

## Seedling recruitment of 11 wetland plant species along a water level gradient: shared or distinct responses?

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Where many different plant species occupy an environmental gradient, the responses of their offspring to that gradient could show one of two patterns. All species could have similar requirements for maximum recruitment, in which case all would show maximum germination and emergence in the same region of the gradient ("shared responses"). Alternatively, each species could have different requirements for recruitment and therefore would show maximum recruitment in different regions of the gradient ("distinct responses"). The objective of this study was to test between these two alternatives in plants occurring along a water level gradient. Seeds of 11 wetland species were allowed to germinate in sand along a gradient of water depth, ranging from 10 cm above to 5 cm below the substrate surface. *Scirpus americanus*, *S. validus*, *Sagittaria latifolia*, *Typha angustifolia*, and *Lythrum salicaria* showed no significant response to this gradient, while *Spartina pectinata*, *Polygonum punctatum*, *Bidens cernua*, *Acorus calamus*, *Alisma plantago-aquatica*, and *Eupatorium perfoliatum* did. However, the six species in the latter group did not exhibit shared preferences along the water depth gradient. These different recruitment patterns were consistent with adult distributions in the field. Most species showed some recruitment at all water levels examined, suggesting that they have broad tolerance limits for water level in the recruitment phase of their life history.

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Lorsque plusieurs espèces de plantes croissent le long d'un gradient environnemental, la réaction de leur progéniture à ce gradient peut appartenir à l'un ou l'autre des deux types suivants. Toutes les espèces pourraient avoir les mêmes exigences pour que leur recrutement soit maximum; dans ce cas, toutes auraient une germination et une émergence maximums dans la même partie du gradient ("réponses partagées"). D'autre part, les espèces pourraient avoir des exigences différentes et, par conséquent, pourraient présenter un recrutement maximum dans différentes parties du gradient ("réponses différentes"). L'objectif de cette étude était d'évaluer cette alternative chez des plantes croissant le long d'un gradient de niveau d'eau. Les graines de 11 espèces d'habitats humides furent mises à germer dans du sable le long d'un gradient de profondeur d'eau, laquelle passait de 10 cm au-dessus à 5 cm au-dessous de la surface du substrat. *Scirpus americanus*, *S. validus*, *Sagittaria latifolia*, *Typha angustifolia* et *Lythrum salicaria* ne manifestent aucune réaction significative à ce gradient, contrairement aux espèces suivantes: *Spartina pectinata*, *Polygonum punctatum*, *Bidens cernua*, *Acorus calamus*, *Alisma plantago-aquatica* et *Eupatorium perfoliatum*. Cependant, ces six dernières espèces ne présentent pas de préférences partagées le long du gradient de profondeur de l'eau. Leurs différents patrons de recrutement correspondent au patron de répartition des individus adultes dans les conditions naturelles. Chez la plupart des espèces, il y a au moins un peu de recrutement à toutes les profondeurs analysées, ce qui laisse croire que ces espèces présentent une grande tolérance à l'égard de la profondeur de l'eau durant la phase de recrutement de leur cycle vital.

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### Introduction

Adult plants are distributed along moisture gradients in habitats ranging from prairies (e.g., Curtis 1955; Dix and Smeins 1966; Walker and Coupland 1970; Platt and Weis 1977) to lakeshores (e.g., Pearsall 1920; Hutchinson 1975; Spence 1982; Keddy 1983); in the latter habitat, conspicuous zonation patterns result. The mechanisms that produce this zonation cannot be understood by describing the distributions of adult plants. Because most species experience the greatest mortality during the recruitment phase (Harper 1977; but see Cavers 1983), recruitment patterns may be important in producing different adult distributions along moisture gradients. One method for investigating recruitment would be to perform detailed life history studies on a single species, with particular emphasis on the many environmental factors that influence recruitment. Alternatively, one could choose a single factor known to be important and compare its impact upon many species at one important stage in their life history. We chose the latter approach in this study.

If we consider possible germination patterns along a gradient where many species of adult plants have different distributions, we can imagine two possible outcomes. (i) All species could have maximum recruitment in a similar region on the gradient

("shared responses"). Both Harper (1967) and Grubb (1977) have observed that all plants share a requirement for a few basic resources (light, carbon dioxide, water, and mineral nutrients) and that there are therefore strong limitations upon specialization or "niche differentiation" in plant communities. Perhaps all seedlings share similar moisture requirements early in establishment and one position on the gradient is most suitable for all. (ii) Alternatively, each species could have maximum recruitment at a different point along the gradient ("distinct responses"). Specialization upon different resource levels or habitats is often implicitly assumed in studies of plant distributions along gradients (e.g., Whittaker 1967; Werner and Platt 1976; Platt and Weis 1977). Often it is also assumed that such specialization resulted from past competition producing coevolved communities, although this assumption has been challenged by Connell (1980). Thus, whether plants have shared or distinct responses to specific gradients has important consequences for understanding the mechanisms that produce pattern in vegetation.

