIP < 1. Therefore, I have also estimated the competitive ability of each species as the number of neighbouring species which suppressed its growth. Species were ranked from strong competitors, which were rarely suppressed, to weak competitors, which were frequently suppressed. The number of suppressions for each species was subtracted from the total number of species in the experiment so that species with high competitive abilities received high scores and those with low abilities received low scores. The correlation between this measure of competitive ability and mean position on the exposure gradient was then tested using 1-tailed Pearson's r. Fig.9 shows that competitive ability was significantly correlated with position on the exposure gradient (r =0.71, P <0.05). These results agree with those given in Fig. 8.

Fig.8 shows that species with high competitive abilities occupy sheltered, nutrient-rich shores while species with low competitive ability are characteristic of disturbed, sandy habitats. This relationship is significant, however, only when the insectivorous Drosera intermedia is excluded from consideration; Drosera has low competitive ability but is found on relatively undisturbed, organic shorelines. Wilson (1985) has shown experimentally that insectivory allows Drosera to avoid competitive suppression by exploiting a nutrient source unavailable to other species. Evidence that the growth of *Drosera* is unaffected by other species is given in Table 2 by the target scores for *Drosera* : RIP ≃ 1 for this species acting as a target, indicating that *Drosera* grows as well with any other species as it does with itself. The ability of *Drosera* to use insects as a nutrient source may allow this small rosette species (1 - 8 cm high, Gleason and Cronquist 1963) to grow in undisturbed, densely vegetated habitats, accounting for its position in Fig.8. In contrast, the study species most morphologically similar to *Drosera*, *Eriocaulon septangulare*, is restricted to disturbed habitats with low standing crop (Fig.8).

Considerable variability remains in the relationship shown in Fig.8 even when *D.intermedia* is excluded. This variability is partly due to problems inherent in the measurement of competitive ability discussed above. There may also exist variability in the relative positions of the species along the exposure gradient produced by the use of presence-absence data to measure distributions: examination of the distribution of biomass of each species along the exposure gradient might produce different results. Lastly, a perfect relationship should perhaps not be expected since relative competitive abilities are almost certainly not the only determinant of species distributions along an environmental gradient. The relative importance of dominance hierarchies in determining species distributions along gradients remains to be explored.

