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GERMINATION OF TEN SHORELINE PLANTS IN RELATION TO SEED SIZE, SOIL PARTICLE SIZE AND WATER LEVEL: AN EXPERIMENTAL STUDY

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SUMMARY

(1) Lakeshore plants are distributed along a gradient of exposure to waves, from sheltered bays to exposed shorelines. Soil particle sizes vary along this gradient, and may influence germination and early establishment. We therefore tested whether species with different-sized seeds germinate at different positions along a particle-sized gradient. In particular, we tested whether there was a shared preference over all species for one position on this gradient.

(2) Seeds of ten wetland plants (*Acorus calamus*, *Alisma plantago-aquatica*, *Bidens cernua*, *B. vulgata*, *Cyperus aristatus*, *Lythrum salicaria*, *Polygonum punctatum*, *Sagittaria latifolia*, *Scirpus americanus*, *Typha angustifolia*) were vernalized and then sown along a particle-size gradient with seven stages ranging from 0·125–0·250 to 8–16 mm. Two water levels, 1 cm and 4 cm below the soil surface, were provided. The proportion of seeds producing established seedlings was determined for each particle size and each species ($n = 5$ replicates).

(3) In the drier treatment, nine out of ten species germinated differentially ($P < 0{\cdot}05$) along the gradient. In the wetter treatment, only three out of ten species so responded. Thus, soil particle size had most influence during drier conditions.

(4) In both wet and dry treatments, those species which did respond significantly ($P < 0{\cdot}05$) to the gradient had a shared preference for the fine soil ($P < 0{\cdot}01$). The single exception was *Acorus calamus* in the dry treatment.

(5) The species with the smallest seeds generally showed the greatest response to the gradient. Large-seeded species therefore had the broadest tolerances for variation in soil particle sizes.

(6) On lakeshores, the fine particles associated with sheltered bays would allow the highest recruitment irrespective of seed size. These effects would be most pronounced during periods of low water. The zonation of adult plants is apparently not produced by species with different-sized seeds requiring different soil particle sizes for maximum germination.

INTRODUCTION

The zonation of plants along environmental gradients has long been of interest to ecologists (Whittaker 1967). It is particularly pronounced on lakeshores where species are distributed along two gradients: water depth and exposure to waves. Yet the mechanisms producing this zonation are still poorly understood (Hutchinson 1975; Spence 1967, 1982). The reviews by Hutchinson and Spence show that past studies have emphasized zonation along the water-depth gradient rather than the exposure gradient, and have emphasized the adult phase of the life cycle rather than the germination and early establishment phase.

The exposure gradient runs parallel to the waterline and produces vegetation zonation from sheltered organic bays to exposed sandy shores. It is particularly interesting because it appears to combine two fundamental gradients: disturbance and 'stress' (Grime 1979; Huston 1979). As exposure increases, disturbance from waves increases. Simultaneously, the potential for recovery from disturbance decreases (i.e. stress increases) since exposed shores have coarse, nutrient-poor soils. The distributions of individual species, and the characteristics of vertical zonation both change along this exposure gradient (Hutchinson 1975; Spence 1982; Keddy 1983, 1985).

Transplanted ramets have been used to investigate the responses of adult plants to exposure (Jupp & Spence 1977; Sharp & Keddy 1985; Wilson & Keddy 1985a, b; Wilson, Keddy & Randall 1985). Experiments with adult ramets, however assume that interactions at the adult stage are largely responsible for vegetation zonation. Grubb (1977) proposed that the recruitment phase might be more important, particularly as mortality rates are highest at this life-history stage (Harper 1977; but see Cavers 1983). Seedling regeneration is known to be important in many wetlands (e.g. Salisbury 1970; van der Valk & Davis 1978; van der Valk 1981; Keddy & Reznicek 1982). Thus, it is possible that zonation patterns could result from differential recruitment patterns rather than from adult interactions alone.

Germination in agricultural species and weeds is significantly affected by subtle variations in the surface texture of the soil (Harper, Williams & Sagar 1965; Harper & Benton 1966; Oomes & Elberse 1976). Since soil particle sizes increase with exposure to waves (e.g. Pearsall 1920), it is possible that differential recruitment along the soil particle-size gradient on lakeshores could produce vegetation zonation. Perhaps each species germinates and establishes most successfully when particle sizes are just slightly larger than seed sizes, thereby maximizing the contact of seeds with the soil.

