Wave disturbance on lakeshores and the within-lake distribution of Ontario's Atlantic coastal plain flora

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Although water level fluctuations may explain the persistence of Atlantic coastal plain species in certain Georgian Bay lakes, they cannot explain the within-lake distribution of this flora. To test whether the within-lake distribution of these species was correlated with disturbance from waves, 25 transects were quantitatively sampled along an exposure gradient in Axe Lake, Ontario. The proportion of Atlantic coastal plain species in a transect increased significantly with exposure ($p < 0.01$). Total frequency of Atlantic coastal plain species reached a maximum at an intermediate level of exposure. Analysis of substrate samples showed that the exposure gradient is a multivariate gradient including not only biomass removal by waves, but sorting of the shoreline substrate. The coarse, nutrient poor sites on exposed shores may allow the persistence of Atlantic coastal plain species in at least two different ways. Their physiological tolerance limits may be narrowly specialized on exposed shorelines. Alternatively, their physiological tolerances may include a broad range of shoreline types, but competition restricts them to those sites least suitable for other species.

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Bien que les fluctuations des niveaux d'eau puissent expliquer la persistance d'espèces de la plaine côtière atlantique dans certains lacs de la baie Georgienne, ces fluctuations ne peuvent expliquer la répartition de cette flore à l'intérieur de chaque lac. Dans le but de vérifier si la répartition de ces espèces dans les lacs est en corrélation avec les perturbations dues aux vagues, 25 transects ont été échantillonnés quantitativement le long d'un gradient d'exposition dans le lac Axe en Ontario. La proportion d'espèces de la plaine côtière atlantique par transect augmente significativement avec l'exposition ($p < 0,01$). La fréquence totale de ces espèces atteint un maximum aux niveaux moyens d'exposition. L'analyse d'échantillons de substrats montre que le gradient d'exposition est un gradient multivarié, qui comprend non seulement le déplacement de biomasse par les vagues, mais aussi le triage du substrat du rivage. Sur les rivages exposés, les sites pauvres en éléments nutritifs sur substrats grossiers peuvent permettre la persistance d'espèces de la plaine côtière atlantique de deux façons au moins. Les limites de tolérance physiologique de ces espèces pourraient être étroitement spécialisées sur les rivages exposés. D'autre part, leur tolérance physiologique pourrait leur permettre de croître sur une grande diversité de types de rivages, la compétition les restreignant aux sites les moins favorables aux autres espèces.

[Traduit par le journal]

Introduction

The presence of plant species in the Great Lakes basin which are disjunct from their main range along the Atlantic coastal plain of eastern North America has long been of interest to phytogeographers (Peattie 1922; McLaughlin 1932; Fernald 1942). More recently, the existence of this flora has been documented in the eastern Georgian Bay area of Ontario (Keddy 1981; Keddy and Reznicek 1982).

Although water level fluctuations may explain the presence or absence of species in a particular lake (Keddy and Reznicek 1982), they cannot account for the uneven distribution of Atlantic coastal plain species around the perimeter of a lake. One factor which may control the horizontal distribution of plants in lakes is the gradient of exposure to wave energy (Pearsall 1920; Spence 1967, 1982; Hutchinson 1975; Keddy 1983; Wilson and Keddy 1985). This gradient may have direct effects on plants (e.g., by uprooting seedlings) or indirect effects (e.g., by eroding and transporting shoreline sediments). This exposure gradient has been documented in one lake with Atlantic coastal plain species (Keddy 1982), and vegetation zonation patterns have been shown to vary with exposure (Keddy 1983). The phytogeographic implications of these data have not been explored. The objective of this paper is to test whether the occurrence of Atlantic coastal plain species was correlated with the amount of wave energy that a shoreline received.

Methods

The data were collected in Axe Lake, Ontario. This small, sandy lake is a remnant of the shoreline of glacial Lake Algonquin, and supports a rich Atlantic coastal plain flora (Keddy 1981). The vegetation data consisted of twenty-five 50 cm wide belt transects and were collected 13–21 July 1979. Each transect ran from 50 cm above to 50 cm below the water line and was divided into 20 height increments of 5 cm each, using an automatic level. Because the water level fell during the study period, all levels were surveyed relative to 0 m on the day sampling was commenced; daily corrections were made for falling water levels. The presence of each species in each height increment was recorded, and the final data consisted of lists of species present or absent in 20 height increments for each of 25 transects. Additional details on data collection and the zonation patterns of these plants are given in Keddy (1983).