Consider the specific case of recruitment along an environmental gradient. Distinct responses could, in themselves, produce zonation patterns, whereas if shared responses occur, other forces (e.g., competition among juveniles and (or) adults,

TABLE 1. The 11 wetland plants examined in this study and selected traits

Species <sup>a</sup>	Family	Perennial (P) or annual (A)	Habitat during growing season	Structure used as a "seed"	Weight per seed (mg) <sup>b</sup>
<i>Spartina pectinata</i> Link.	Poaceae	P	Upper shoreline	Caryopsis	2.65 <sup>c</sup>
<i>Acorus calamus</i> L.	Araceae	P	Upper shoreline	Seed	0.80
<i>Lythrum salicaria</i> L.	Lythraceae	P	Upper shoreline	Seed	0.053
<i>Eupatorium perfoliatum</i> L.	Asteraceae	P	Upper shoreline	Achene	0.12
<i>Typha angustifolia</i> L.	Typhaceae	P	Upper shoreline	Achene	0.055
<i>Polygonum punctatum</i> Ell.	Polygonaceae	A	Upper shoreline	Achene	1.79
<i>Bidens cernua</i> L.	Asteraceae	A	Upper shoreline	Achene	1.11
<i>Scirpus americanus</i> Pers.	Cyperaceae	P	Shallow water	Achene	3.34
<i>Scirpus validus</i> Vahl.	Cyperaceae	P	Shallow water	Achene	0.63
<i>Alisma plantago-aquatica</i> L.	Alismataceae	P	Shallow water	Achene	0.52
<i>Sagittaria latifolia</i> Willd.	Alismataceae	P	Shallow water	Achene	0.38

<sup>a</sup>Nomenclature follows Gleason and Cronquist (1963).

<sup>b</sup>Seeds were dried for 1 day at 100°C; values are based on one batch of  $n = 100$  seeds.

<sup>c</sup>Weight includes palea, lemma, and glumes.

predation) must be invoked. For wetland plants, moisture gradients may be particularly important during recruitment. If water levels on a shoreline remain relatively constant, there will be a strong moisture gradient near the water line. Alternatively, recruitment may be most abundant during low water years (Salisbury 1970; van der Valk and Davis 1978; van der Valk 1981; Keddy and Reznicek 1982), in which case moisture gradients could result from variation in substrate microtopography.

This study examines the recruitment of 11 plant species along a water depth gradient to test whether they have shared or distinct responses. Because there is considerable evidence that wetland species respond to differences between flooded and nonflooded conditions (van der Valk 1981), the gradient provided eight levels between these extremes.

### Methods

The seeds of 11 species (Table 1) were collected from several wetlands in Lanark County and the adjacent Regional Municipality of Ottawa-Carleton, Ont., between 11 and 20 October 1982. (Throughout this paper "seed" will be used in the functional sense to describe a propagule containing a single embryo.) Seeds were air dried at 22°C for 5 days and then kept dry at 5°C in plastic containers in the dark. On 10 December 1982 they were transferred to storage at 2°C in the dark, in mesh bags in plastic containers filled with a moist mixture of peat and sand. In the case of *Polygonum punctatum*, all the seeds had germinated before being removed from the 2°C refrigerator. Consequently, they were replaced by seeds that had received identical treatment except that they had been stored in tap water.

Recruitment was tested along a water depth gradient ranging from treatments with water above the soil surface ("submersed") to those with water levels below the soil surface ("emersed"). The depth of water included eight levels, above (+10, +5, +2, and +1 cm), at (0 cm), or below (-1, -2, and -5 cm) the substrate surface. This gradient was produced in the University of Ottawa greenhouse by using five blocks of eight aquaria, with the water levels assigned at random in each block. Each Plexiglas aquarium (57.5 × 30.5 × 26 cm) was fitted with a tray containing 11 inserts (12.5 × 8 × 6 cm), each filled to 5.5 cm with compacted, unsterilized sand from a quarry. The 12th insert space was used for marking water depths in emersed treatments so that they could be inspected and adjusted daily. A standard sieve series was used to obtain the particle size distribution of the sand: coarse sand (>500 μm), 1%; medium sand (250–500 μm), 88.5%; fine sand (125–250 μm), 10%; and very fine sand (<125 μm), 0.5%. No germination was observed in pots of unsown controls set out in the greenhouse at water depths corresponding to our gradient.