All species on such a gradient could share similar requirements for maximum recruitment, and thus 'prefer' the same portion of the gradient. Alternatively, all species could have different requirements for optimal recruitment, in which case different sections of the gradient may be 'preferred' by different species. These alternatives were briefly discussed by Pimm (1978), who uses the terms *shared preference* and *distinct preference*, respectively, to describe the possible outcomes. Some ecologists (e.g. Whittaker 1967; Platt & Weis 1977) assume distinct preference. However, experimental work often supports the idea of shared preference (e.g. Harper & Benton 1966; Colwell & Fuentes 1975; Austin & Austin 1980; Wilson & Keddy 1985a).

If distinct preference occurred, zonation patterns could be caused by differing regeneration requirements of the component species. If shared preference were found, some other mechanism (e.g. competition among adult ramets) would be required to explain zonation.

This study tests these alternatives. To increase the chance of detecting different germination responses to different particle sizes, we chose a wide range of seed sizes. We collected seeds, vernalized all under similar conditions, and tested for shared or distinct preference in patterns of recruitment along a particle-size gradient.

Lakeshore environments are also influenced by water depth (Hutchinson 1975; Spence 1982; Keddy & Reznicek 1982). Drier conditions are found higher on shorelines, and during periodic low water levels. We therefore included two water table levels in this experiment. Our prediction was that soil particle size would have more effect on recruitment when the soil was drier.

MATERIALS AND METHODS

The particle-size gradient

The particle-size gradient was prepared by sifting granite, sand and gravel obtained from a local quarry into seven particle sizes. Using a standard sieve series and a Tyler sifting machine the following classes were obtained: 0·13–0·25 mm, 0·25–0·50 mm, 0·50–1·00 mm, 1·00–2·00 mm, 2·00–4·00 mm, 4·00–8·00 mm, 8·00–16·0 mm. To minimize any chemical differences between the seven classes, all fractions were thoroughly washed with tap water.

The experiment was set up in the University of Ottawa glasshouse. Each unit of the experiment consisted of a plastic tray (26 × 52 × 5 cm), subdivided into twelve compartments by a plastic insert and filled with a particular particle size. The compartments were first filled with a 3-cm deep layer of unsorted and unwashed sand (85% by weight composed of 0·25–0·50 mm particle sizes), and then covered with a 2-cm layer of one of the particle size classes. This two-layer design was necessary because some particle-size fractions were difficult to obtain. One compartment per tray was left empty to allow adjustment of water levels. Openings in the bottom of the inserts permitted free movement of water within each tray. Half of the trays had the water level maintained at 1 cm below the soil surface (wetter treatment), and others had the water level maintained at 4 cm below the soil surface (drier treatment); all trays were carefully levelled. The trays were randomized within five blocks, each block containing fourteen trays (seven particle sizes × two water levels). Thus, each treatment for each species occurred once in each block.

Seed collection and storage

The seeds of ten wetland species (*Acorus calamus*, *Alisma plantago-aquatica*, *Bidens cernua*, *B. vulgata*, *Cyperus aristatus*, *Lythrum salicaria*, *Polygonum punctatum*, *Sagittaria latifolia*, *Scirpus americanus*, *Typha angustifolia*; names follow Gleason & Cronquist (1963)) were collected from several wetlands in Lanark County (45°05′N, 76°15′W) and the adjacent Regional Municipality of Ottawa–Carleton, Ontario, Canada (45°20′N, 75°50′W) between 11 and 20 October 1982. In each case, they were air dried at 22 °C for 5 days, and then stored at 5°C in sealed plastic containers in the dark. On 10 December 1982, they were transferred to moist or wet storage at 2 °C in the dark for 5 months. Moist storage refers to seeds stored in mesh bags in plastic containers filled with a moist mixture of peat and sand. Wet storage refers to seeds covered in tap water in plastic containers. Both methods were used for each species because there appeared to be no consensus in the literature about optimum storage for seeds of these wetland plants. Preliminary germination trials in May 1983 on moistened filter paper in Petri dishes showed that storage in peat and sand generally yielded better germination after 14 days. We therefore used seeds from moist storage in this experiment, except in the case of *Polygonum punctatum*, where all seeds in the moist conditions had germinated prior to being removed from the refrigerator.