Because no two botanists would completely agree on what constitutes a list of Atlantic coastal plain species (see, for example, Peattie 1922; McLaughlin 1932; Fernald 1942), I prepared two lists for Axe Lake, a conservative and an extreme one. If similar results were obtained with both, it would mean that the results were not dependent upon one particular phytogeographer's opinion. The conservative list consisted of *Rhexia virginica, Juncus militaris, Nymphoides cordata, Utricularia purpurea, U. resupinata*, and *Xyris difformis*. The extreme list also included *Cladium mariscoides, Drosera intermedia, Juncus pelocarpus, Myriophyllum tenellum, Muhlenbergia uniflora, Potamogeton confervoides, P. oakesianus, Utricularia cornuta, Viola lanceolata*. (Nomenclature follows Gleason and Cronquist (1963) except for the use of *Xyris difformis* Chapman for *X. caroliniana* Walt.). Total frequency of Atlantic coastal plain species in a transect was determined by summing all occurrences of the above species in the 20 height increments examined.

The vegetation data were the dependent variable. The independent variable was exposure. Exposure is a multivariate gradient incorporating many direct and indirect effects. For this study, it was necessary only to rank the vegetation transects in order from low to high exposure. The transects represented a range of exposure levels from a sheltered bay to an exposed beach and, if they are simply ranked in the order in which they occurred along the perimeter of the lake, then this order is strongly correlated with exposure (Keddy 1982). Because this exposure gradient was ordinal, the Spearman rank correlation coefficient, r_s, (Siegel 1956) was used to test whether the occurrence of coastal plain species varied along it.

Physical characteristics of the exposure gradient

Three sample units were taken from each transect, one 25 cm vertically above the waterline, the second at the waterline, and the third 25 cm below the waterline. Each sample unit was composed of five soil cores (10 cm deep, 3 cm diameter) collected in a 50 × 50 cm quadrat, one core from the centre and one from each corner. The five cores were combined into one substrate sample unit and frozen at −5°C 8 h later. The pH values for each unit were determined in the field using a portable meter; where no interstitial water was present, sample units were wetted with 5 mL of distilled water.

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

One subsample of each sample unit was analyzed for nutrients and conductivity by the University of Guelph Soil Test Laboratory, Guelph, Ontario. K, Mg, and Ca were measured using the neutral normal ammonium extract method and P was measured by the Olsen extract procedure (Black 1965). Because available nutrients are dynamic, especially in shoreline soils which may be oxidized or reduced depending on the 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 between sample units by one or two orders of magnitude (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 to first remove organic content with peroxide, the high organic content of the sample units (up to 50%) required removing organic matter 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 sample units were very sandy and clay and silt proportions were less than 10%. Therefore, each subsample was ignited, cooled, and weighed to determine 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. This could produce a spurious positive correlation between organic content and silt and clay content. This was corrected by determining the ash content of sample units of known organic content; this produced an ash to organic content ratio 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 was 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 was calculated as the standard deviation around the mean of the five sand fractions; and (*iii*) silt and clay content, expressed as a percentage of the weight of inorganic matter.

Correlations among the 17 measured environmental variables were calculated by Pearson's correlation coefficient, r.

Results

Figure 1 shows that the proportion of Atlantic coastal plain species increased significantly with exposure ($p < 0.01$) for both the conservative list and extreme list. The total frequency of Atlantic coastal plain species was highest at an intermediate level of exposure (Fig. 2). Thus the distribution of the Atlantic coastal plain flora was not random with respect to exposure. To better illustrate the restricted within-lake distributions of many Atlantic coastal plain species, Fig. 3 compares the distributions of *Rhexia virginica* and *Xyris difformis* along the exposure gradient to that of *Lysimachia terrestris*. *Rhexia virginica* and *X. difformis* have disjunct populations in the Georgian Bay area, and are considered rare in Ontairo (Sharp and Keddy 1983; Randall and Keddy 1983); *L. terrestris* is common in wetlands throughout this geographic region.