The seeds (38 000) were counted and planted over a 5-day period (one block per day). One hundred seeds per replicate were sown for each species at each water level in each block except for *Typha latifolia*, *Spartina pectinata*, and *Polygonum punctatum*, for which 50 seeds were used per replicate. Seeds for a species were counted and stored on moist filter paper at 22°C until the end of the day when all species were sown. They were randomly assigned to an insert and then evenly scattered over the soil surface and lightly pressed flat into the soil by hand. To prevent seeds from floating, they were covered by sand until they were barely visible to the naked eye; water levels were then raised to the required depth.

In this study recruitment refers to the germination and early establishment phase in a species' life history. In dicotyledons it means that the cotyledons were expanded or that the hypocotyl length exceeded 2.5 cm when the seed coat prevented full expansion of the cotyledons. Seedling recruitment in monocots means that the first foliage leaf had emerged from the coleoptile. Recruited seedlings were counted and clipped off each day for the 1st week and every other day for the next 3 weeks.

Oxygen concentrations in the water in the zero-depth treatment and the submersed treatments were obtained using a model 53 Clark oxygen electrode. Five-millilitre samples of water at the soil surface were obtained with a 10-cm<sup>3</sup> syringe previously flushed with N<sub>2</sub>. O<sub>2</sub> concentrations could not be obtained accurately in emersed treatments by using these methods.

Soil moisture content was determined for emersed treatments and the +1-cm submersed treatment. The upper 0.5 cm of soil (30 mL) was removed from one insert of each aquarium in each block. The soil was dried at 110°C for over 24 h and percent moisture content was calculated.

A one-way ANOVA was performed for each species to test for the equality of recruitment means among eight depths. Only those species showing significant treatment effects were compared using Kendall's coefficient of concordance (Siegel 1956). For each species, mean seedling recruitment values were ranked and assigned to the corresponding water level. The null hypothesis was that the rankings of the water levels for the species were not concordant ("distinct responses") with the alternate hypothesis being that the rankings were concordant ("shared responses").

### Results

Only 6 of the 11 species showed significant differences in recruitment along the water level gradient (Fig. 1). As a group these six species did not have concordant responses to the gradient (Kendall's  $W = 0.14$ ,  $k = 6$ ,  $n = 8$ ,  $p < 0.05$ ); therefore, the null hypothesis of nonconcordant early seedling establishment responses along the gradient was accepted.

Considering adult distributions, of the subset of five species

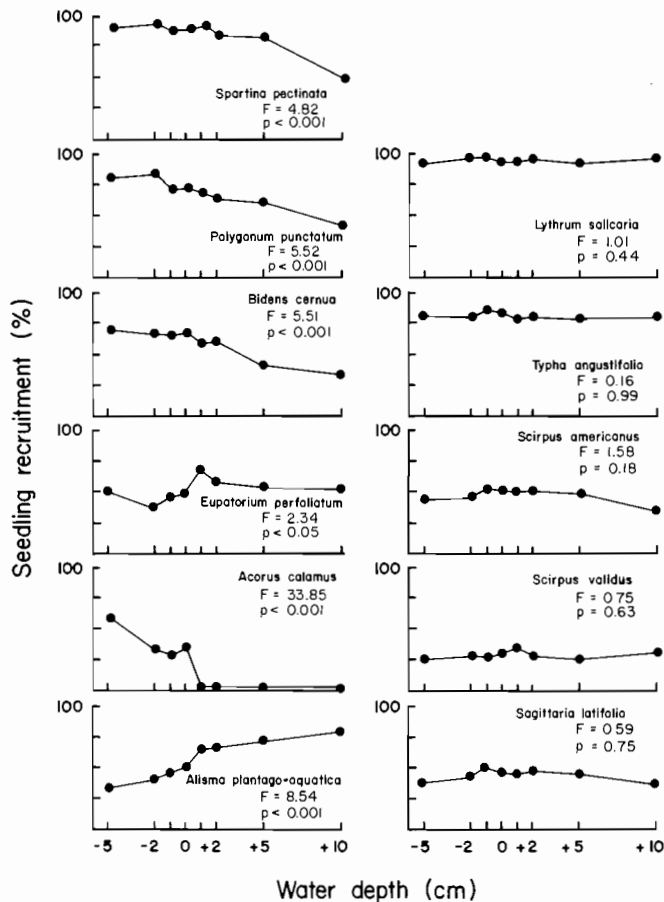


FIG. 1. Recruitment plotted against position along a water depth gradient for 11 wetland plant species. Water depth varied from 5 cm below to 10 cm above the soil level. Species are arranged within each column by position on shoreline (upper shoreline to emergent); the left column contains species showing significant responses to the water depth gradient ( $n = 5$  replicates,  $F$  values calculated using one-way ANOVA,  $df = 7,32$ ).