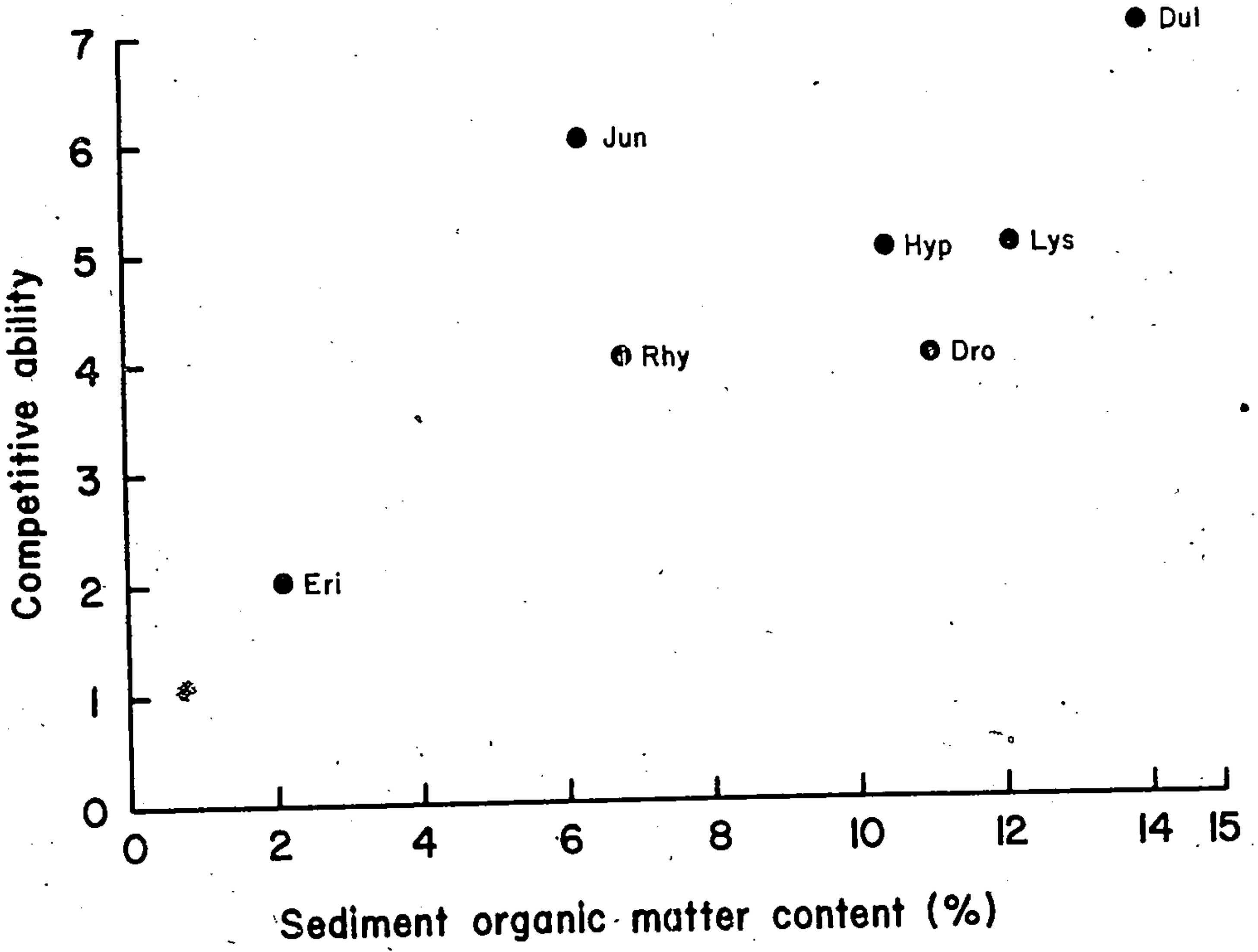
Previous experimental work has described the rôle of competition in producing zonation patterns (e.g. Connell 1961, Austin and Austin 1980, Lubchenco 1980, Grace and Wetzel 1981), but the relationship between position in a competitive hierarchy and distribution along a natural gradient for multiple-species sets has not been examined. Those studies which have considered this relationship have estimated competitive ability using species characters likely to be related to competitive success. Grime and Hunt (1975) examined the relationship between maximum potential growth rates and field distributions within a local flora. As they noted, however, high growth rates are found in both competitive and ruderal species. Boorman (1982) also suggested that a relationship might exist between growth rates and the distributions of sand dune plants. Menges and Waller (1983) used published maximum heights to relate competitive ability to occurrence in productive, undisturbed habitats within a floodplain. Experimentally-measured competitive abilities allow a direct test of the predicted relationship between competitive ability and distribution.

Yodzis (1978) has discussed the effects of disturbance on community structure. He notes that the shape of diversity-disturbance relationships would depend on the competitive relationships of the species removed by disturbance. In particular, if disturbance removed competitive dominants, then intermediate levels of disturbance could lead to increased species diversity (see Huston 1979, Grime 1979).

Alternatively, if disturbance removed competitive subordinates, then diversity should simply decrease with increasing disturbance. Fig.8 suggests that disturbance eliminates competitive dominants, thereby allowing competitive subordinates to occupy more disturbed or stressed sites. The diversity-disturbance relationship in shoreline plant communities is also consistent with this postulated mechanism. Species richness reaches a maximum at intermediate levels of disturbance in Axe Lake (Keddy 1983). A similar, but weaker, intermediate disturbance relationship has also been documented on a second lakeshore exposure gradient (Keddy 1984). There may be a basic morphological explanation for disturbance selectively removing competitive dominants. The very attributes which contribute to competitive dominance (such as tall, leafy shoots, Grime 1979) may make them susceptible to wave damage. Conversely, the morphologies most resistant to wave damage (small rosettes) may be weak competitors since they are unable to shade taller species. This could be the mechanism producing the situation postulated by Yodzis (1978), where competitive dominants are selectively reduced by disturbance.