Sowing and maintenance

The seeds were counted and one block was planted on each of 5 consecutive days, 14–18 June 1983. Seeds were surface dry when counted, then were placed between moist filter paper in Petri dishes and kept refrigerated until planting later the same day. Depending on the number of seeds available, fifty or 100 seeds of each species were planted. The only exception was *Bidens vulgata*, where seed shortages restricted us to a total of three replicates of forty seeds each. Species were assigned randomly to the compartments within the trays; one compartment per tray was left without seeds as a control. Seeds were sprinkled onto the soil; the compartment was then flooded and allowed to drain. Adding seeds in this manner imitated field conditions and facilitated good seed–

soil contact. Since the seed hairs of *Typha angustifolia* prevented contact between seed and water, these seeds were gently pressed into the soil before the water level fell. Care was taken to keep all seeds away from the sides of compartments. The experiment was maintained in a glasshouse at the University of Ottawa between 14 June and 12 July 1983; most germination occurred within the first 10 days. Water levels of the trays were adjusted once or twice daily depending on water loss. Fluctuations were kept within 0·5 cm.

The percentage of seeds germinating and acquiring a root and leaves (recruitment) was determined daily for the first 5 days of emergence and on alternate days thereafter. Dicotyledonous seedlings were regarded as established when rooted and with a pair of leaves open to more than 45°; for monocotyledonous species, the appearance of the first leaf marked establishment. Seedlings were removed or clipped off as they were recorded.

The moisture content of each treatment at the end of the experiment was determined by removing 50 ml of soil from the surface of four randomly selected compartments in each treatment. Water content was then determined by weight loss on drying at 100 °C, and expressed as ml of water per ml of soil.

A one-way analysis of variance was employed for each species to test the significance of response to the gradient. Homogeneity of variances was first tested using Bartlett's test, and appropriate transformations performed when necessary. For the group of species with significant responses, Kendall's coefficient of concordance (Siegel 1956) was used to test whether they exhibited a common response or different responses to the gradient.

RESULTS

In the drier treatment, all species except *Polygonum punctatum* were significantly ($P < 0{\cdot}05$) affected by the gradient (Fig. 1). The species in Fig. 1 are arranged in order of seed size, as measured by the length (mm) of the longest axis. In this drier treatment, the responses of the species were concordant (Kendall's coefficient of concordance, $W = 0{\cdot}699$, $n = 7$, $k = 9$, $P < 0{\cdot}01$). Figure 1 shows that the concordance results from shared preference for fine particles. The only species that did not exhibit this trend was *Acorus calamus* (Fig. 1).

In contrast, in the wetter treatment, overall germination was higher and response to the gradient was reduced (Fig. 2). Only three of the ten species responded significantly ($P < 0{\cdot}05$), again with a common preference for fine particles (Kendall's coefficient of concordance, $W = 0{\cdot}960$, $k = 3$, $n = 7$, $P < 0{\cdot}01$).

The water content of the soil decreased with increasing particle size (Fig. 3). Two-factor analysis of variance showed that both main effects (particle size, water level) and their interaction were significant ($P < 0{\cdot}001$). However, the assumption of homogeneous variances was violated, since the treatments with intermediate particle sizes had higher variances; this problem could not be corrected by conventional transformations.

DISCUSSION

Particle size had a significant effect on recruitment in the wetland species studied, particularly when the water level was at least 4 cm below the soil surface. Raising the water level reduced the effect of particle size on recruitment.