that grow above the water line (Table 1), responses are still not significantly concordant (Kendall's  $W = 0.39$ ,  $k = 5$ ,  $n = 8$ ,  $p < 0.05$ ). Inspection of Fig. 1 suggests that a subset of four of the five species had a concordant response; *Spartina pectinata*, *Polygonum punctatum*, *Bidens cernua*, and *Acorus calamus* all decreased in percent seedling establishment as water depth increased.

Mean moisture content varied significantly ( $F = 49.65$ ,  $p < 0.001$ ) along this gradient, from 38% below water (saturation) to 27% in the driest treatment. Mean oxygen concentrations were similar for the zero-depth treatment and all submersed treatments (92–94% saturation).

## Discussion

### Recruitment and zonation

Our principal objective was to test whether 11 wetland plant species had shared or distinct recruitment patterns. The six species that responded to the gradient did not show a shared (concordant) response. Previous studies of germination and early establishment responses of groups of species along a moisture gradient have found both shared and distinct responses. Pickett and Bazzaz (1978) tested the early establishment responses of six successional field species along a six-level soil moisture gradient and found similar responses. They

suggest that the absence of differential establishment responses to the moisture gradient may reflect the fact that soil moisture content is usually high during the time of maximal germination, in early spring, and moisture gradients form later in the year when adult responses are more important. In contrast, Harper and Sagar (1953) found distinct early establishment responses for three species of *Ranunculus* that coexist in ridge and furrow grassland. The responses along a three-level water gradient paralleled the adult field distributions along a moisture gradient where *R. bulbosus* tends to occupy the ridges, *R. repens* the furrows, and *R. acris* the intermediate zone. Rabinowitz (1978) tested for shared preference in four genera of mangrove seedlings and concluded that there was no single preferred habitat. Zonation could also not be attributed to distinct preference because seedlings often grew better in habitats occupied by adults of other species. She proposed that zonation is controlled by passive sorting of mangrove propagules.

The above examples illustrate a second point relevant to recruitment patterns and zonation. If distinct preference is found, the patterns in recruitment may be similar to adult distributions (Harper and Sagar 1953) or they may be different from them (Rabinowitz 1978). In the six species that responded to our gradient, comparison of Table 1 and Fig. 1 shows some similarity between adult distributions and seedling requirements. Recruitment in the emergent *Alisma plantago-aquatica* increased with water depth, whereas it decreased with water depth for species from the upper shoreline such as *Spartina pectinata* and *Acorus calamus* (Fig. 1).

### Physical factors varying with water level

Soil moisture (Harper 1977), oxygen concentration (Bewley and Black 1982; Barclay and Crawford 1982), temperature fluctuations, and light characteristics (Bannister 1976) are all known to be the basis for differences in germination requirements. Our objective was not to determine which, if any, of these factors caused the observed recruitment patterns. The water depth gradient included variation in moisture and oxygen availability. While anoxic conditions did not occur in this study, a steep oxygen concentration gradient could be expected between submersed treatments and emersed treatments, as the latter would have seeds partly exposed to atmospheric oxygen concentration through soil pore systems. Different water levels might also have produced different daily temperature fluctuations or changes in light quantity and wavelength.

## Conclusion

These data show that some shoreline plants had distinct rather than shared germination requirements and that these differences are consistent with the distributions of adults. Thus, there is evidence that different species are specialized upon different sections of the moisture gradient at the recruitment phase of their life histories. All species except *Acorus calamus*, however, showed at least 25% establishment in all treatments. Since water level fluctuations are frequent on shorelines (e.g., Salisbury 1970; van der Valk and Davis 1978; van der Valk 1981; Keddy and Reznicek 1982), selection may be against narrowly specializing on a particular water level for recruitment. Rabinowitz (1978) similarly proposed that in mangrove swamps, the environment fluctuates too much to permit specialization. Specialization by adult plants on freshwater shorelines may similarly be of limited value (Keddy 1984).

The mechanisms producing lakeshore zonation are poorly understood (Spence 1982); in particular little is known about

recruitment patterns along lakeshore water level gradients. In wetlands, where recruitment is highest during low water periods (van der Valk 1981), little is known of species' responses to moisture gradients under such conditions. This study shows that recruitment requirements differ along an experimental moisture gradient, which may in turn produce different distributions of adult plants.

