

Effects of water level, shade and time on germination and growth of freshwater marsh plants along a simulated successional gradient

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Summary

1 We examined the effect of soil organic content (1.4, 3.6, 7.2% soil C), water level (+2, –1, –4 cm from soil surface) and duration (13 or 33 days) on 10 species that varied in abundance during succession in freshwater marshes. We also determined the effect of shade (0, 40, 80% shade) and soil organic content (1.4 and 7.2% soil C) on germination of six species over 62 days with water 0.5 cm below the soil surface.

2 Water level consistently affected species germination on both dates. Above-ground biomass was generally higher with increasing organic content of soil, but shade had little effect on germination or height.

3 The hydrologic zone in which species were found in the field was a good indicator of the response of germination to hydrology. Both early successional species and species widespread across the successional gradient show similar germination on all organic contents, while later successional species appear to germinate best at higher organic contents.

4 Successional changes in soils are capable of affecting plant community development, independent of disturbance.

Key-words: establishment, hydrology, *Phalaris arundinacea*, restoration, wetland

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Introduction

Succession has often been studied in the context of competition, but fewer studies have focused on the role of germination, notably on the effects of successional increases in soil organic matter on germination. Freshwater wetlands are particularly appropriate systems in which to study the potential for germination to affect plant community structure during succession because there is evidence that they are not immigration limited (Weiher & Boylen 1994) and the increase in organic content of soils during wetland succession is well documented (Dansereau & Segadas-Vianna 1952; Gorham 1957). Although plant competition (Wilson & Keddy 1986a) and the competitive ability of individual species (Wilson & Keddy 1986b; Gaudet & Keddy 1995) are

positively correlated with soil organic matter, immigration is still capable of affecting herbaceous community composition after 5 years in wetland microcosms (Weiher & Keddy 1995). Additionally, hydrologic changes often leave large areas of unvegetated soils open to colonization (van der Valk & Davis 1976; Keddy & Reznicek 1982). In the absence of regeneration from surviving individuals (e.g. Grubb 1977), seed banks and dispersal must drive the establishment of new plant communities. Because seed banks of freshwater wetlands often differ substantially from the plant community (van der Valk 1981; Leck 1989), disturbances have the potential to result in dramatic changes in vegetation. Species-specific germination responses will depend on site-specific environmental conditions such as hydrology, successional status, and shade from remnant vegetation or litter.

Germination and establishment are obviously critical first steps in the development of a plant community. However, the assumption that life-history strategies of mature plants will reflect the strategies of seeds and seedlings (e.g. MacArthur & Wilson 1967) has been discredited for freshwater marsh plants (Shipley *et al.* 1989). There can be differences in the location on environmental gradients favoured by seedlings and adults, such as in Panamanian mangroves, where seedlings germinate best in hydrologic conditions from which

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adults are excluded (Rabinowitz 1978). Other studies found that germination differences resulting from microtopographic variation of 1–5 cm were capable of changing plant community composition in microcosms (Vivian-Smith 1997), while wetland plant communities subjected to experimental flooding were structured by historical germination for 1–2 years (Seabloom *et al.* 2001). However, others have found that the conditions that maximized germination corresponded to those where mature plants were most abundant in the field (Keddy & Ellis 1985). The decoupling of seed and adult plant traits indicates the need for detailed studies on the effect of environmental gradients on wetland species.

Environmental gradients cannot structure plant communities through germination if species either do not vary, or vary similarly across the gradient (Keddy & Ellis 1985; Moore & Keddy 1988). Other structuring forces could be dependent on plant adult traits, such as competition, or they could vary based on allogenic effects on adults and seedlings, such as disturbance and herbivory. Any differential germination may, or may not be sufficient to explain community structure, and its response to soil successional changes may also explain locations of plant species on successional gradients (e.g. Peterson & Bazzaz 1978).

Factors that may affect germination rates in freshwater marshes include hydrology, soil characteristics, temperature fluctuations and light conditions. Many wetland species require mudflat conditions to germinate (van der Valk 1981), but some emergent species, such as *Typha latifolia* (Sifton 1959; Keddy & Ellis 1985), germinate best in flooded conditions. Soil characteristics, such as particle size (Keddy & Constabel 1986) and small differences in organic matter (Moore & Keddy 1988), interact with hydrology to cause differential germination. Nitrate at moderate levels increases germination (Peterson & Bazzaz 1978; Baskin & Baskin 1998), and various soil organic compounds can both inhibit and stimulate germination (Hilhorst & Karssen 2000). Temperature fluctuations are particularly important in wetlands, with 42% of 66 species tested responding to temperature fluctuations, compared to approximately 10% from other ecosystems (Thompson & Grime 1983). Large temperature fluctuations are thought to be good indicators of gaps in vegetative cover (Thompson *et al.* 1977; Fenner 1985) and can also indicate exposure of soil from falling water level (Fenner 1985). Both temperature fluctuations and light are sometimes necessary for germination (Pons 2000), and species requiring light for germination also generally respond negatively to a reduction in the ratio of red : far-red light found under vegetation canopies (Gorski *et al.* 1977). Much less is known about the interactions of factors in ecologically realistic settings than their individual effects. This is particularly true for interactions involving soil organic matter effects on germination, which have only rarely been examined (e.g. Moore & Keddy 1988).