In conclusion, the results suggest that the competitive abilities of plant species may vary predictably, so that superior competitors are frequently found in habitats where stress and disturbance (sensu Grime 1979) are minimal and diffuse competition is intense (Wilson and Keddy 1986). Because stress and disturbance vary along other environmental gradients (e.g. altitude on mountains, height in the rocky intertidal zone, depth in the abyssal seas), competitive hierarchies may be correlated with zonation patterns in other multi-species communities.

FIG.9. The relationship between the competitive abilities and mean positions on the exposure gradient, of seven plant species, where the competitive ability of each species is calculated as the number of neighbour species by which it is suppressed (see Discussion). Relative competitive ability is correlated with position on the exposure gradient (r =0.71, P <0.05). Species names are abbreviated as in Fig.7.


Dul
Jun
Hyp
Lys
Rhy
Dro
Eri
Competitive ability
0
1
2
3
4
5
6
7
0
2
4
6
8
10
12
14
15
Sediment organic matter content (%)

GENERAL DISCUSSION

Figure 1 shows that the plant species are distributed differentially along the exposure gradient in Ontario lakes. Further, the rank order of species along the gradient is the same in four different lakes (App. 1), suggesting that the factors controlling species distributions are at work regardless of the particular lake considered.

In spite of their different distributions, the species have similar physiological response curves when grown in sediment from various points along the exposure gradient in a pot experiment (Fig.2) and when grown along the natural gradient in the absence of neighbours (Fig.3b). Therefore, with the exception of Lobelia dortmanna, the different field distributions are not attributable to the species having different physiological responses to physical factors varying along the exposure gradient. The species have different ecological response curves but similar physiological response curves, suggesting that competition may be partially responsible for the differential field distributions shown in Fig.1.

It has been suggested that the differential field distributions of species along an environmental gradient is evidence that species have specialized on different parts of a resource spectrum, and that such specialization has resulted from competition-driven selection (Whittaker 1965, Werner and Platt 1976). Experimental evidence suggests, however, that different ecological response curves do not necessarily mean that plant species are physiologically incapable of exploiting an identical range of resources in the absence of interspecific competition. Descriptive studies of field distributions do not provide evidence for physiological specialization on different habitats. In the case of shoreline plants, it may be unreasonable to expect a species to specialize on disturbed, nutrient-poor shores as long as opportunities occasionally arise which permit species such as Eriocaulon septangulare or Juncus pelocarpus to exploit nutrient-rich habitats and accumulate more biomass, presumably resulting in higher seed set and increased fitness. Such opportunities may arise through occasional disturbance on sheltered shores.

Given that species accumulate biomass most rapidly on sediment from sheltered bays (Fig.2), it might be expected that diffuse competition would be most intense there. My results suggest that the effect of neighbours in restricting biomass accumulation by individuals is greatest in habitats that support high standing crop (Fig.4), where sediments are nutrient-rich and disturbance is low (Fig.5). Although predictable variation in diffuse competition along environmental gradients is an assumption central to current models of species diversity (Grime 1973, Connell 1978, Huston 1979), it has not previously been experimentally examined.

Because diffuse competition varies along the exposure gradient, species distributions might be expected to be related to their competitive abilities. Species with relatively high competitive abiltity should be found in habitats where competition is intense whereas species with low competitive ability should occur elsewhere. Figures 8 and 9 suggest that this prediction is corroborated in the shoreline plant community: tall, dominant species occupy habitats with high standing crop and intense competition while smaller competitive subordinates are found on nutrient-poor habitats that are subject to disturbance from wave action. This relationship between species competitive abilities and field distributions has not previously been investigated.