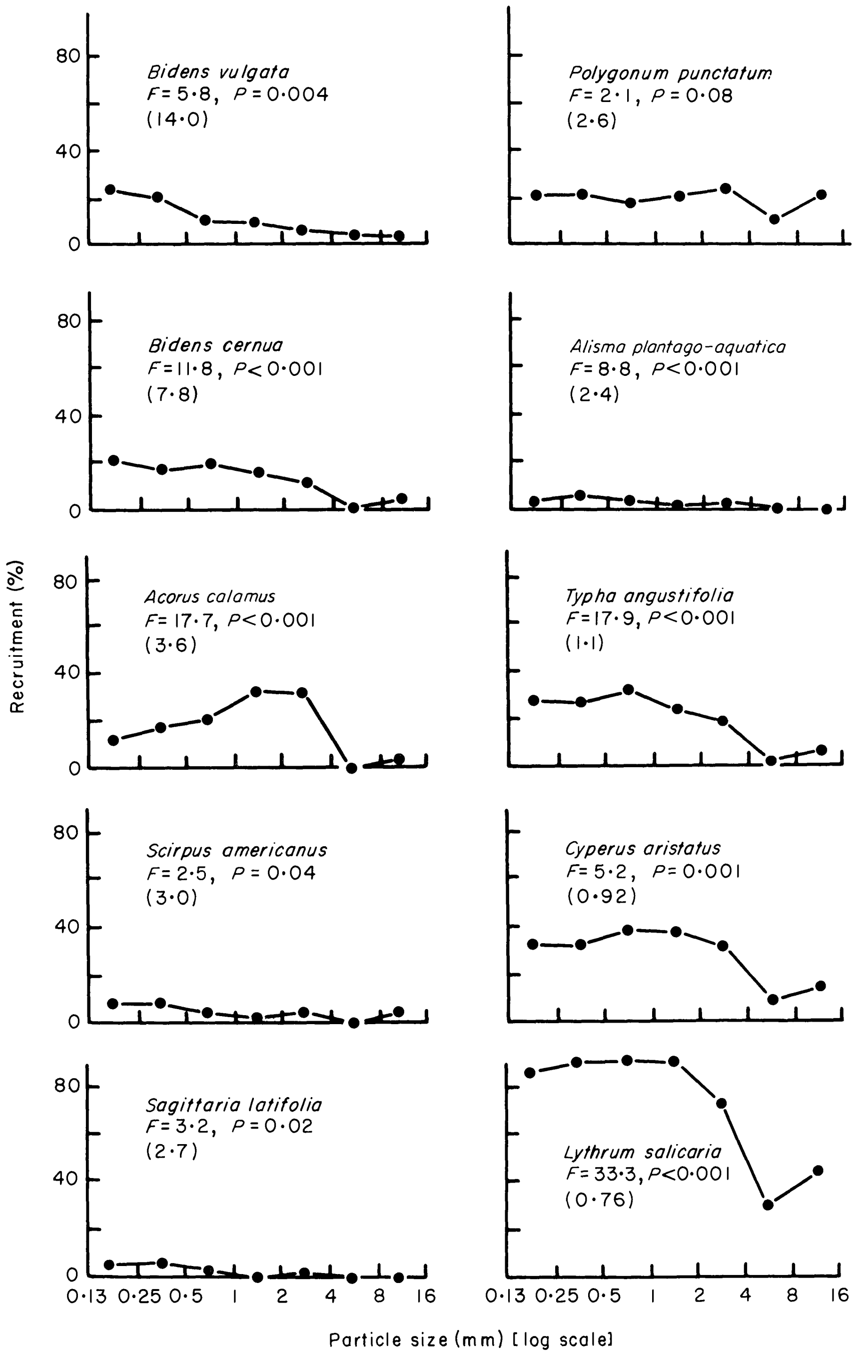

FIG. 1. Recruitment of ten wetland species along a particle-size gradient with the water table 4 cm below the soil surface (dry series). Species are arranged in declining order of seed size beginning with the left-hand column (top) and then moving to the right-hand column (bottom). *F* values are for one-way analysis of variance with five replicates; untransformed data were used for graphs; number in parentheses is the length of the longest axis of the seed (mm).