This study examined the effects of a simulated soil successional gradient (differing organic matter contents),

a hydrologic gradient and light-availability (shade treatments) on germination of emergent marsh species which varied in abundance among early and late successional freshwater marshes in northern Indiana, USA (Kellogg & Bridgman 2002). Our objectives were to determine whether (i) soil, hydrology, or interactive effects drive germination and growth rate of seedlings; (ii) increased temporal homogeneity of environmental conditions changes the relative germination rates among species (i.e. did rankings differ after 2 and 4 weeks); (iii) optimum germination conditions reflected the mature plants' distribution; (iv) the successional status of mature plants affects germination and seedling response to shade.

Methods

ORGANIC MATTER AND HYDROLOGY EFFECTS ON GERMINATION

This experiment was conducted in a greenhouse at the University of Notre Dame from May–June, 2000. The greenhouse is constructed of quartz glass, which transmits 95% of solar radiation and natural light was supplemented with grow-lights (40 watt wide spectrum, General Electric Lighting, Cleveland, Ohio, USA) for 12 hours each day. Temperatures during the experiment ranged from 16 to 32 °C.

Seeds from 10 locally common marsh species, *Alisma subcordatum* Raf., *Calamagrostis canadensis* (Michaux) Beauv., *Leersia oryzoides* (L.) Sw., *Penthorum sedoides* L., *Phalaris arundinacea* L., *Sagittaria latifolia* Willd., *Scirpus acutus* Muhl., *Scirpus cyperinus* (L.) Kunth, *Scirpus validus* Creber, and *Typha × glauca* Godr. were used. All seeds (with the exception of *L. oryzoides*) were local genotypes and were obtained from a local native plant nursery (J. F. New and Associates, Inc., Walkerton IN), where they were refrigerated after harvest. Seeds were not tested for viability, but those selected were firm, had an unbroken seed coat and were similar in size. Seeds that remained ungerminated were firm and had no evidence of fungal growth, also indicating viability (Baskin & Baskin 1998).

We used a fully crossed factorial design to test the effects of soil organic matter percentage and hydrology on germination. The soil treatment had three levels consisting of 10% (1.4% soil C, pH = 6.1), 25% (3.6% soil C, pH = 5.8), and 50% (7.2% soil C, pH = 5.7) by volume of a Histosol (Houghton muck; 31% C, 2.5% N, 0.1% P) from a local wetland mixed with washed and sieved sand (playground sand; Quikrete, Atlanta GA). The Histosol had all roots removed, and was dried and sieved to pass a 2-cm mesh prior to the experiment. The hydrology treatment also had three levels consisting of water to 4 cm below, 1 cm below and 2 cm above soil surface, maintained daily using deionized water. Seeds were stored in deionized water for 1 month in the dark at 4 °C prior to the experiment. Fifty seeds from each species were evenly distributed on the soil surface of each of three replicates per treatment.

All seeds were flattened against the soil by hand, except in the flooded treatments, when they were allowed to sink at their own rate. All treatments were randomly placed in the greenhouse and were re-randomized twice during the study. A set of control pots of soil with no seeds was placed in each treatment combination to determine if viable seeds of any of the experimental species were present in the soil seed bank (they were not). Soil percent moisture was measured in the top 1 cm of soil by comparing wet weight to weight after drying for 72 h at 65 °C. This moisture measurement reflects percent water holding capacity of the soil and does not take into account water that drained from soils as they were collected.

Germinated seedlings (defined as shoot emergence) were counted every 2–3 days. Few seedlings died after germination, so seedling numbers analysed are good indicators of total germination on the day measured. Seedling above-ground weight was determined at the completion of the experiment after drying at 65 °C for 48 h. Species were compared based on the number of seedlings on days 13 and 33, and on the mean individual above-ground biomass of seedlings on day 33.

Nylon mesh bags of 3 g H-OH resins (Rexyn I-300 research grade resin, Fisher Scientific stock #R208-500) were used to compare nitrate levels in each soil treatment (Binkley & Hart 1989). This was done as part of another experiment, so resin bags were placed only in pots with water levels 1 cm below the soil. Five pots for each treatment were placed in the greenhouse for 100 days (early June until mid-October 2000) with one resin bag per pot buried approximately 5 cm beneath the soil surface. After removal, the bags were rinsed in DI water, air-dried and stored until extraction with 50 mL 2 M potassium chloride for 1 hour. Extracts were analysed on a Lachat QuikChem 8600 autoanalyser (method 12-107-04-1-B, Lachat Instruments, Milwaukee WI, USA).