In summary, shoreline plant species are distributed differentially along the exposure gradient in spite of the fact that the species have significantly similar physiological response curves along the same gradient: species tend to accumulate biomass most rapidly on nutrient-rich sediments from sheltered bays. Further, species distributions along the gradient are related to their competitive abilities, such that dominant species occupy sheltered shores where diffuse competition is most intense. These experiments suggest that competition for space in sheltered bays is partly responsible for the distribution patterns of plant species along the exposure gradient in nature.

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APPENDIX 1

AGREEMENT OF SPECIES DISTRIBUTIONS AMONG FOUR LAKES

To test whether species were distributed along the exposure gradient in the same rank order in different lakes, the range of sediment organic matter content found in the field was broken down onto five broad classes and the relative frequency of occurrence of the six most common species was calculated for each of the four most intensively sampled lakes. The figures in the table below represent the organic matter class in which each species was most abundant. The relative positions of species along the gradient in each lake were then expressed as ranks and tested for agreement among lakes using Kendall's *W*. The ranking of species along the exposure gradient was similar among lakes (*P* < 0.01).

	Species*					
Lakes	TRI	DUL	LYS	DRO	ERI	JUN
Axe	5	4	5	2	1	1
Black Oak	5	5	4	3	3	1
Matchedash	5	5	2	4	1	1
Three Mile	4	5	3	4	3	1

* Species names abbreviated as follows: TRI - *Triadenum fraseri*, DUL - *Dulichium arundinaceum*, LYS - *Lysimachia terrestris*, DRO - *Drosera intermedia*, ERI - *Eriocaulon septangulare*, JUN - *Juncus pelocarpus*.

APPENDIX 2

PHYSIOLOGICAL RESPONSE CURVE DATA

(CHAPTER 1)

Mean dry weight (g) and 95% lower and upper confidence limits of each species grown at ten levels of sediment organic matter content (N = 5 replicates). Levels are arranged from lowest to highest organic matter content values.

		Level									
Species*		1	2	3	4	5	6	7	8	9	10
TRI	x̄	0.61	0.58	0.53	0.81	0.82	0.87	0.95	0.50	0.80	1.04
	LCL	0.31	0.46	0.38	0.34	0.44	0.69	0.36	0.00	0.27	0.41
	UCL	0.92	0.71	0.68	1.07	1.21	1.05	1.55	1.05	1.33	1.67
DUL	x̄	1.62	1.66	1.94	2.50	2.24	2.70	5.20	7.30	9.94	10.17
	LCL	0.91	1.17	1.22	1.50	1.87	2.44	3.58	5.90	7.95	7.14
	UCL	2.32	2.15	2.65	3.51	2.60	2.96	6.82	8.70	11.93	13.19
LYS	x̄	1.29	1.38	1.39	1.41	1.52	1.58	1.34	3.01	6.84	5.17
	LCL	0.21	0.81	0.66	1.12	0.94	0.00	0.90	1.04	4.64	3.20
	UCL	2.37	1.96	2.13	1.70	2.10	3.42	1.77	5.00	9.04	7.14
CAL	x̄	3.34	3.05	4.29	4.08	4.32	5.15	4.18	5.52	9.44	9.32
	LCL	2.83	2.56	1.38	3.46	3.25	2.78	2.99	3.71	6.97	4.74
	UCL	3.86	3.55	7.20	4.70	5.40	7.53	5.36	7.33	11.91	13.91
DRO	x̄	0.39	0.29	0.37	0.32	0.33	0.30	0.28	0.56	0.60	0.48
	LCL	0.11	0.14	0.12	0.12	0.19	0.12	0.22	0.30	0.18	0.19
	UCL	0.66	0.44	0.62	0.52	0.46	0.49	0.33	0.82	1.02	0.77
HYP	x̄	0.30	0.49	0.40	0.49	0.53	0.41	0.72	0.43	0.34	0.40
	LCL	0.24	0.30	0.29	0.29	0.21	0.22	0.37	0.16	0.12	0.21
	UCL	0.36	0.68	0.50	0.70	0.86	0.59	1.07	0.70	0.57	0.59
XYR	x̄	1.32	1.51	1.63	2.83	2.19	2.23	3.06	3.46	2.38	4.72
	LCL	0.48	0.81	1.13	1.51	1.57	1.80	1.36	2.26	1.23	1.76
	UCL	2.16	2.22	2.14	4.15	2.81	2.65	4.76	4.65	4.14	7.67
CLA	x̄	4.10	3.85	3.57	4.60	4.30	5.49	5.94	7.29	5.24	6.98
	LCL	3.10	2.61	1.67	2.29	3.32	3.79	3.73	2.83	2.88	3.03
	UCL	5.09	5.08	5.97	6.91	5.27	7.19	8.15	11.74	7.60	10.92
JUN	x̄	2.39	2.31	4.18	4.38	2.69	3.54	4.38	12.08	9.97	6.18
	LCL	0.56	0.80	2.42	0.08	1.05	2.25	1.50	2.51	3.56	4.73
	UCL	4.22	3.82	5.93	8.66	4.32	4.82	7.25	21.65	16.37	7.63