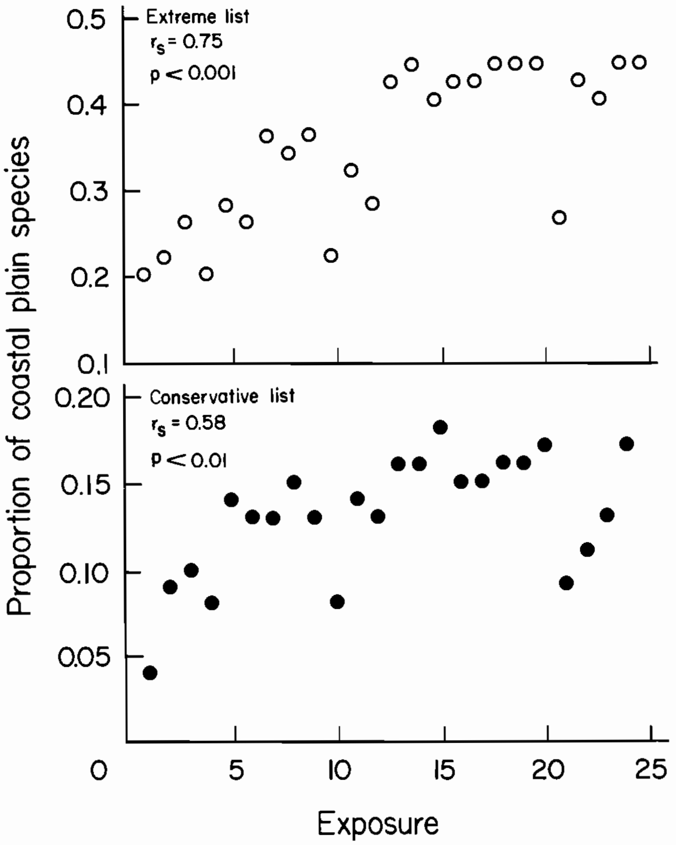

FIG. 1. The proportion of Atlantic coastal plain species in a transect plotted against exposure, for the extreme list (top) and the conservative list (bottom); r_s, Spearman rank correlation coefficient.

While these data demonstrate correlation, the search for mechanisms is complicated by the multivariate nature of the exposure gradient. Table 1 shows a correlation matrix for characteristics of this gradient including sample units from the three different depths ($n = 75$). Note that all four nutrients were significantly negatively correlated with exposure ($r > -0.36$) as were loss on ignition, conductivity, and silt and clay content. The sand sorting coefficient was positively correlated with exposure.

Discussion

There have been many recent discussions of natural disturbance and diversity in vegetation (e.g., Grime 1977; Grubb 1977; Connell 1978; Huston 1979; White 1979); it is thought that regular disturbance prevents competitive dominants from excluding weaker competitors. A similar point was raised much earlier by Griggs (1940), who proposed that rare plant species are weak competitors, and persist only where environ-

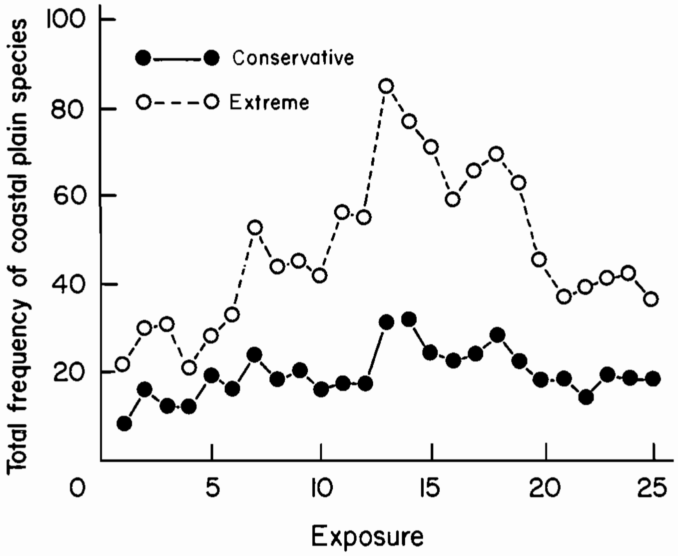

FIG. 2. The total frequency of coastal plain species in a transect plotted against exposure, for the extreme list and the conservative list.

mental conditions prevent competitive exclusion. Huston (1979) proposed that the species composition of vegetation was the result of two factors : (*i*) rate of disturbance and (*ii*) rate of increase after disturbance. While increased exposure will produce increased disturbance, the substrate data suggest that it will also decrease the rate of recovery from disturbance, since exposed shores have coarse, nutrient-poor substrates. Wilson and Keddy (1985) found that shoreline species grew most rapidly in substrate from organic bays. Thus the exposure gradient may consist of Huston's two axes superimposed: increased disturbance not only uproots seedlings and removes biomass, but also removes the fine substrate particles with associated nutrients thereby lowering growth rates.