For number of seedlings, repeated measures ANOVA (rmANOVA) was conducted, and both independent factors had significant interactions with day sampled ($P = 0.02$), so ANOVAs were run separately for each day. Differences among species (within treatments) and among treatments (within each species) were compared using ANOVA and Fisher's least significant difference (LSD) *post hoc* tests for each day. Seedling biomass was compared among treatments using ANOVA and Fisher's LSD *post hoc* tests. Soil moisture was compared among soil-hydrology treatments using ANOVA and Fisher's LSD *post hoc* tests. Nitrate levels were compared among soil mixtures using ANOVA and Fisher's LSD *post hoc* tests. Significance for all statistical tests was determined at $P \leq 0.05$.

FIELD SURVEY OF VEGETATION

Vegetation at various stages of succession was sampled in the field in unplanted freshwater marsh restorations and in two undrained reference sites in northern Indiana

(Kosciusko, Newton, Noble, St. Joseph counties) USA. Restored sites consisted of two 5-year-old, two 10-year-old, three 22–23-year-old sites, and three 41–47-year-old sites, and had previously been cultivated for at least 45 years following initial drainage. Historical photos, documents and personal interviews confirmed that no wetland areas remained prior to restoration. Because restored sites were neither planted or seeded, and the wetland seed bank was expected to have been reduced by draining and farming, wetland vegetation was expected to be due almost entirely to colonization. The reference wetlands have never been drained. Sites ranged in size from 0.2 to 2 ha and had no surface inlets, with the exception of two 47-year-old-sites that were approximately 32 ha and had inlets draining fields cultivated in row crops approximately 0.5 km from the sampled plots. Vascular plant cover was estimated (as a percentage) for eight 1-m² plots in each wetland including three saturated plots (0–5 cm standing water) in August 1997 and five saturated plots in August 1998. Plots were randomly chosen and all species examined in this analysis were present in at least nine sample plots.

Soil percent carbon for each wetland was determined from the mean of three plots in the saturated zone of each wetland. Each 1-m² plot had cores removed from opposite corners of the quadrat, which were consolidated for analysis. Cores from restored sites consisted of the organic layer (1–6 cm depth) with litter and roots removed and the top 5 cm of mineral soil. The organic layer was assessed in the field by changes in colour and texture. Cores from the reference sites were all organic, so the top 10 cm was sampled. Soils were dried, ground and analysed using a Perkin Elmer (Shelton, Connecticut) PE-2400 CHN analyser. Vegetation cover in the field was compared to germination rates on day 33 for three soil organic classes (0–2.49% (four wetlands), 2.5–4.99% (four wetlands), 5–7.5% (two wetlands) soil C). Additionally, vegetation cover was analysed for the two undrained wetlands that had much greater soil C than the restored sites (mean 27%). This comparison was done for the six species that consistently germinated across treatments in the soil-hydrology experiment.

SHADE EFFECTS ON GERMINATION

This experiment was conducted in a climate-controlled greenhouse at the University of Notre Dame from March–May 2001. Conditions were as above except that the greenhouse glass transmitted 75% of solar radiation, and temperatures during the experiment ranged from 25 to 29 °C.

We studied five of the six species that had germinated freely in the soil-hydrology study (*L. oryzoides*, *Phalaris arundinacea*, *Sagittaria latifolia*, *Scirpus cyperinus*, *Scirpus validus*) plus *Typha latifolia* L., which replaced *Typha* × *glauc*, whose seeds were no longer available. Three ungerminated *L. oryzoides* seeds showed evidence of fungal growth, but all other seeds appeared viable. All seeds were stored dry in the dark at 4 °C

prior to the experiment, with the exception of *Sagittaria latifolia*, which was shipped wet.

We used a fully crossed factorial design to test the effects of two levels of a soil treatment (10% and 50% by volume of a Histosol mixed with sand, as in the previous experiment) and three levels of shade (0%, 40%, and 80%). The shade was provided by nylon shade cloth (Plaspack Corporation, Antigo WI) on a wooden frame. Water levels were maintained 0.5 cm below the soil surface daily using deionized water. Fifty seeds from each species were placed on the soil surface of each of three replicates per treatment and flattened against the soil by hand. All treatments were randomly placed in the greenhouse and were re-randomized three times during the study. No seeds germinated in control pots of soil used to assess the soil seed bank.

