

Effects of a water-depth gradient on the germination of lakeshore plants

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The germination requirements of many wetland species commonly found in the seed bank are poorly understood. The purpose of this study is to explore the germination responses of lakeshore plant species to a water-depth gradient on each of two soil types normally found on shorelines and to test whether germination patterns predict field distributions of adults. Germination patterns were determined in a greenhouse by sowing seeds of 24 lakeshore species along an artificial water-depth gradient, using two soil types (sand and organic soil). Those species showing significant treatment effects were then tested for similar or different germination patterns, using Kendall's coefficient of concordance. Species had similar germination patterns ($n = 5$, $P = 0.02$) on sand. Species had different germination patterns ($n = 7$, $P > 0.50$) on the organic soil. Mean water-depth of germination was significantly correlated with the mean depth occupied by adults in the field for seven species ($r = 0.81$, $P = 0.04$). This study shows that germination requirements are important in controlling recruitment of wetland species after disturbance.

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Les exigences de la germination de plusieurs espèces marécageuses communément présentes dans les réservoirs séminaux sont méconnues. Le but de la présente étude est d'examiner les réactions germinatives d'espèces riveraines à un gradient de profondeur d'eau sur chacun de deux types de sols présents d'habitude sur la berge, et de vérifier l'hypothèse que le type de germination permet de prédire la distribution des plants adultes sur le terrain. Les types de germination ont été déterminés en serre en semant des graines de 24 espèces riveraines le long d'un gradient de profondeur d'eau pour deux types de sols (sable et sol organique). Les espèces qui ont montré des effets de traitement significatifs ont ensuite été testées pour des types de germinations semblables ou différents à l'aide du coefficient d'accord de Kendall. Les espèces avaient le même type de germination sur le sable ($n = 5$, $P = 0,02$); elles avaient des types différents de germination ($n = 7$, $P > 0,50$) sur le sol organique. Dans le cas de sept espèces, il y avait une corrélation significative entre la profondeur d'eau moyenne pour la germination et la profondeur moyenne occupée par les adultes sur le terrain. La présente étude montre que les exigences de la germination sont importantes dans le contrôle du recrutement des espèces marécageuses à la suite de perturbations.

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Introduction

Several recent reviews have emphasized the importance of the regeneration niche when considering factors that determine species distributions and abundances in vegetation (Grubb 1977; Grime 1979; Werner 1979). The regeneration niche is of particular importance in some wetlands because of the frequent occurrence of catastrophic disturbances that remove established vegetation (Harris and Marshall 1963; Salisbury 1970; van der Valk and Davis 1978; Leck and Graveline 1979; van der Valk 1981; Keddy and Reznicek 1985). Furthermore, many wetland plant species have enormous persistent seed banks (van der Valk and Davis 1976, 1978; Thompson and Grime 1979), which are important in the colonization of recently disturbed habitat. Lakeshores are an ideal system for exploring wetland processes since the wetland vegetation is arranged along two gradients: water depth and exposure to waves (Keddy 1983). The latter gradient is often correlated with a soil-texture gradient, ranging from sand in wave-exposed shores to highly organic soil in protected bays (Keddy 1983). This study explores regeneration in sand and in organic soil along the water-depth gradient, in a range of species typical of shoreline wetlands on the southern Precambrian shield.

A central question in the study of seed banks and vegetation is the manner in which germination requirements control recruitment from the former to the latter. This is particularly evident in habitats where microenvironments vary, since minor

differences in habitat can produce very different rates of germination and establishment (Harper et al. 1965). There is an unlimited array of factors that can potentially influence germination. Examples include light intensity (King 1975) and quality (Grime and Jarvis 1975; King 1975), diurnal temperature fluctuations (Thompson et al. 1977), substrate texture (Harper et al. 1965; Keddy and Constabel 1985), soil nitrate levels (Williams and Harper 1965), soil salinity (Chapman 1974), litter (Goldberg and Werner 1983), and moisture levels (Harper and Sagar 1953; Keddy and Ellis 1985). On lakeshores, many of these factors covary with one another along the water-depth and exposure gradients. Irradiance, oxygen concentration, and temperature fluctuations tend to decline with increasing water depth. Soil organic content, nutrients, and water-retention capacity tend to decrease with increasing exposure to waves. In this study, the water-depth gradient was simulated in a glasshouse and the germination patterns of a variety of lakeshore species were determined. The water-depth gradient was duplicated on two soil types differing in soil organic content.