The specific causes of the restricted distributions of Atlantic coastal plain species along this gradient are not known. These species may have physiological tolerance limits and life histories which are specialized upon a narrow range of conditions produced along the exposure gradient. They may competitively exclude other species from this, their optimum habitat. This is assumed in many theoretical models (MacArthur 1972; May 1981) and is an underlying assumption in gradient analysis of vegetation (Whittaker 1967). Alternatively, these species might grow best on more sheltered shores were it not for the presence of competitors there. If this were the case, the Atlantic coastal plain species would have broad tolerance limits but weak competitive ability. Their persistence on exposed shores would then be viewed as either greater ability to tolerate disturbance (the ruderal strategy), or greater ability to withstand stress (the stress tolerator strategy), or both (Grime 1977). Only field experiments can distinguish between these alternatives.

The advantage of using transects in this analysis was that all shoreline species were considered simultaneously. This could also be considered a disadvantage, since species with very different morphologies and life histories are included in the same data set. The above results could therefore be refined if sampling were restricted to specific water depths; then floating-leaved species could be examined independently of emergent or upper shoreline species. This study also uses data from a single year. Weins (1981) has criticized the use of single sample surveys since observed correlations may vary from year to year. In Axe Lake, repeated visits to the study area over a period of 5 years have not revealed any obvious shifts in the distribution of species such as *Rhexia virginica* or *Xyris difformis*, or of vegetation zones in general. It is therefore unlikely that major differences would be found from one year to the next.

