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

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SUMMARY

(1) The distributions of twelve shoreline plant species were measured along a gradient of substratum organic content in six Canadian lakes.

(2) The organic content gradient reflects varying amounts of wave energy arriving on shorelines; it is positively correlated with substratum silt and clay content and with concentrations of P, K, Ca and Mg.

(3) The frequencies of occurrence of eleven species varied significantly ($P < 0{\cdot}05$) along the gradient. Different species reached maximum frequency at different substratum organic contents.

(4) The same species were grown singly at ten different substratum organic contents. Biomass accumulated after one growing season varied significantly ($P < 0{\cdot}05$) with substratum organic content for each of eleven species. The physiological response curves of the species along the gradient were similar ($P < 0{\cdot}01$).

(5) The experiment suggests that the differential distributions of the species along the gradient are not entirely attributable to differential physiological responses.

INTRODUCTION

The distribution of freshwater plant species along gradients of depth and exposure has been extensively studied, but recent reviews (Hutchinson 1975; Spence 1982) have given little consideration to the possible importance of competition between species in producing zonation. 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). Similarly, Grace & Wetzel (1981) and Snow & Vince (1984) present evidence that competition produces zonation in marshes. 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 when grown along the gradient in the absence of neighbours (Mueller-Dombois & Ellenberg 1974; Ernst 1978; Austin & Austin 1980). If, however, 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, the zonation might result from biological interactions in the field. The purpose of this study was to describe the distributions of a set of species along a naturally-occurring gradient and then experimentally to test the similarity of their physiological response curves along the gradient.

The community chosen for study was composed of shoreline plants distributed along a gradient of substratum organic content that runs parallel to the water-line of lakes in central Ontario, Canada; one end of the organic-content gradient is found on sand beaches and the other in organic bays. The community studied occurs in a horizontal band 10–25 cm vertically above the summer water-level. The gradient is produced by different intensities of wave energy arriving at different parts of a shoreline (Pearsall 1920; Spence 1967, 1982; Hutchinson 1975; Keddy 1982, 1984). Variations in organic content also affect the vertical zonation of species (Pearsall 1920; Thunmark 1931; Hutchinson 1975; Keddy 1983), but this study is concerned only with horizontal changes in species abundances.

Our study had three objectives: (i) to measure the correlation between substratum organic content and other abiotic variables; (ii) to examine the distributions of twelve species of varying morphologies along the gradient in order to test whether the species were distributed differentially—this was done in several lakes to test whether distribution patterns were consistent at different locations; (iii) to test whether the twelve species had different or similar physiological responses when grown singly along the gradient.

METHODS

Organic content gradient: correlated variables

Abiotic variables along the gradient were measured along a 600-m section of the north end of Axe Lake, Ontario, Canada (45°23′N, 79°30′W) (Keddy 1981). Twenty-five sites along the shore were randomly chosen for sampling on 22 July 1979. Three samples were taken from each site: one 0·25 m vertically above the waterline, the second at the waterline, and the third 0·25 m below the waterline. Each sample comprised five soil cores (10-cm deep, 3-cm diameter) collected in a 0·5 × 0·5 m quadrat; one core from the centre and one from each corner. The five cores were combined into one substratum sample and frozen 8 h later to −5 °C. The pH values for each were determined in the field using a portable meter; where no interstitial water was present, samples were wetted with 5 ml of distilled water. Also, the slope of the shoreline for each site was calculated from levellings.

Each sample was later thawed, dried at 85 °C, and then thoroughly mixed. The samples were analysed for organic content, sand fractions, silt and clay content, sorting coefficient (see below), nutrient status (concentrations of P, K, Mg, and Ca), and conductivity, using the following procedures.

One subsample of each was analysed for nutrients and conductivity by the University of Guelph Soil Test Laboratory, Guelph, Ontario. Potassium, magnesium and calcium were measured using standard methods (Black 1965) after the neutral normal-ammonium extraction method and phosphorus was measured after the Olsen extraction procedure (Black 1965). Because available nutrients are highly reactive, especially in shoreline soils which may be oxidized or reduced depending on water levels (Ponnamperuma 1972), the absolute values are less important than the differences found between samples collected from different sites at the same time. All nutrients varied considerably among samples (e.g. P, 1–43 mg l^{-1}; K, 4–180 mg l^{-1}; Mg, 5–131 mg l^{-1}; Ca, 25–675 mg l^{-1}).