In any multispecies community found along an environmental gradient, there are three possible patterns of germination: (i) germination of the species does not vary along the gradient, (ii) the species have similar germination patterns, or (iii) the species have different germination patterns. If the species exhibit constant germination along the water-depth gradient or if the species exhibit similar patterns, then other forces (e.g., competition, herbivory, stress, disturbance) acting after germination determine the abundance and distribution of adults in this community. However, in the case of different

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patterns where germination maxima are correlated with adult distributions, it is possible that differences in germination requirements are sufficient to produce different distributions of adults. The latter case would also suggest that species could coexist by partitioning the environment as seedlings (Grubb 1977) possibly leading to a reduction in competitive interactions of adults (MacArthur 1972; Werner 1979; May 1981; Schoener 1983).

The objectives of this study were (i) to explore the germination responses of wetland plant species to a range of water depths often encountered in emergent wetland communities, (ii) to test for shared or distinct germination patterns, and (iii) to test whether the responses of species to a water-depth gradient could predict the field distribution of adults.

Materials and methods.

Germination patterns

Seeds were collected from Axe Lake, Ont., Canada (45°23' N, 79°30' W) and an adjacent beaver pond during 23–25 September 1983. The geology, vegetation, and distributions of species within Axe Lake are described by Keddy (1981, 1983). In this study we define a seed as a propagule containing a single embryo. Seeds were air dried at 20°C for 1 month before being transferred to plastic containers, which were kept dry at 4°C in the dark. From 9 to 14 December 1983 the seeds were transferred to nylon mesh bags in plastic containers filled with moist sand (75% saturated) and were kept in the dark at 4°C. The seeds remained in these stratifying conditions until 21 May 1984.

The experimental water-depth gradient included treatments in which water levels were above (–20, –10, –5, –2 cm), at (0 cm), and below (+2, +5, +10 cm) the soil surface. This gradient was created on two soil types: sand (organic content: 0.59%) (measured as in Dean 1974) and organic soil (organic content: 3.12%). Organic contents are expressed as the percentage of dry soil mass lost on ignition at 500°C. The experiment was conducted in a greenhouse, using plastic tubs (length, 56.5 cm; width, 37 cm; height, 35 cm). The experiment consisted of five blocks with eight tubs for each block. Water-level treatments were randomly assigned to the tubs and each tub was divided to include both soil types. Each tub was divided into two by a 0.5 cm thick Plexiglas insert (width, 37 cm; height, 35 cm) and each half of each tub was divided into 24 sections (length, 5 cm; width, 7 cm) with 0.25 cm thick Plexiglas strips. The tubs were filled to a level of 13 cm with commercially obtained sand on one side and organic soil (topsoil mixed with sand) on the other. Plexiglas strips were sunk into the soil to a level of 1.5 cm to prevent seed dispersal between sections. Water levels were adjusted daily or twice daily.

Seeds were planted over a 5-day period (one block per day) beginning 4 June 1984. Fifty seeds of each species were sown in each treatment. The seeds had been counted out 2 weeks before sowing and had been stored dry in Petri dishes in the dark at 4°C until sown. The seeds were then randomly assigned to a section, scattered over the soil surface, and covered with approximately 0.25 cm of soil. Water levels were then raised to the required depth. On 16 June 1984 an algicide, Cutrine Plus (<0.2 ppm Cu), was added to the underwater treatments to minimize algal growth.

In this study, germination refers to early recruitment (i.e., germination and subsequent emergence) and a seed was deemed to have germinated when a green shoot appeared above the soil surface. Recruited seedlings were counted and either removed (small seedlings) or clipped below the hypocotyl (large seedlings) weekly. Eight weeks after the experiment was begun, the soil in each of the treatments was stirred to complete germination. However, the stirring had little effect in stimulating further germination. The experiment was terminated after 10 weeks (4 June 1984 to 17 August 1984) because germination had ceased.