Germinated seedlings were counted every 2–3 days, and germination was defined as emergence of plant parts above the soil. Seedling mortality was again negligible. Species were compared based on the number of seedlings on days 10, 32 and 62, and on mean height of seedlings on day 62. The seeds were allowed longer to germinate than the prior experiment due to their dry storage and the reduced temperature fluctuations in

the solarium used for this experiment. Data were analysed as above, with the exception that results from the two soils were not different for germination or mean height, so both soil types were pooled for subsequent analysis.

Results

ORGANIC MATTER AND HYDROLOGY EFFECTS ON GERMINATION

Comparisons among species

Repeated measures ANOVA of percentage germination on days 13 and 33 showed significant interactions between day sampled and species ($P < 0.001$), soil ($P = 0.04$), and hydrology ($P < 0.001$). Soil did not affect the number of seedlings on day 13 but there was a species–hydrology interaction ($P < 0.001$) (Table 1). Germination by day 33 (Table 2) had a species–soil–hydrology interaction ($P < 0.001$). Mean above-ground biomass of seedlings on day 33 (Table 3) had significant species–hydrology and species–soil interactions ($P = 0.02$ and $P < 0.001$, respectively).

Table 1 Mean percentage germination (1 SE) on day 13 from soil/hydrology experiment (soils pooled). Species abbreviations are: PA, *Phalaris arundinacea*; LO, *Leersia oryzoides*; PS, *Penthorum sedoides*; SC, *Scirpus cyperinus*; TG, *Typha × glauca*; SV, *Scirpus validus*; SL, *Sagittaria latifolia*; AS, *Alisma subcordatum*; SA, *Scirpus acutus*; CC, *Calamagrostis canadensis*

Hydrology	Species									
	PA	LO	PS	SC	TG	SV	SL	AS	SA	CC
Flooded	29 (6) ^a	4 (2) ^{bc}	5 (3) ^{bc}	1 (1) ^c	8 (3) ^b	0 (0) ^c	0.4 (0.3) ^c	0.4 (0.3) ^c	0 (0) ^c	0 (0) ^c
1 cm below surface	15 (1) ^a	1 (0.5) ^b	15 (4) ^a	3 (1) ^b	20 (5) ^a	0 (0) ^b	0 (0) ^b	0 (0) ^b	0.4 (0.3) ^b	0 (0) ^b
4 cm below surface	12 (4) ^a	2 (1) ^b	23 (7) ^c	5 (3) ^{ab}	11 (5) ^{ad}	3 (2) ^{bd}	0 (0) ^b	0 (0) ^b	0 (0) ^b	0 (0) ^b

Superscript letters indicate significant differences (Fisher's LSD, $P = 0.05$) among species within each treatment.

Table 2 Mean percentage germination (1 SE) on day 33 for all soils from soil/hydrology experiment. Soil abbreviations are: low OM (10% organic soil), int. OM (25% organic soil), high OM (50% organic soil). Species abbreviations as Table 1

Hydrology and soil	Species									
	PA	LO	PS	SC	TG	SV	SL	AS	SA	CC
Flooded										
Low OM	55 (15) ^a	7 (3) ^b	1 (1) ^b	13 (6) ^b	3 (3) ^b	2 (1) ^b	3 (2) ^b	0 (0) ^b	0 (0) ^b	0 (0) ^b
Int. OM	27 (7) ^a	9 (3) ^{bc}	15 (4) ^c	6 (3) ^{bd}	2 (1) ^{bd}	5 (2) ^{bd}	0 (0) ^d	0 (0) ^d	0 (0) ^d	0 (0) ^d
High OM	29 (4) ^a	9 (2) ^b	19 (12) ^{ab}	17 (6) ^{ab}	12 (6) ^b	5 (1) ^b	0 (0) ^c	0 (0) ^c	1 (1) ^c	1 (1) ^c
1 cm below soil										
Low OM	59 (10) ^a	6 (3) ^b	29 (7) ^c	87 (8) ^d	37 (10) ^c	1 (1) ^b	1 (1) ^b	0 (0) ^b	1 (1) ^b	0 (0) ^b
Int. OM	65 (4) ^a	11 (2) ^b	57 (10) ^a	68 (14) ^a	15 (10) ^b	1 (1) ^b	4 (2) ^b	0 (0) ^b	0 (0) ^b	0 (0) ^b
High OM	81 (7) ^a	10 (6) ^c	28 (9) ^{bc}	55 (26) ^{ab}	19 (11) ^c	4 (2) ^c	0 (0) ^c	0 (0) ^c	0 (0) ^c	0 (0) ^c
4 cm below soil										
Low OM	33 (2) ^a	7 (3) ^b	38 (9) ^a	34 (15) ^a	9 (5) ^b	0 (0) ^b	3 (2) ^b	0 (0) ^b	1 (1) ^b	0 (0) ^b
Int. OM	50 (11) ^a	7 (2) ^b	51 (7) ^a	84 (8) ^c	31 (10) ^d	4 (4) ^b	0 (0) ^b	0 (0) ^b	0 (0) ^b	2 (2) ^b
High OM	59 (5) ^a	7 (1) ^b	37 (12) ^c	85 (15) ^d	21 (12) ^{bc}	8 (2) ^b	0 (0) ^b	0 (0) ^b	1 (1) ^b	5 (5) ^b

Superscript letters indicate significant differences (Fisher's LSD, $P = 0.05$) among species within each soil-hydrology treatment combination.