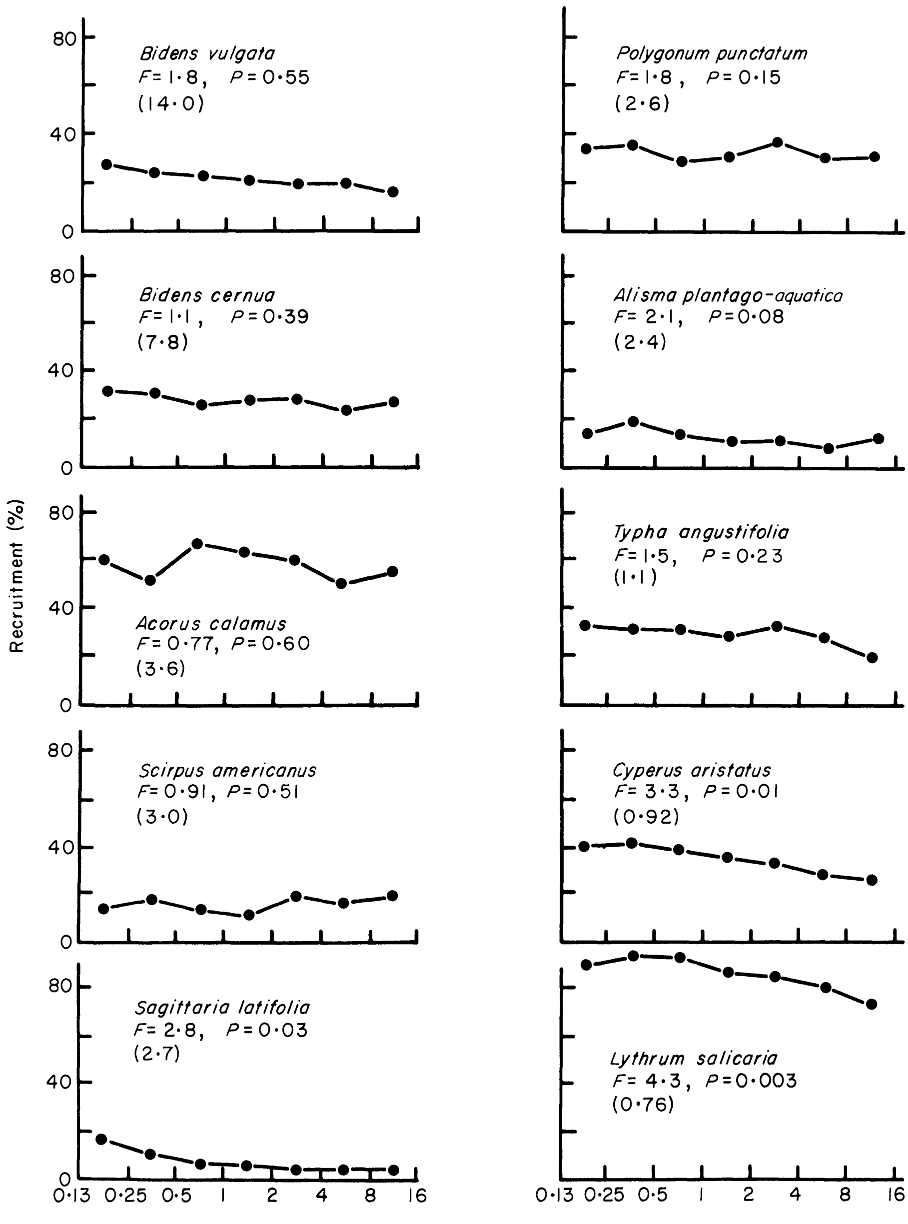

FIG. 2. Recruitment of ten wetland species along a particle-size gradient with the water table 1 cm below the soil surface (wet series). Species are arranged in declining order of seed size beginning with the left-hand column (top) and then moving to the right-hand column (bottom). *F* values are for one-way analysis of variance with five replicates; untransformed data were used for graphs; number in parentheses is the length of the longest axis of the seed (mm).

Despite a wide range of seed sizes and shapes, most species had maximum recruitment at the fine end of the gradient. The strongest response was shown by the species with the smallest seeds, *Cyperus aristata*, *Lythrum salicaria*, and *Typha angustifolia*. Their