For species that had at least 10% total germination in at least one treatment, Friedman's nonparametric test (Siegel 1956) was per-

TABLE 1. Species that had a minimum of 10% germination in at least one treatment (column A), and species that had less than 10% germination in all treatments (column B)

A	B
<i>Bidens cernua</i> L.	<i>Cladium mariscoides</i> (Muhl.) Torr.
<i>Glyceria canadensis</i> Trin.	<i>Drosera intermedia</i> Hayne
<i>Juncus militaris</i> Bigel.	<i>Dulichium arundinaceum</i> (L.) Britt.
<i>Lobelia dortmanna</i> L.	<i>Eleocharis palustris</i> (L.) R. and S.
<i>Lycopus uniflorus</i> Michx.	<i>Hypericum boreale</i> (Britt.) Bickn.
<i>Rhexia virginica</i> L.	<i>Hypericum ellipticum</i> Hook.
<i>Sagittaria latifolia</i> L.	<i>Juncus brevicaudatus</i> (Engelm.) Fern.
<i>Typha latifolia</i> L.	<i>Juncus canadensis</i> J. Gay
<i>Viola lanceolata</i> L.	<i>Muhlenbergia uniflora</i> (Muhl.) Fern.
<i>Xyris difformis</i> Chapman	<i>Myrica gale</i> L.
	<i>Rhynchospora fusca</i> (L.) Ait. f.
	<i>Scirpus torreyi</i> Olney.
	<i>Triadenum fraseri</i> (Sach.) Gl.
	<i>Utricularia cornuta</i> Michx.

NOTE: Species names are as in Gleason and Cronquist (1963).

formed for each species on each soil type to test for the equality of means among the eight water depths. Depths were ranked according to level of germination; the rankings were done separately for each block.

Those species showing a significant pattern along the water-depth gradient were compared using Kendall's coefficient of concordance (Siegel 1956) to test for similar or different germination patterns. Two tests were done, one for each soil type.

Field distributions

The distributions of adults along the water-depth gradient at Axe Lake were determined during July 1979 (Keddy 1983). The presence of each species was recorded at 20 relative heights (beginning 0.5 m underwater and extending to 0.5 m above water) along each of 25 transects. The number of times a species was found at a particular depth over the 25 transects was then calculated for each species.

A Pearson correlation was performed between the mean depth of germination on the experimental water-depth gradient and the mean depth of occurrences of adults along the water-depth gradient in the field. The correlation included only those species that had a significant germination pattern along the water-depth gradient in the experiment.

Results

Germination patterns

Ten species of 24 had greater than 10% germination in at least one of the treatment levels provided (Table 1). Of the 10 species analyzed individually with Friedman's nonparametric test, 9 demonstrated a significant difference ($P < 0.05$) in recruitment along the water-depth gradient on one or both soil types (Fig. 1).

Because species' germination patterns along the water-depth gradient likely differed between the two soil types, Kendall's coefficient of concordance was performed separately for each soil type to test for similar or different germination patterns. Using only species that had a significant pattern along the water-depth gradient in each analysis, it was found that species had significantly concordant patterns on sand (Kendall's $W = 0.48$, $k = 5$, $df = 7$, $P = 0.02$), whereas on the organic soil species did not have significantly concordant patterns (Kendall's $W = 0.11$, $k = 7$, $df = 7$, $P > 0.50$). Thus, species had similar germination patterns on sand, with maximum germination occurring at water depths near the soil surface (Fig. 1). In

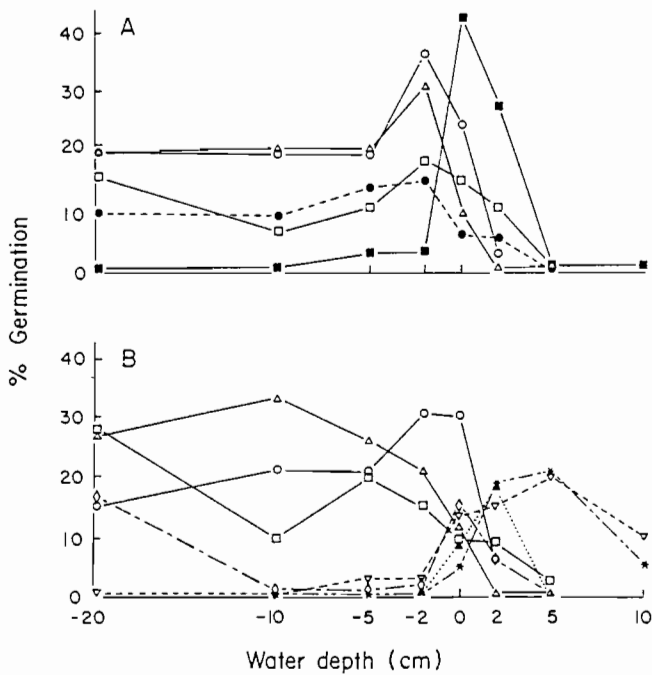


FIG. 1. Mean germination ($n = 5$ replicates) along the water-depth gradient for those species in which germination varied significantly with depth. (A) Sand; (B) organic soil. ■—■, *Bidens cernua*; ◇—◇, *Juncus militaris*; □—□, *Lobelia dortmanna*; ▽—▽, *Lycopus uniflorus*; ▲—▲, *Rhexia virginica*; △—△, *Typha latifolia*; *—*, *Viola lanceolata*; ●—●, *Xyris difformis*.

contrast, species had different germination patterns on organic soil.