Table 3 Mean seedling above-ground biomass ($\text{g} \times 10^3$) (1 SE) on day 33 from soil/hydrology experiment. Results for species–hydrology and species–soil interaction are shown. Abbreviations as Tables 1 and 2

Hydrology or soil	Species									
	PA	LO	PS	SC	TG	SV	SL	AS	SA	CC
Hydrology										
Flooded	2.4 (0.3) ^a	7.0 (1.6) ^b	0.1 (0.05) ^c	0.1 (0.01) ^c	0.4 (0.2) ^c	0.7 (0.1) ^c	0.3 (0.2) ^c	0 (0) ^c	0.8 (0.8) ^c	0.02 (0.02) ^c
1 cm below surface	2.6 (0.3) ^a	7.7 (4.1) ^b	0.2 (0.1) ^a	0.3 (0.1) ^a	1.1 (0.3) ^a	0.5 (0.1) ^a	0.3 (0.3) ^a	0 (0) ^a	0.1 (0.1) ^a	0 (0) ^a
4 cm below surface	3.1 (0.5) ^a	3.9 (1.1) ^a	0.1 (0.05) ^b	0.2 (0.05) ^b	0.9 (0.2) ^b	0.4 (0.2) ^b	0.05 (0.04) ^b	0 (0) ^b	0.2 (0.1) ^b	0.2 (0.1) ^b
Soil										
Low OM	2.1 (0.3) ^a	2.6 (0.5) ^a	0.04 (0.01) ^b	0.2 (0.1) ^b	0.5 (0.2) ^b	0.2 (0.1) ^b	0.3 (0.2) ^b	0 (0) ^b	0.1 (0.1) ^b	0 (0) ^b
Int. OM	2.9 (0.4) ^a	6.5 (1.4) ^b	0.1 (0.03) ^c	0.2 (0.1) ^c	1.1 (0.4) ^c	0.5 (0.1) ^c	0.3 (0.3) ^c	0 (0) ^c	0 (0) ^c	0.1 (0.1) ^c
High OM	3.1 (0.3) ^a	9.7 (4.0) ^b	0.4 (0.1) ^a	0.2 (0.1) ^a	0.8 (0.3) ^a	0.9 (0.1) ^a	0 (0) ^a	0 (0) ^a	0.2 (0.1) ^a	0.2 (0.1) ^a

Superscript letters indicate significant differences (Fisher's LSD, $P = 0.05$) among species within each treatment.

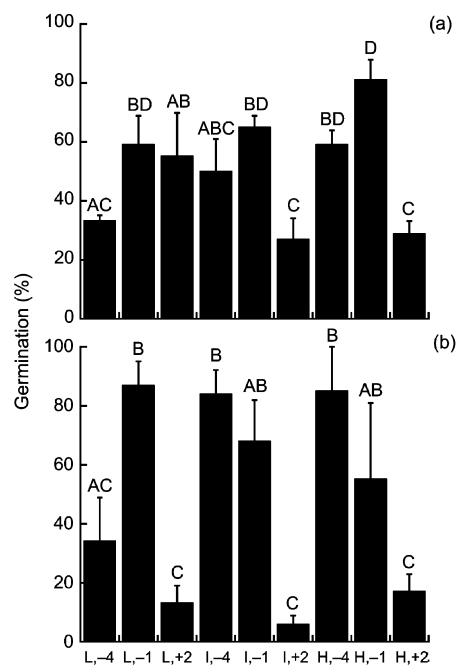


Fig. 1 Percentage germination after 33 days for (a) *Phalaris arundinacea* and (b) *Scirpus cyperinus*. Letters indicate significant differences between treatments for each species (Fisher's LSD, $P = 0.05$) and error bars indicate 1 SE. Treatment abbreviations are as follows: L, low organic soil; I, intermediate soil; H, high organic soil; -4, water level 4 cm below soil; -1, water level 1 cm below soil; +2, water level 2 cm above soil.