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- BANNISTER, P. 1976. Introduction to physiological plant ecology. Blackwell Scientific Publications, Oxford.
- BARCLAY, A. M., and R. M. M. CRAWFORD. 1982. Plant growth under strict anaerobiosis. *J. Exp. Bot.* **33**: 541–549.
- BEWLEY, J. D., and M. BLACK. 1982. Physiology and biochemistry of seeds in relation to germination. Vol. 2. Viability, dormancy and environmental control. Springer-Verlag, Berlin.
- CAVERS, P. B. 1983. Seed demography. *Can. J. Bot.* **61**: 3578–3590.
- CONNELL, J. H. 1980. Diversity and the coevolution of competitors, or the ghost of competition past. *Oikos*, **35**: 131–138.
- CURTIS, J. T. 1955. A prairie continuum in Wisconsin. *Ecology*, **36**: 558–566.
- DIX, R. L., and F. F. SMEINS. 1966. The prairie, meadow, and marsh vegetation of Nelson County, North Dakota. *Can. J. Bot.* **45**: 21–58.
- GLEASON, H. A., and A. CRONQUIST. 1963. Manual of vascular plants of northeastern United States and adjacent Canada. Willard Grant Press, Boston, MA.
- GRUBB, P. J. 1977. The maintenance of species richness in plant communities: the importance of the regeneration niche. *Biol. Rev. Cambridge Philos. Soc.* **52**: 107–145.
- HARPER, J. L. 1967. A Darwinian approach to plant ecology. *J. Ecol.* **55**: 242–270.
- . 1977. Population biology of plants. Academic Press, London, U.K.
- HARPER, J. L., and G. R. SAGAR. 1953. Some aspects of the ecology of buttercups in permanent grassland. *Proc. Br. Weed Control Conf.* **1**: 256–264.
- HUTCHINSON, G. E. 1975. A treatise on limnology. Vol. 3. Limnological botany. John Wiley & Sons, New York, NY.
- KEDDY, P. A. 1983. Shoreline vegetation in Axe Lake, Ontario: effects of exposure on zonation patterns. *Ecology*, **64**: 331–344.
- . 1984. Plant zonation on lakeshores in Nova Scotia, Canada: a test of the resource specialization hypothesis. *J. Ecol.* **72**: 797–808.
- KEDDY, P. A., and A. A. REZNICEK. 1982. The role of seed banks in the persistence of Ontario's coastal plain flora. *Am. J. Bot.* **69**: 13–22.
- PEARSALL, W. H. 1920. The aquatic vegetation of the English Lakes. *J. Ecol.* **8**: 163–201.
- PICKETT, S. T. A., and F. A. BAZZAZ. 1978. Germination of co-occurring annual species on a soil moisture gradient. *Bull. Torrey Bot. Club*, **105**: 312–316.
- PLATT, W. J., and I. M. WEIS. 1977. Resource partitioning and competition within a guild of fugitive prairie plants. *Am. Nat.* **111**: 479–513.
- RABINOWITZ, D. 1978. Early growth of mangrove seedlings in Panama, and an hypothesis concerning the relationship of dispersal and zonation. *J. Biogeogr.* **5**: 113–133.
- SALISBURY, E. J. 1970. The pioneer vegetation of exposed muds and its biological features. *Philos. Trans. R. Soc. London Ser. B*, **259**: 207–255.
- SIEGEL, S. 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill, New York, NY.
- SPENCE, D. H. N. 1982. The zonation of plants in freshwater lakes. *Adv. Ecol. Res.* **12**: 37–125.
- VAN DER VALK, A. G. 1981. Succession in wetlands: a Gleasonian approach. *Ecology*, **62**: 688–696.
- VAN DER VALK, A. G., and C. B. DAVIS. 1978. The role of seed banks in the vegetation dynamics of prairie glacial marshes. *Ecology*, **59**: 322–335.
- WALKER, B. H., and R. T. COUPLAND. 1970. Herbaceous wetland vegetation in the aspen grove and grassland regions of Saskatchewan. *Can. J. Bot.* **48**: 1861–1878.
- WERNER, P. A., and W. J. PLATT. 1976. Ecological relationships of co-occurring goldenrods (*Solidago*: Compositae). *Am. Nat.* **110**: 959–971.
- WHITTAKER, R. H. 1967. Gradient analysis of vegetation. *Biol. Rev. Cambridge Philos. Soc.* **42**: 207–264.