There was a significant correlation ($r = 0.81$, $df = 5$, $P = 0.04$) between mean depth of germination in the greenhouse and mean depth of occurrence of adults in the field (Fig. 2). In this analysis, data from both soil types for both adults and seedlings were combined to increase sample sizes. *Sagittaria latifolia* and *Typha latifolia* were not included in the analysis because of insufficient data on adult distributions.

Discussion

In this study many species failed to germinate regardless of water depth; this may be because of the hardened seed coats or pericarps characteristic of many wetland species (e.g., *Cladium mariscoides*, *Scirpus torreyi*) (Sculthorpe 1967; Hutchinson 1975; Hook 1984), which may require special pre-treatments such as mechanical breaking, bacterial activity, or drying to stimulate germination. The moisture regime during cold stratification has also been found to be important to several species (Bannister 1976; Moore 1985), enhancing or retarding germination.

Lakeshore water levels fluctuate widely from year to year and within a year (Keddy 1984; Keddy and Reznicek 1982, 1985). Prolonged periods of high water levels gradually eliminate emergent plant species (van der Valk and Davis 1978) or woody plants (Keddy and Reznicek 1985). Low water periods eliminate species intolerant of drying (e.g., submerged species), which are then replaced by species emerging from the seed bank (Salisbury 1970; van der Valk and Davis 1976, 1978; van der Valk 1981; Keddy and Reznicek 1982; 1985). Many of the genera used in this experiment have widespread occurrence in wetland seed banks (e.g., *Bidens*, *Juncus*, *Lycopus*, *Sagittaria*, *Typha*, and *Viola*) (Keddy and Reznicek

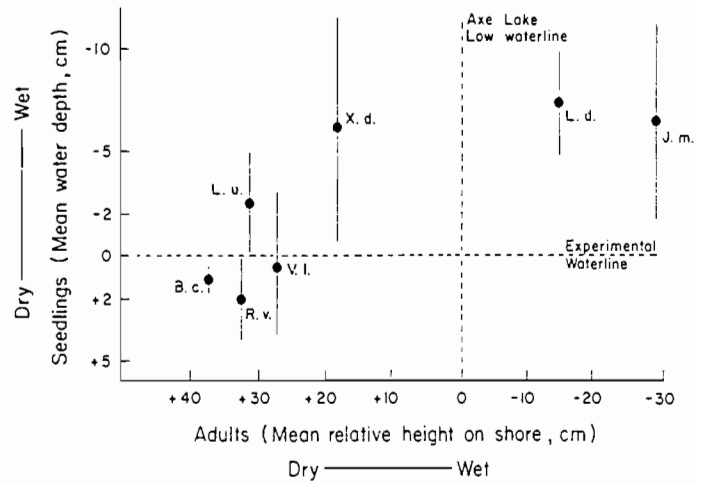


FIG. 2. The relationship between mean depth of germination (with 95% confidence limits) in the greenhouse and mean depth of adult occurrences at Axe Lake for seven lakeshore plant species ($r = 0.81$, $df = 5$, $P = 0.04$). Mean depth of germination was calculated by averaging germination patterns from sand and organic soil types. B.C., *Bidens cernua*; R.V., *Rhexia virginica*; L.u., *Lycopus uniflorus*; V.l., *Viola lanceolata*; X.d., *Xyris difformis*; L.d., *Lobelia dortmanna*; and J.m., *Juncus militaris*.

1985)). This fact combined with the prominent role of natural water-level fluctuations (disturbances) suggests that regeneration by seeds is important in many wetlands. The difficulty is in predicting which species will regenerate after a disturbance. van der Valk (1981) stated that wetland species can be broken into two major groups based on establishment requirements: drawdown species, which establish when there is no standing water, and standing water species, which establish when there is standing water. Figure 1B indicates that a 4-cm change in water level (from -2 to +2 cm) would dramatically alter species composition. This result is consistent with van der Valk's (1981) hypothesis that only two water-level states (flooded or unflooded) are necessary to predict vegetation changes after disturbance. Figure 2 indicates that after disturbance, high shoreline species will be the primary colonizers if unflooded conditions exist, while low shoreline species will colonize the disturbed habitat if flooded conditions exist.