A second subsample was used for particle-size analysis. Although the standard method (Black 1965) is first to remove organic content with peroxide, the high organic content of the samples (up to 50%) required that organic matter be removed by ignition at 400 °C for 24 h prior to particle-size analysis. This temperature may consolidate the clay portion of a sample (Folk 1968), but most of the samples were very sandy; and clay and silt proportions were less than 10%. Therefore each subsample was ignited, cooled, and weighed to determine its organic content and then sorted in sieves with mesh sizes of 1, 0·5, 0·25, 0·10, and 0·05 mm to separate to very coarse, coarse, medium, fine, and very fine sand. Material that passed through the 0·05-mm sieve was weighed as silt and clay.

Combustion of organic matter leaves an ash residue which falls into the silt and clay category when sieved and this could produce a spurious positive correlation between the organic content and the silt and clay content. It was corrected for by determining the ash content of a sample of known organic content; this produced an ash to organic content quotient by weight of approximately 0·05. Then, for each sample unit, the expected weight of ash (from the known loss-on-ignition multiplied by 0·05) was subtracted from that of silt- and clay-sized particles. In all cases, only a small amount of ash was present.

The data on soil particle size were in three parts: (i) five sand fractions, where each was the percentage of the total weight of sand; (ii) a sorting coefficient, a measure of variability among the sand classes (Folk 1968), which is calculated as the standard deviation of the five sand fractions; and (iii) silt and clay content, expressed as a percentage of the weight of inorganic matter.

Correlations among the eighteen measured environmental variables were calculated by Pearson's correlation coefficient, *r*.

Field distributions of shoreline species

The field distributions of twelve shoreline species—*Calamagrostis canadensis, Cladium mariscoides, Drosera intermedia, Dulichium arundinaceum, Eriocaulon septangulare, Hypericum ellipticum, Juncus pelocarpus, Lobelia dortmanna, Lysimachia terrestris, Rhynchospora fusca, Triadenum fraseri* and *Xyris difformis*—were measured (nomenclature follows Gleason & 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 although *X. difformis* is considered rare in Ontario (Randall & 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 in the following central Ontario lakes (lake locations and number of samples taken from each lake are also given): Axe Lake (172 samples), Black Oak Lake (45°30′N, 80°13′W; 80 samples), 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). These 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 these lakes were once part of glacial Lake Algonquin (Chapman 1975). The aquatic flora of the lakes in this region has been described by Miller & Dale (1979), Keddy (1981) and Keddy & Reznicek (1982). Each sampled lake contained most of the study species; lakes with human dwellings were avoided. Within a lake, all the shoreline—except bedrock, peat bog and shrub (e.g. *Myrica gale*) 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: 2 m 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 substratum was sampled from the centre of the hoop by taking a trowel-full of soil 5 cm deep—the average maximum rooting depth. Because it was not possible to freeze soil samples at the lakes, samples were sealed in polyethylene bags and stored in the shade for about 3 weeks, after which they were frozen for 1–2 months until analysis for organic content. Organic content was determined for each substratum sample according to Dean (1974) and expressed as the percentage loss-of-sample-mass upon ignition.

The range of organic content found 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, and so on. The rankings produced a numerical expression of the abundance of each species along the gradient. The agreement of the distributions of the different species along the gradient was tested using Kendall's coefficient of concordance (W) (Siegel 1956).

Agreement of field distributions among lakes

To test whether particular species were always found at the same relative position along the organic-content gradient in different lakes, the range of organic 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-content classes to those occurring most frequently in low organic-content classes. The agreement of species ranking along the gradient among lakes was also 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 history of human activity. 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 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 organic contents were formed by mixing a known volume of sand and organic sediment. Each was mixed for 1 h by hand and then put into watertight pots (15·5-cm diameter). Samples of each of the treatments were frozen for later determination of organic content.

Approximately seventy-five ramets of each study species were collected at Axe Lake on 25 May 1982. The plants were carefully removed from the substratum, rinsed, and stored in lake water for up to 4 days, until planted. For each species, we attempted to select individuals of equal size and stage of development. For rhizomatous species (e.g. *Cladium mariscoides* and *Dulichium arundinaceum*) this entailed cutting the rhizome at a fixed number of nodes.

Five ramets of each species were planted in individual pots for each organic content. In spite of the 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 south-west of the study area. Soil in the pots was saturated by daily watering with deionized water.

The plants were harvested over 5 days beginning 1 September 1982. Whole plants were washed to remove soil and dried to constant weight at 100 °C, allowed to cool for 1 h, and weighed.

Biomass values were log-transformed to meet the assumptions of analysis of variance and the significances 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, and so on. The agreement of ranks among species along the gradient levels was tested using Kendall's W.