Comparisons within species

Phalaris arundinacea had higher germination in flooded conditions than other hydrologies on day 13 (Table 1, $P \leq 0.035$). The seedling mass was greater in high organic soil than other soils ($P \leq 0.05$), and in intermediate than in low organic soil ($P = 0.03$) (Table 3). Germination by day 33 was affected by a soil–hydrology interaction for *Phalaris arundinacea* (Fig. 1a, $P = 0.025$) as well as for *Scirpus cyperinus* (Fig. 1b, $P = 0.04$).

Penthorum sedoides had higher germination by day 33 in intermediate than low organic soils ($P = 0.02$), and a trend toward more seedlings in intermediate than high organic soils ($P = 0.078$). Germination by day 33 was also lower in flooded conditions than other hydrologies ($P \leq 0.002$). Seedling biomass was greater in high and intermediate than in low organic soils.

The other seven species showed few or no differences among treatments. *L. oryzoides* had greater biomass in high organic soil (Table 3, $P \leq 0.01$). *Scirpus validus* had more seedlings by day 33 in high than low organic soil (Table 2, $P = 0.008$), and greater biomass in high organic soils than others (Table 3, $P \leq 0.006$). *A. subcordatum*, *Calamagrostis canadensis*, *Sagittaria latifolia*, and *Scirpus acutus*, which did not consistently germinate, did not differ among treatments for any measurement. Field abundance across an organic content gradient for all other species is compared with their germination in Fig. 2.

Environmental factors

Soil percent moisture in the top 1 cm was greater with increasing organic content ($P < 0.001$), but was not affected by hydrology. All soil types were different ($P < 0.01$) becoming moister with increasing organic content ($17.5 \pm 0.5\%$ (1 SE) vs. $21.7 \pm 0.8\%$, and $32.9 \pm 1.4\%$ for low, intermediate and high).

Nitrate levels differed among soils ($P = 0.002$), with intermediate soils ($0.16 \pm 0.005 \text{ mg-NO}_3 \text{ g-resin}^{-1} \text{ day}^{-1}$) having higher nitrate levels ($P \leq 0.05$) than low ($0.09 \pm 0.026 \text{ mg-NO}_3 \text{ g-resin}^{-1} \text{ day}^{-1}$) or high ($0.04 \pm 0.012 \text{ mg-NO}_3 \text{ g-resin}^{-1} \text{ day}^{-1}$) which did not differ significantly ($P = 0.13$).

SHADE EFFECTS ON GERMINATION

Repeated measures ANOVA revealed significant day–species ($P < 0.001$), and day–shade ($P = 0.008$) interactions. Soil organic content was not a significant factor,

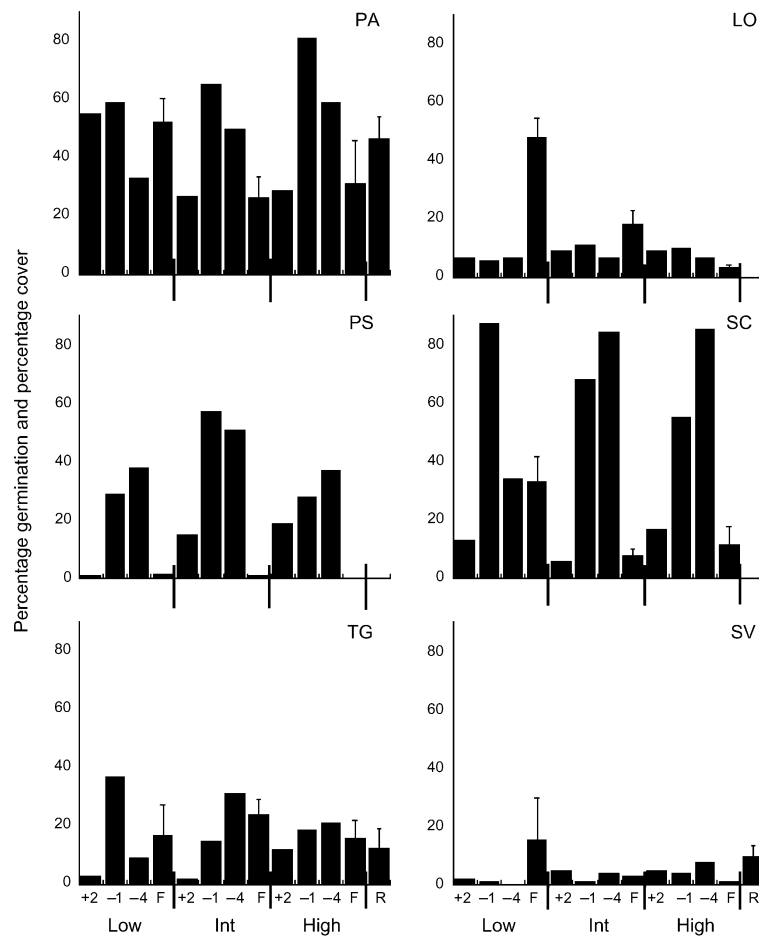


Fig. 2 Mean percent germination (+2, -1, -4) and field cover (F) over soil organic content gradient for species that germinated consistently across treatments. Species abbreviations are as Table 1. Soil abbreviations are as follows: Low, 0–2.49% soil C; Int, 2.5–4.99% soil C; High, 5.0–7.5% soil C. R = undrained reference wetlands (27% mean soil C). Error bars are 1 SE for all cover data, while SE for germination is listed in tables.

