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Seed dispersal, germination and seedling growth of six helophyte species in relation to water-level zonation

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SUMMARY

1. Seed dispersal, germination, and seedling growth characteristics of six helophyte species, *Iris pseudacorus, Phalaris arundinacea, Phragmites australis, Typha angustifolia, T. latifolia* and *Scirpus lacustris*, were investigated in relation to their water-level zonation.
2. The experiments demonstrated a large variation in these characteristics between the species.
3. Propagule floating capacities range from < 1 h (*S. lacustris*) to > 1000 h (*I. pseudacorus*).
4. Seed germination in a water-level gradient revealed two groups with respect to germination percentage – exposed soil species (*I. pseudacorus, Phalaris arundinacea, Phragmites australis*) and submerged soil species (*T. angustifolia, T. latifolia*).
5. There were two contrasting types of seedling growth response to submergence and exposure: one group of species formed longest leaves under exposed conditions (*Phalaris arundinacea, Phragmites australis, I. pseudacorus*), and the other under submerged conditions (*S. lacustris, T. latifolia, T. angustifolia*).
6. The results suggest that early life-history characteristics of the species relate to their locations in the riparian zonation: *Phalaris arundinacea* and *Iris pseudacorus* at the higher end, *Phragmites australis* intermediate, and *Typha* spp. and *Scirpus lacustris* at the lower end. Species occurring at lower locations show adaptations to (periodical) flooding of the soil (submersed germination and growth), while those from higher locations require prolonged exposed soil conditions to germinate and to survive the establishment stage.

Introduction

Regeneration and establishment patterns of emergent macrophyte species depend on hydrological conditions. Characteristics related to seed dispersal, seed bank formation, germination and seedling survival determine the success of establishment of species (Harper, 1977). Differences between species concerning these early life-history components may contribute to the zonation of helophyte vegetation over the water depth gradient along water bodies (Parker & Leck, 1985; Galinato & Van der Valk, 1986).

Hydrochory (transport of seeds by floating on water) appears to be the primary mode of dispersal in helophytes (Van der Pijl, 1982; Skoglund, 1990; Grelsson & Nilsson, 1991). Germination and seedling survival are the next 'sieves' in the life history of plants through which hydrology might play a structuring role in the development of vegetation zonation (Keddy & Ellis, 1985; Moore & Keddy, 1988).

In our ongoing study of hydrological factors that determine the riparian zonation of helophytes, several