RESULTS

Organic content gradient

The organic-matter content of the field samples ranged from 0·13% to 89·9%; samples with low values were most abundant. Organic content was positively correlated ($P < 0\cdot05$) with percentage of substratum particles between 0·1 mm and 0·05 mm diameter ($r = 0\cdot61$), silt and clay fractions ($r = 0\cdot64$), Mg ($r = 0\cdot89$), Ca ($r = 0\cdot93$), K ($r = 0\cdot88$), P ($r = 0\cdot91$) and conductivity ($r = 0\cdot93$). It was negatively correlated ($P < 0\cdot05$) with percentage of substratum particles 0·25–0·10 mm diameter ($r = -0\cdot36$), sorting coefficient ($r = -0\cdot30$) and water depth ($r = -0\cdot46$). Variables not significantly correlated with organic content included pH, percentages of substratum particles between 0·25 mm and 1·00 mm diameter, and slope.

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 contents greater than the highest of the experimental gradient (Table 1). Also, the lowest three organic contents of the experimental gradient were pooled into one level and the next two were pooled into a second level; the dry weights of plants grown at these organic contents were pooled into

TABLE 1. Manipulations used to make the substratum organic contents of the experimental gradient similar to the classes of organic content found along the field gradient in experiments on the distribution of shoreline vegetation in Ontario.

Experimental substrata			Field substrata	
Original level	Organic content (%) mean ± 1 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 ± 0·08			
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	12·6 ± 0·37	6	6	8·00–16·0
10	20·7 ± 0·53	7	7	16·0–24·0

the new levels for statistical analysis. The highest five organic-content levels of the experimental gradient were not changed. This manipulation produced seven organic-content classes that were comparable between the field and experimental data (Table 1). The same species and organic-content classes were necessary to test concordance of data within both the field and experimental studies. Therefore, some field samples were not considered in this set of analyses, including samples with organic contents of 6·00–7·99% and greater than 24·0%.

Field distributions of shoreline plants

Abundance varied significantly ($P < 0{\cdot}05$) along the field gradient for all species but *Rhynchospora fusca*, and species had different patterns of distribution (Kendall's W, s =

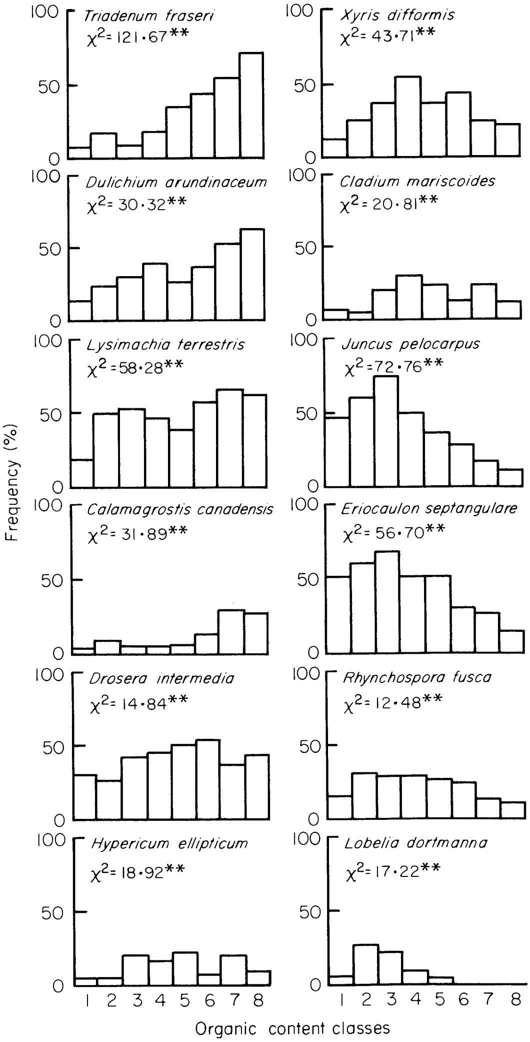

FIG. 1. The field distributions of twelve shoreline species along an organic content gradient in Canadian lakes. Relative abundance along the gradient varied significantly. Symbols: $^{*}P < 0{\cdot}05$; $^{**}P < 0{\cdot}01$; d.f. = 7 for all species except *Calamagrostis canadensis* (d.f. = 6) and *Lobelia dortmanna* (d.f. = 2), for which classes were combined to meet the assumptions of the χ^2 test.

581, $k = 7$, $N = 12$, $P > 0{\cdot}05$). Figure 1 shows that some species have peak abundances at the more organic end of the gradient (*Dulichium arundinaceum, Lysimachia terrestris*), some at the sandy end (*Eriocaulon septangulare, Juncus pelocarpus*) and others were intermediate (*Cladium mariscoides, Xyris difformis*).