Table 4 Mean percentage germination (1 SE) on days 10 and 32, and mean seedling height (1 SE) on day 62 from shade germination experiment (both soil types pooled). Species abbreviations are: PA, *Phalaris arundinacea*; TL, *Typha latifolia*; LO, *Leersia oryzoides*; SC, *Scirpus cyperinus*; SV, *Scirpus validus*; SL, *Sagittaria latifolia*

Measurement	Species					
	PA	TL	LO	SC	SV	SL
Day 10	1 (0.4) ^a	2 (0.4) ^b	1 (0.5) ^{ac}	0 (0) ^c	0 (0) ^c	0.2 (0.2) ^c
Day 32	8 (2) ^a	3 (1) ^b	1 (1) ^{bc}	0.2 (0.2) ^{bc}	0 (0) ^c	0.3 (0.2) ^{bc}
Mean height (cm)	6.4 (0.6) ^a	0.9 (0.3) ^{bc}	1 (0.5) ^c	0.1 (0.05) ^b	0.03 (0.03) ^b	0.07 (0.06) ^b

Superscript letters indicate significant differences (Fisher's LSD, $P = 0.05$) among species within each measurement.

so all subsequent analyses were run with both soil types pooled. There were no treatment effects on germination on days 10 and 32 or seedling height, although species was significant in all cases ($P < 0.001$) (Table 4). However, a significant species–shade interaction affected final germination rates (day 62, $P = 0.002$). Subsequent ANOVAs for each shade treatment showed differences among species ($P < 0.001$) (Table 5), but *Phalaris arundinacea* was the only species that showed a shade effect ($P = 0.057$).

Discussion

Although germination was initially affected only by hydrology, the composition of the community, establishment and initial growth rates can be structured by soil organic content. A successional increase in organic matter in soils is well documented for peatlands (Dansereau & Segadas-Vianna 1952; Gorham 1957), and has also been noted in disturbance mediated successional gradients in freshwater lacustrine wetlands

Table 5 Mean percentage germination (1 SE) on day 62 from shade germination experiment (both soil types pooled). Species abbreviations as in Table 4

Treatment	Species					
	PA	TL	LO	SC	SV	SL
No shade	22 (8) ^a	3 (1) ^b	1 (1) ^b	0.3 (0.3) ^b	0 (0) ^b	0.3 (0.3) ^b
40% shade	10 (3) ^a	2 (1) ^b	1 (1) ^b	0 (0) ^b	0 (0) ^b	0.3 (0.3) ^b
80% shade	4 (2) ^a	1 (1) ^b	1 (1) ^b	0 (0) ^b	0 (0) ^b	0 (0) ^b

Superscript letters indicate significant differences (Fisher's LSD, $P = 0.05$) among species within each shade treatment.

(Wilson & Keddy 1985, 1986a,b). Effects on germination may be mediated by pH, nitrate levels, soil organic compounds and differences in irradiance. It is unlikely that pH affected germination, as the limited information on wetland plants indicates that they can germinate across much wider ranges than encompassed by this study (Simpson 1966; Rivard & Woodard 1988). Nitrate is known to increase germination in many species (Baskin & Baskin 1998), and is thought to be an indicator of disturbance and therefore gaps in vegetation. Intermediate organic soils had the highest nitrate levels, probably due to increased binding sites in high organic soils (Stevenson 1994), but rarely showed the highest germination. Although high nitrate levels may inhibit germination (Peterson & Bazzaz 1978), a more likely explanation is that it is less common in wetlands due to periodically anaerobic conditions, and is therefore a less reliable indicator of disturbance, and thus potential gaps, than in other systems. Soil organic compounds can both inhibit and promote germination (Hilhorst & Karssen 2000) and, in this experiment, more organic soils generally promoted germination. Increased organic matter in soils can also lower irradiance to the seed, possibly causing changes in favoured germination conditions (Moore & Keddy 1988). Biomass, for those species with differences among treatments, was higher with increasing organic matter, and was probably due to increased nutrients.

Organic content also affected soil moisture content, and this had effects for some species. Although *Scirpus cyperinus* generally germinated well in non-flooded conditions, there was a small reduction in final germination on the driest low organic soils. It has been found that particle size did not affect germination when water levels were near the surface, but did as the water level was lowered (Keddy & Constabel 1986) and differing levels of organic matter may have similar effects.