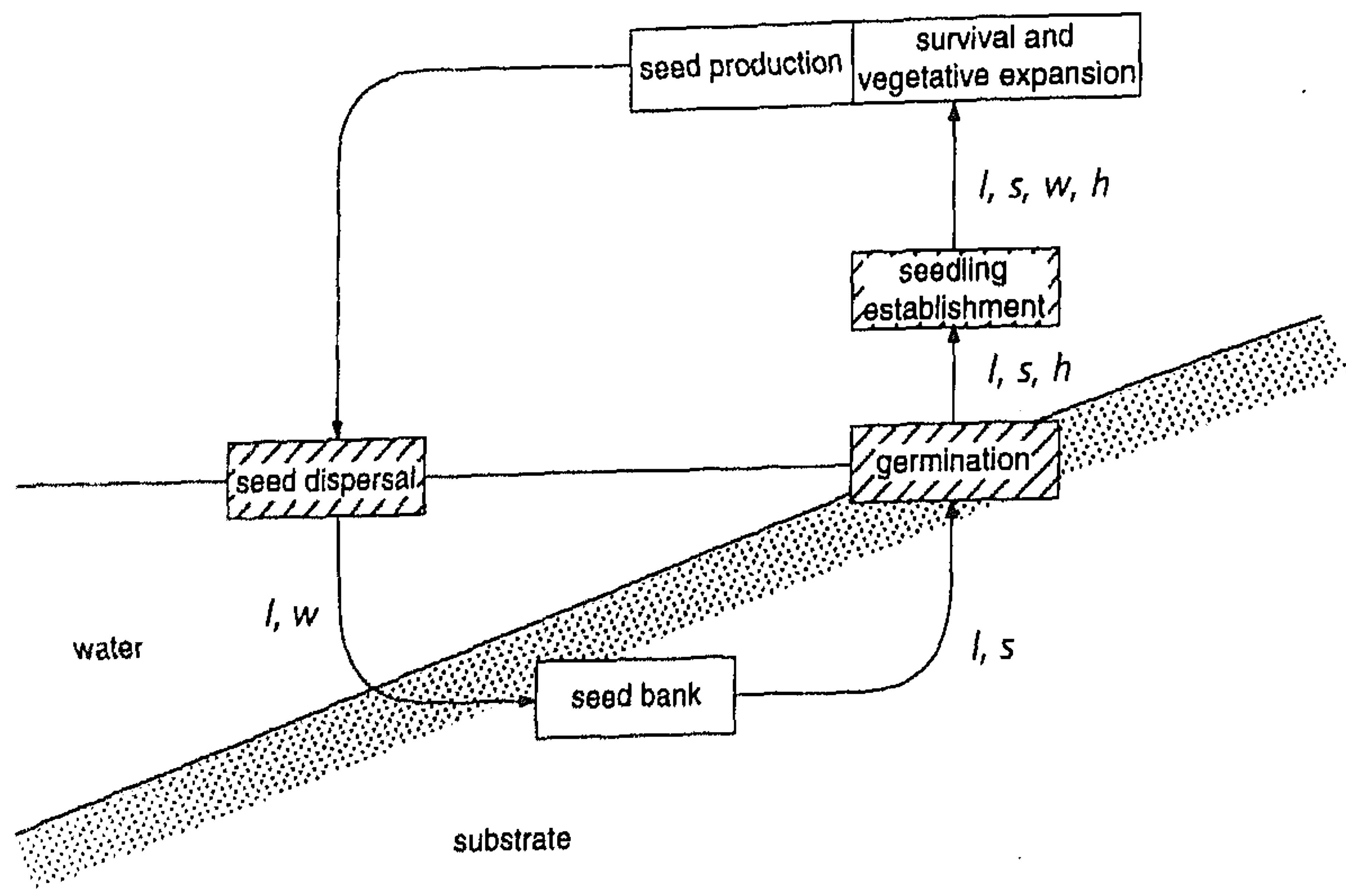

Fig. 1 Schematic model of life history stages of helophytes on shorelines. The stages considered in this article have been shaded. Determining factors: *l*, water level; *s*, soil type; *w*, wave action; *h*, herbivory.

stages of the life history of species are being considered (Fig. 1). For the present paper, we investigated variation in hydrochorous dispersal capacity, germination and seedling growth for six helophyte species. The species studied are common along large, eutrophic waters in the south-western part of the Netherlands. They occur in the littoral vegetation along formerly estuarine freshwater areas: *Iris pseudacorus* L. and *Phalaris arundinacea* L., which occur in higher locations; *Phragmites australis* (Cav.) Trin. ex Steudel, which shows a wide range of occurrence in the zonation; and *Scirpus lacustris* L., *Typha angustifolia* L. and *Typha latifolia* L. from the lower parts of emergent vegetation.

Materials and methods

Study material

Comparative experiments were set up using seed material from river bank stands of *I. pseudacorus*, *Phalaris arundinacea*, *Phragmites australis*, *S. lacustris*, *T. angustifolia* and *T. latifolia*.

Ripe propagules were collected, and stored under dry conditions for a maximum of 6 months at a temperature of 4 °C. In the following, the term 'seed' refers to the dispersal unit of the plant, a propagule containing a single embryo. 'Germination' was defined as the first appearance of the hypocotyl.

The origins of seed samples of each species are presented in Table 1; propagule type, individual propagule weight (thirty seeds per species) and production of propagules per plant (thirty flowering plants of each species) were determined for the populations sampled.

Buoyancy of seeds

In September–November 1990, two batches of 100 dry seeds for each species were released on the water surface of separate 30 × 20 × 20-cm polythene containers half filled with tap-water. The seeds were kept floating freely by means of a continuous flow of air at the water surface from a rubber tube attached to the sides of the containers. Counts were made over a period of 6 weeks of the number of seeds that had sunk. Periods after which 50% and 90% of the seeds had sunk (Ft_{50} and Ft_{90}) were determined.

In an additional test, the seed coats of three seeds of *I. pseudacorus* were removed prior to release. Seeds that germinated during the experiment were recorded.

Germination of seeds

Dry seeds were treated with added tap-water in darkened bottles in a cold room (4 °C) for 2 months prior to the experiment, as earlier tests showed that such a procedure was necessary to obtain germinable seeds. Petri dishes (diameter 9.5 cm) were filled with fine-grained sand (organic matter content < 0.1%). In each of three dishes per species, 100 seeds were pushed to a depth of about 1 mm into the soil (for *I. pseudacorus* twenty-five seeds were used per Petri dish). The dishes were placed at random in 40 × 30 × 10-cm polythene trays under three different moisture conditions: (a) moist, no standing water but sprayed with tap-water daily (soil moisture content *c.* 3%); (b) saturated, water level at soil surface (± 1 mm; soil moisture content *c.* 18%); and (c) flooded, water level 5 cm above soil surface.