Our results also indicated that substrate organic content may influence absolute germination levels of several species. For instance, several species had much greater germination on sand (e.g., *Bidens cernua*, *Xyris difformis*), while others had maximum germination on organic soil (e.g., *Juncus militaris*). Some were unaffected by soil organic content (*Lobelia dortmanna*, *Sagittaria latifolia*). Maximum germination on the two substrate types was consistent with field distributions. For instance, *J. militaris* was abundant on shorelines with substrate organic content $> 3.7\%$, while *X. difformis* was associated with sandy shorelines (organic content $< 3.7\%$) (Keddy 1981). Therefore, our results indicate that substrate organic content can influence the species that are able to establish after disturbance.

The question of similar or different germination patterns is most relevant to species that can potentially interact; this study included only species found between the shrub and floating-plant zones on lakeshores. Within this shoreline association, we found similar germination patterns on sand and different germination patterns on the organic soil. Variation in several environmental factors along the water-depth gradient may

TABLE 2. Studies that have examined germination patterns of two or more species along environmental gradients

Gradient	Plant association	Germination	Reference
Moisture	<i>Ranunculus</i> spp.	Different*	Harper and Sagar 1953
	Successional field spp.	Similar	Pickett and Bazzaz 1978
	Sand-dune annuals	Similar*	Pemadesa and Lovell 1975
Water potential	Forest and prairie annuals	Similar*	Raynal and Bazzaz 1973
Water tension	Range grasses	Similar*	Knipe and Herbal 1960
	Various herbs	Similar*	Harper and Benton 1966
Water depth	River shoreline herbs	Different	Keddy and Ellis 1985
Saltwater depth†	Mangrove spp.	Different	Rabinowitz 1978
Salinity	Halophytes	Similar*	Chapman 1974
Particle size	Wetland herbs	Similar	Keddy and Constabel 1985
Soil type	Forest and prairie annuals	Different*	Raynal and Bazzaz 1973
Temperature	Old-field spp.	Similar*	Shontz and Oosting 1970
	Desert annuals	Different	Went 1949

*Determined by inspection of the data.

†Adults were present throughout this study.

explain the contrasting results obtained on the two soil types. Irradiance and moisture content measurements, both in the greenhouse experiment and at Axe Lake, indicate that both of these factors have a greater range over the water-depth gradient on the organic soil than occurs on sand (Moore 1985). These differences may explain why species were able to partition the water-depth gradient, in terms of their germination patterns, on the organic soil but not on sand. For instance, *Typha latifolia* had maximum germination at -2 cm on sand, as did 3 of the other 4 species considered, but on the organic soil, maximum germination occurred at -10 cm, unlike any other species.

Several studies of recruitment along environmental gradients have found that species have similar germination patterns (Table 2). For instance, Harper and Benton (1966) found that of 12 species sown along a water-tension gradient, 9 had maximal germination at the wettest end, 2 were not affected by the gradient, and 1 did not germinate. Similarly, Keddy and Constabel (1985) sowed 11 wetland plant species along a gradient of soil particle sizes to test whether seeds of different sizes germinated best on soil types with specific particle sizes. They found that the species had similar germination patterns, with maximal germination occurring on small particle sizes irrespective of the seed size sown.

Different germination patterns along environmental gradients have also been demonstrated (Table 2). Keddy and Ellis (1985) found that of 11 riparian species sown along a water-depth gradient, 6 had different germination patterns, while the other 5 had no significant pattern of germination. Harper and Sagar (1953) found that three species of *Ranunculus* coexisting in ridge and furrow grassland have different germination patterns along a moisture gradient, with maximal germination for *R. bulbosus* occurring at the dry end, *R. acris* in the middle, and *R. repens* at the wet end. As in this study (Fig. 2), the above studies found that the different germination patterns of the species studied paralleled their respective field distributions as adult plants. At present we lack the information necessary to predict which environmental gradients, or which habitats, are likely to be characterized by similar or different patterns of germination.

In certain wetlands (e.g., prairie glacial marshes, freshwater tidal marshes, lakeshores) disturbance can lead to mass germination from buried seeds. While it may be possible to predict the kinds of species emerging, thereby predicting future

kinds of vegetation (van der Valk 1981), our results show that minor changes in water level or substrate type will cause significant changes in the species that germinate. At the same time, these results add to a growing literature showing that manipulations of soil moisture, soil texture, or substrate type will dramatically alter the species composition of recently disturbed sites.

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