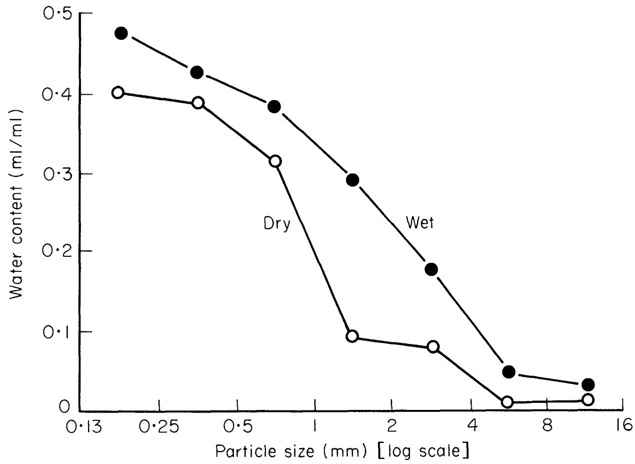

FIG. 3. Mean water content of soil (ml water per ml of soil) as a function of particle size for dry and wet treatments in experiments on the germination of wetland plants ($n = 4$ replicates).

germination declined steeply at the coarse end of the gradient in the drier treatment (Fig. 1). Also, two of these species, *L. salicaria* and *C. aristata*, were among the three species that retained a statistically significant response to the gradient at the high water level. The third species was *Sagittaria latifolia*, a species with very flat seeds. Both small and flat seeds have high surface area to volume ratios, and should therefore be particularly sensitive to drying (Harper & Benton 1966). Thus, while there was shared preference, large-seeded species apparently were less affected by the gradient.

In the drier treatments, the recruitment of small-seeded species (e.g. *L. salicaria*, *C. aristata*, *T. angustifolia*), showed a sharp increase in the coarsest particles. This probably resulted from the small seeds falling into the moist pores between the particles.

Our results are consistent with the conclusion of Harper, Williams & Sagar (1965) that microtopography exerts its effects largely through modifying seed–water relationships. Three observations lead to this conclusion: (i) comparison of recruitment at two water levels (Figs 1 and 2) shows that the response of seeds to the particle-size gradient was diminished when water was more readily available; (ii) the decline in recruitment from fine to coarse soils parallels the measured reduction in water content along the gradient; (iii) total recruitment was higher on the wetter gradient. Thus, water availability appeared to limit recruitment on our gradient. A particle-size gradient in a drying wetland can, from the viewpoint of a seed, act as a moisture availability gradient.

Water level fluctuations are common in wetlands, both among years and within years. Our results suggest that species which germinate during high-water years will be minimally affected by the particle-size gradient. Many species, however, emerge from buried seed reserves only during years with low water levels (Salisbury 1970; van der Valk 1981; Keddy & Reznicek 1982). Under these conditions, one would expect highest recruitment in those patches with the smallest particle sizes. Similarly, species which germinate early in the year should be less affected by soil particle sizes than species which germinate later in the year when water levels have fallen. Since water levels can fall many centimetres within a few days, comparison of Figs 1 and 2 will illustrate the dramatic changes in recruitment patterns which could result from falling water levels during the summer.

These results also have broader implications for the distribution and abundance of shoreline vegetation. The germination responses observed here will apparently intensify the other effects produced by waves. Waves not only remove biomass from plants, but produce nutrient-poor substrata. Shoreline plants have significantly less growth in substrata from exposed shores (Sharp & Keddy 1985; Wilson & Keddy 1985), so that plant associations on those shores will have low rates of recovery after disturbance The germination data in this paper show that the coarse substrata on exposed shores reduce recruitment as well as growth.

Although there is conspicuous vegetation zonation along gradients of particle size on lakeshores, there is no evidence that species with different-sized seeds have different optima for recruitment along this gradient. Rather, species apparently have shared preference for the small particle sizes found in sheltered bays. If differences in recruitment patterns do produce zonation, some other environmental factor varying with exposure is apparently responsible.

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REFERENCES

Austin, M. P. & Austin, B. O. (1980). Behaviour of experimental plant communities along a nutrient gradient. *Journal of Ecology*, **68,** 891–918.

Cavers, P. B. (1983). Seed demography. *Canadian Journal of Botany*, **61,** 3578–3590.

Colwell, R. K. & Fuentes, E. R. (1975). Experimental studies of the niche. *Annual Review of Ecology and Systematics*, **6,** 281–309.

Gleason, H. A. & Cronquist, A. (1963). *Manual of Vascular Plants of Northeastern United States and Adjacent Canada.* Willard Grant, Boston.