The relative germination success of species changed over time in non-flooded but not in flooded conditions. These changes show that differences in duration of exposure to germination conditions and in hydrology may interact to structure vegetation communities. In some marsh communities prone to fluctuations in water levels and drought, emergence from seed bank depends on frequency and duration of particular

hydrologic conditions (e.g. Casanova & Brock 2000), but our results show an effect in much more hydrologically constant environments.

Five of the six species that germinated consistently showed similar patterns across the organic gradient, but the field distribution of *Phalaris arundinacea* and *Typha × glauca*, which were widespread across the organic gradient, contrasted with *L. oryzoides*, *Penthorum sedoides* and *Scirpus cyperinus*, which were most abundant in early succession. Evolutionarily selected germination traits can be expected to differ from traits in mature plants (Shipley *et al.* 1989). In this case, the two widespread species have high competitive ability, while at least one of the other species (*L. oryzoides*), the only other species for which data are available, had medium competitive ability (Gaudet & Keddy 1995). In fact, *Phalaris arundinacea* generally germinated best over all treatments and this, combined with its competitive ability, is probably responsible for its success as an invasive grass in many wetlands. The ability to germinate well across a wide range of organic and hydrologic conditions is equally important for species such as *L. oryzoides* which are less competitive and appear to be adapted to germinate opportunistically after disturbance, followed by rapid seedling growth. The one species whose germination is clearly correlated with field distribution is *Scirpus validus*, where both increase with organic matter. *Phalaris arundinacea* and *Typha × glauca* are more widespread across the organic gradient than found by Gaudet & Keddy (1995) for shoreline plant communities, probably due to less frequent disturbances in isolated wetlands. The effects on germination of successional age may be greater than indicated by our experiment, because seeds may experience more extreme organic gradients. Our organic contents were based on means for the upper 6–10 cm of soil, although organic material accumulates at the soil surface during succession.

Some species, *Alisma subcordatum*, *L. oryzoides*, *Penthorum sedoides* and *Scirpus cyperinus*, that are typical of early successional wetlands were found only in non-flooded conditions in the field (Kellogg & Bridgman 2002 and unpublished data). *Penthorum sedoides* and *Scirpus cyperinus* were the only early successional species greatly affected by treatments, and they germinated better in the non-flooded conditions that are similar to their field distributions. *Penthorum sedoides* germinated at higher percentages in intermediate soils, which had the highest nitrate levels, consistent with the induction of germination by nitrate (Baskin & Baskin 1998), and its increased abundance in drier areas.

The three species, *Calamagrostis canadensis*, *Sagittaria latifolia* and *Scirpus acutus*, that are found most often in old successional sites (Wilson & Keddy 1985; Kellogg & Bridgman 2002) never germinated to high frequencies, and may have specific germination requirements that were not met in this study. All species with seedling biomass differences had higher biomass in the

more organic soils, indicating that initial growth is primarily controlled by nutrients.

Although shade tolerance when germinating is a common adaptation of late successional species (e.g. Orozco-Segovia & Vazquez-Yanes 1989), shade had little effect on germination of these species. Most herbaceous wetland plants, however, require mudflat conditions for successful germination (van der Valk 1981), and shade tolerance therefore confers little benefit. Herbaceous wetland microcosms have also been found to be open to colonization even after 5 years, due to seasonal dieback (Weiher & Keddy 1995). The generally lower germination rates in the shade than in the soil/hydrology experiment may be due to the reduced temperature fluctuations. Temperature fluctuations are good indicators of gaps in vegetative cover and exposure of soil after falling water levels (Thompson *et al.* 1977; Fenner 1985), and act as a cue for germination of wetland plants (Thompson & Grime 1983). Temperature fluctuations have also been found to be necessary, in combination with other factors such as light (Pons 2000), for breaking dormancy. The lack of effect of organic content on germination may be due to the drying, which, in aquatic seeds, can induce dormancy (Muenscher 1936; Sharp 1940; Baskin & Baskin 1998) and lower germination rates (Else & Riemer 1984).

Germination has been found to structure freshwater marsh communities in mesocosms after 3 months (Stockey & Hunt 1994) and, after 1–2 years, in experimental wetlands undergoing water level fluctuations (Seabloom *et al.* 2001). These results can aid in the prediction of plant community response to succession and disturbance, and it may also be possible to favour certain plant species by managing the organic content of the soil and the hydrology. Specifically, greater germination of species other than the invasive grass, *Phalaris arundinacea*, may be enhanced by drier conditions and lower organic soils. Successional changes in soils are capable of affecting plant community development but, since light interception by a mature canopy is unlikely to change these effects, disturbance is not necessary for these effects to be exhibited.

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