Agreement of field distributions among lakes

Six species (*Dulichium arundinaceum, Drosera intermedia, Eriocaulon septangulare, Juncus pelocarpus, Lysimachia 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. These species agreed in their rankings along the gradient among lakes (Kendall's W, $s = 216$, $k = 4$, $N = 6$, $P < 0{\cdot}01$) suggesting that the zonation pattern is similar regardless of the lake considered.

Measurement of physiological response curves

Biomass varied significantly ($P < 0{\cdot}05$) with position on the level for all species but *Drosera intermedia.* The physiological response curves of the species along the gradient were similar (Kendall's W, $s = 1914$, $k = 7$, $N = 12$, $P < 0{\cdot}01$). Most species achieved their maximum dry weight at the organic end of the gradient (Fig. 2). One species, *Hypericum ellipticum*, achieved its maximum biomass at an intermediate organic content. No species performed best at the sand end of the gradient.

DISCUSSION

The organic-content gradient was strongly correlated with other variables important to plant growth, including nutrient concentrations and particle sizes. It is a multivariate gradient; substratum-organic 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. The distributions of species vary significantly along the organic content gradient and the pattern is similar among the different lakes, suggesting that the mechanism is independent of the particular lake considered. The most striking feature of the results, in light of the differential field distributions of the species, is the similarity of their physiological response curves. This suggests that zonation may not be entirely attributable to individual physiological responses of a species to changing physical factors; interactions with other plants may also be important in determining its distribution within a zonation pattern.

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 substrata 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 & 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. It is assumed, secondly, that the plants were allowed sufficient growth time for differences among them to appear; the 90-day time-span of the experiment includes the period of highest growth rates (Auclair, Bouchard & Pajaczowski 1976).

A feature common to recent reviews concerning the mechanisms that produce shoreline zonation is limited consideration of the possible importance of between-species competition (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

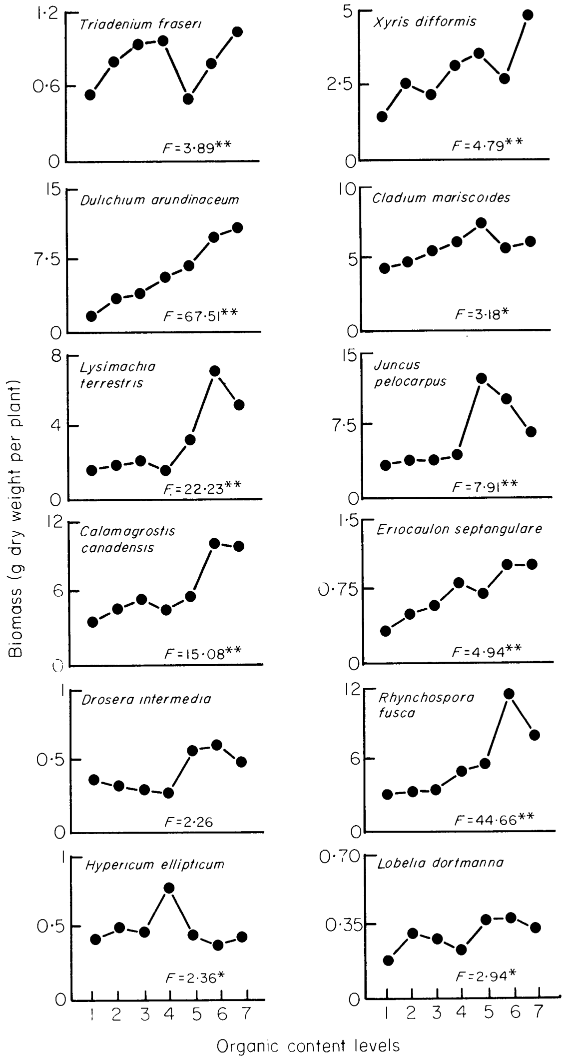

FIG. 2. Biomass as a function of substratum organic content in an experiment with twelve shoreline species grown singly. Significance symbols: *$P < 0{\cdot}05$; **$P < 0{\cdot}01$.

for zonation. These results are consistent with those of Misra (1938) who found that *Potamogeton pectinatus* grew best on the organic substratum upon which it was most commonly found, but that *Isoetes lacustris*, which was most abundant on sandy substrata, also grew best on substratum with high organic content; Misra (1938) speculated that between-species competition might affect the distribution of some aquatic plants. When considering vertical zonation, Buttery & Lambert (1965) proposed that competition produced the zonation of *Glyceria maxima* and *Phragmites communis*. Similarly, Grace & Wetzel (1981) showed that between-species competition determined the vertical distributions of two species of *Typha*.

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.

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