Grime, J. P. (1979). *Plant Strategies and Vegetation Processes.* Wiley, Chichester.

Grubb, P. J. (1977). The maintenance of species richness in plant communities: the importance of the regeneration niche. *Biological Reviews*, **52,** 107–145.

Harper, J. L. (1977). *Population Biology of Plants.* Academic, London.

Harper, J. L. & Benton, R. A. (1966). The behaviour of seeds in soil. II. The germination of seeds on the surface of a water supplying substrate. *Journal of Ecology*, **54,** 151–166.

Harper, J. L., Williams, J. T. & Sagar, G. R. (1965). The behaviour of seeds in soil. I. The heterogeneity of soil surfaces and its role in determining the establishment of plants from seed. *Journal of Ecology* **53,** 273–286.

Huston, M. (1979). A general hypothesis of species diversity. *American Naturalist*, **113,** 81–101.

Hutchinson, G. E. (1975). *A Treatise on Limnology. Vol.* 3. *Limnological Botany.* Wiley, New York.

Jupp, B. P. & Spence, D. H. N. (1977). Limitations of macrophytes in a eutrophic lake, Loch Lever II. Wave action, sediments and waterfowl grazing. *Journal of Ecology*, **65,** 431–446.

Keddy, P. A. (1983). Shoreline vegetation in Axe Lake, Ontario: effects of exposure on zonation pattern: *Ecology*, **64,** 331–344.

Keddy, P. A. (1985). Plant zonation on lakeshores in Nova Scotia, Canada: a test of the resourc specialization hypothesis. *Journal of Ecology*, **72,** 797–808.

Keddy, P. A. & Reznicek, A. A. (1982). The role of seed banks in the persistence of Ontario's coast plain flora. *American Journal of Botany*, **69,** 13–22.

Oomes, M. J. M. & Elberse, W. T. (1976). Germination of six grassland herbs in microsites with differe water contents. *Journal of Ecology*, **64,** 745–755.

Pearsall, W. H. (1920). The aquatic vegetation of the English Lakes. *Journal of Ecology*, **8,** 163–201.

Pimm, S. L. (1978). An experimental approach to community structure. *American Zoologist*, **18,** 797–808.

Platt, W. J. & Weis, I. M. (1977). Resource partitioning and competition within a guild of fugitive prai plants. *American Naturalist*, **111,** 479–513.

Salisbury, E. (1970). The pioneer vegetation of exposed muds and its biological features. *Philosophical Transactions of the Royal Society of London, Series B*, **259,** 207–255.

Sharp, M. J. & Keddy, P. A. (1985). Biomass accumulation by *Rhexia virginica* and *Triadenum fraseri* along two lakeshore gradients: a field experiment. *Canadian Journal of Botany* (in press).

Siegel, S. (1956). *Nonparametric Statistics for the Behavioral Sciences.* McGraw-Hill, New York.

Spence, D. H. N. (1967). Factors controlling the distribution of freshwater macrophytes with particular reference to the lochs of Scotland. *Journal of Ecology*, **55,** 147–170.

Spence, D. H. N. (1982). The zonation of plants in freshwater lakes. *Advances in Ecological Research*, **12,** 37–125.

Valk, A. G. van der (1981). Succession in wetlands: A Gleasonian approach. *Ecology*, **62,** 688–696.

Valk, A. G. van der & Davis, C. B. (1978). The role of seed banks in the vegetation dynamics of prairie glacial marshes. *Ecology*, **59,** 322–335.

Whittaker, R. H. (1967). Gradient analysis of vegetation. *Biological Reviews*, **42,** 207–264.

Wilson, S. D. & Keddy, P. A. (1985a). Plant zonation on a shoreline gradient: physiological response curves of component species. *Journal of Ecology*, **73,** 851–860.

Wilson, S. D. & Keddy, P. A. (1985b). The shoreline distribution of *Juncus pelocarpus* along a gradient of exposure to waves: an experimental study. *Aquatic Botany* **21,** 277–284.

Wilson, S. D., Keddy, P. A. & Randall, D. L. (1985). The distribution of *Xyris difformis* along a gradient of exposure to waves: an experimental study. *Canadian Journal of Botany* **63,** 1226–1230.

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