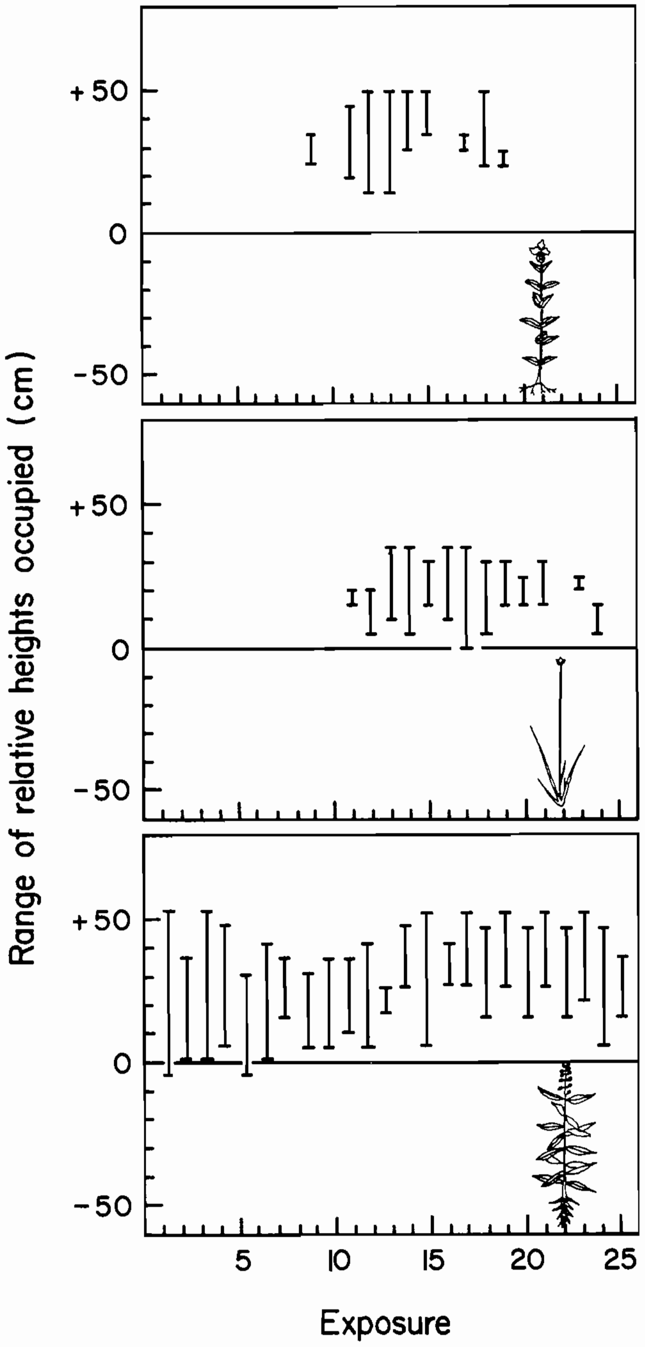

FIG. 3. The distribution of two Atlantic coastal plain species (*Rhexia virginica* (top), *Xyris difformis* (middle)), compared with *Lysimachia terrestris* (bottom) along a gradient of exposure. The bars show the range of relative heights occupied by a species in a transect. Both *R. virginica* and *X. difformis* reach a maximum range of relative heights at an intermediate level of exposure, and *X. difformis* appears most tolerant of exposure. Note that both are more narrowly distributed along the exposure gradient than *L. terrestris*.

Few lakes in Ontario contain many Atlantic coastal plain species. Natural disturbance from water level fluctuations may

TABLE 1. Correlation matrix among 17 characteristics of the lakeshore examined ($N = 75$, $r > 0.23$, $p < 0.05$; $r > 0.30$, $p < 0.01$)

	Particle sizes (mm)							Chemistry							
	>1	1−0.5	0.5−0.25	0.25−0.10	0.10−0.05	Silt/clay	Sorting coefficient	P	K	Mg	Ca	pH	Conductivity	Loss on ignition	Relative height[a]
Particle sizes															
>1 mm	1.00														
1−0.5 mm	0.77	1.00													
0.5−0.25 mm	0.52	0.51	1.00												
0.25−0.10 mm	−0.63	−0.68	−0.53	1.00											
0.10−0.05 mm	0.15	0.19	−0.34	−0.59	1.00										
Silt/clay	0.26	0.34	−0.06	−0.64	0.77	1.00									
Sorting coefficient	−0.70	−0.75	−0.59	−0.97	−0.52	0.58	1.00								
Chemistry															
P	0.09	0.07	−0.07	−0.27	0.39	0.53	−0.25	1.00							
K	0.11	0.07	−0.11	−0.29	0.45	0.66	−0.28	0.93	1.00						
Mg	0.19	0.16	−0.12	−0.46	0.63	0.77	−0.41	0.86	0.94	1.00					
Ca	0.15	0.17	−0.13	−0.44	0.61	0.72	−0.39	0.90	0.92	0.96	1.00				
pH	0.31	0.43	0.25	−0.30	0.02	0.08	−0.32	−0.23	−0.21	−0.14	−0.12	1.00			
Conductivity	0.02	0.05	−0.19	0.24	0.45	0.57	−0.19	0.96	0.90	0.85	0.91	−0.19	1.00		
Loss on ignition	0.12	0.10	−0.22	−0.36	0.61	0.64	−0.30	0.91	0.88	0.89	0.93	−0.17	0.93	1.00	
Relative height[a]	−0.21	−0.43	−0.43	0.07	0.39	0.24	0.11	0.36	0.32	0.33	0.31	−0.44	0.36	0.46	1.00
Exposure[b]	0.34	−0.59	−0.02	0.49	−0.49	−0.55	0.51	−0.36	−0.36	−0.47	−0.49	−0.02	−0.37	−0.47	0.00

[a] Vertical position of sample with respect to waterline (−25, 0, and 25 cm).

[b] Horizontal position along exposure gradient (sample units numbered 1−25 along shoreline from sheltered bay to exposed beach).

explain the presence of such species in some lakes (Keddy and Reznicek 1982). In lakes where water level fluctuations are infrequent, exposed shorelines may allow small populations of these species to persist during long high water periods. This might provide a supplement to buried seeds, particularly if buried reserves of seeds survived for only limited periods of time. The restricted distribution of Atlantic coastal plain species in Ontario, both within and among lakes, may therefore be attributed in part to disturbance by waves.

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