APPENDIX 2 (CONTINUED).

ERI	$\bar{x}$	0.27	0.25	0.34	0.55	0.51	0.57	0.76	0.68	0.91	0.91
	LCL	0.05	0.02	0.14	0.15	0.18	0.20	0.28	0.29	0.79	0.00
	UCL	0.48	0.50	0.55	0.96	0.84	0.94	1.24	1.07	1.02	1.95
RHY	$\bar{x}$	1.72	1.69	2.20	3.20	3.46	3.30	4.52	5.46	10.98	7.87
	LCL	1.23	1.30	1.68	2.61	2.45	1.65	3.29	3.36	7.03	6.23
	UCL	2.21	2.07	2.72	3.78	4.48	4.95	5.75	7.55	14.93	9.51
LOB	$\bar{x}$	0.14	0.15	0.25	0.30	0.28	0.26	0.23	0.36	0.37	0.32
	LCL	0.07	0.03	0.13	0.00	0.08	0.11	0.15	0.24	0.23	0.15
	UCL	0.20	0.27	0.37	0.63	0.49	0.41	0.31	0.47	0.51	0.49

* Species names are abbreviated as follows: TRI - Triadenum fraseri, DUL - Dulichium arundinaceum, LYS - Lysimachia terrestris, CAL - Calamagrostis canadensis, DRO - Drosera intermedia, HYP - Hypericum ellipticum, XYR - Xyris difformis, CLA - Cladium mariscoides, JUN - Juncus pelocarpus, ERI - Eriocaulon septangulare, RHY - Rhynchospora fusca, LOB - Lobelia dortmanna.

APPENDIX 3.

PHYSIOLOGICAL RESPONSE CURVE DATA (CHAPTER 2)

Mean dry weight (g) and 95% lower and upper confidence limits of ramets grown at seven locations along the exposure gradient at Axe Lake (N=10 replicates). Missing values (indicated by --) signify ramet death. Stations are arranged from most to least exposed.

		Stations						
Species*		1	2	3	4	5	6	7
DUL	$\bar{x}$	0.03	0.25	0.45	1.24	0.83	0.28	2.19
	LCL	–	–	0.13	0.47	0.45	0.11	1.36
	UCL	–	–	0.76	2.02	1.21	0.44	3.02
TRI	$\bar{x}$	0.09	0.03	0.12	0.10	–	0.04	0.17
	LCL	0.02	–	0.06	–	–	-0.03	-1.19
	UCL	0.16	–	0.17	–	–	0.11	1.52
LYS	$\bar{x}$	0.10	0.01	0.20	0.38	0.10	0.07	0.13
	LCL	–	–	0.12	0.03	0.05	0.02	0.08
	UCL	–	–	0.28	0.73	0.15	0.11	0.19
CLA	$\bar{x}$	1.36	1.41	1.88	1.65	0.59	1.24	3.51
	LCL	0.85	0.17	1.15	-0.42	-2.61	0.51	-2.59
	UCL	1.86	2.65	2.61	3.71	3.80	1.96	9.61
RHY	$\bar{x}$	0.06	–	0.10	0.10	0.06	0.09	0.15
	LCL	0.03	–	0.06	-0.13	-0.26	0.04	0.01
	UCL	0.09	–	0.14	0.32	0.37	0.14	0.29
XYR	$\bar{x}$	0.05	–	0.10	0.07	0.08	0.05	0.15
	LCL	–	–	0.07	-0.10	–	0.02	0.07
	UCL	–	–	0.13	0.24	–	0.07	0.22
JUN	$\bar{x}$	0.01	–	0.04	0.07	0.02	0.06	0.25
	LCL	–	–	0.01	-0.02	-0.01	-0.04	0.05
	UCL	–	–	0.06	0.16	0.04	0.16	0.45
ERI	$\bar{x}$	–	–	0.07	0.16	0.07	0.06	0.16
	LCL	–	–	0.03	–	0.00	0.02	0.06
	UCL	–	–	0.11	–	0.13	0.10	0.26
LOB	$\bar{x}$	–	–	0.03	0.05	0.06	0.02	0.01
	LCL	–	–	0.02	0.02	-0.11	0.02	0.00
	UCL	–	–	0.05	0.08	0.23	0.03	0.03

APPENDIX 3 (CONTINUED)

* Species names are abbreviated as follows: DUL - *Dulichium arundinaceum*, TRI - *Triadenum fraseri*, LYS - *Lysimachia terrestris*, CLA - *Cladium mariscoides*, RHY - *Rhynchospora fusca*, XYR - *Xyris difformis*, JUN - *Juncus pelocarpus*, ERI - *Eriocaulon septangulare*, LOB - *Lobelia dortmanna*.

APPENDIX 4

DIFFUSE COMPETITION EXPERIMENT DATA

Mean dry weight (g) of each species (with lower and upper 95% confidence limits) grown in cleared and uncleared plots at eight stations along the exposure gradient at Axe Lake (*N* = 10 replicates). Stations are arranged from most to least exposed.

			Station							
Species			1	2	3	4	5	6	7	8
Juncus pelocarpus										
	Cleared	$\bar{x}$	.020	.010	.137	.018	.029	.032	.024	.065
		LCL	.011	.005	-.084	.013	.019	.014	.014	.018
		UCL	.029	.014	.357	.023	.039	.050	.035	.112
	Uncleared	$\bar{x}$	.015	.016	.045	.017	.027	.022	.021	.022
		LCL	.008	.008	-.015	.006	.017	.006	.011	.006
		UCL	.021	.025	.105	.027	.036	.039	.031	.037
Lysimachia terrestris										
	Cleared	$\bar{x}$	.271	.128	.132	.216	.226	.184	.244	.168
		LCL	.152	.057	.086	.170	.131	.137	.181	.120
		UCL	.389	.200	.178	.261	.322	.232	.307	.217
	Uncleared	$\bar{x}$	.275	.099	.168	.106	.169	.117	.215	.179
		LCL	.152	.051	.089	.071	.131	.066	.117	.107
		UCL	.398	.147	.247	.141	.207	.167	.313	.250
Rhynchospora fusca										
	Cleared	$\bar{x}$	.058	.035	.043	.072	.100	.067	.103	.091
		LCL	.046	.028	.030	.032	.049	.051	.060	.067
		UCL	.071	.042	.057	.111	.150	.083	.146	.115
	Uncleared	$\bar{x}$	.063	.041	.054	.051	.118	.049	.072	.060
		LCL	.046	.027	.047	.040	.068	.029	.027	.042
		UCL	.081	.055	.061	.062	.167	.068	.117	.079