Table 1 Origins and characteristics of the seeds of helophytes used in the experiments

Species	Origin	Type of propagule and usual dispersal mode	Individual propagule weight (mg) (mean ± SD, n = 30)	Number of propagules produced per flowering shoot (mean ± SD, n = 30)
Typha angustifolia	51°46′N 4°48′E	Stalked capsule with long hairs, released October/winter and borne by air and/or water	0.027 ± 0.008	$(1.6 \pm 0.6).10^5$
Typha latifolia	51°48′N 4°46′E	Stalked capsule with long hairs, released October/winter and borne by air and/or water	0.088 ± 0.015	$(3.5 \pm 0.8).10^5$
Phragmites australis	51°44′N 4°39′E	Plumed fruit including lemma and palea, released in winter and borne by air and/or water	0.16 ± 0.02	1509 ± 933
Phalaris arundinacea	51°44′N 4°39′E	Short bristled fruit, released July/August by falling down	0.32 ± 0.07	393 ± 120
Scirpus lacustris	51°51′N 4°52′E	Hard coated ± triangular fruit, released August/September by falling on the water surface, zoochory probable	1.63 ± 0.13	412 ± 120
Iris pseudacorus	51°45′N 4°51′E	Hard coated seed, released September by falling on the water surface	122.43 ± 31.20	47 ± 15

The trays were covered with transparent foil to prevent evaporation, and placed in a climate chamber at 20–25 °C, with a photoperiod of 12L : 12D. Light was provided by Philips TLD 18 W/33 tubes situated 100 cm above the soil surface, producing 40–50 μE $m^{-2} s^{-1}$ (PAR) at soil level.

Germinated seeds were counted daily for 6 weeks. The period after which 50% of the final number of germinated seeds had germinated (Gt_{50}) was determined, as well as the final proportion of germinated seeds.

Seedling growth in relation to flooding

One-week-old seedlings raised from seeds incubated on trays filled with garden pond soil were planted individually in 6 × 6 × 5-cm PVC pots. The following treatments were applied: (i) permanently flooded for 6 weeks; (ii) 5 weeks flooded, followed by 1 week drained; (iii) 5 weeks drained, followed by 1 week flooded; (iv) permanently drained for 6 weeks. Sixteen pots per species per treatment were randomly placed in containers in blocks of four. Light and temperature conditions were similar to those in the previous experiment. The containers could be either flooded (10 cm of water above the soil level) or drained (water level just below soil surface).

The length of the plant from the shoot base to the tip of the longest leaf was measured at the end of the experiment after 6 weeks of growth. All plants were harvested and dry weight biomasses of above-ground and below-ground parts were determined after drying for 24 h at 105 °C.

Statistical treatment

Differences between species in Ft_{50}, Ft_{90}, germination percentage, Gt_{50}, final shoot length and above-ground seedling biomass were analysed with ANOVA. No significant block effects were revealed in the seedling growth experiment, whereafter they were neglected in the computations. An angular transformation was carried out for proportion values. Least significant differences (at $P < 0.05$) were determined for contrasts between mean values.

Results

Individual propagule weights and the numbers of seeds produced per flowering shoot of the six species are shown in Table 1.

Buoyancy of seeds

Most of the seeds of *S. lacustris* floated for less than an hour. The propagules of *Phragmites australis*, *Phalaris*

Table 2 Floating periods for 50% (Ft_{50}) and 90% (Ft_{90}) of batches of 100 seeds released on the water surface. Means and SD are shown; significant differences are indicated by different symbols

Species	Ft_{50} (h)	Ft_{90} (h)
Scirpus lacustris	0.5 ± 0.3[a]	1.1 ± 0.6[a]
Typha angustifolia	10.9 ± 6.2[a]	27.6 ± 9.9[b]
Phalaris arundinacea	19.9 ± 11.4[a]	38.3 ± 8.8[b]
Phragmites australis	40.9 ± 16.6[b]	65.0 ± 13.2[c]
Typha latifolia	55.2 ± 2.1[b]	81.4 ± 19.3[c]
Iris pseudacorus	> 1000	> 1000

arundinacea and *Typha* spp. floated for 1 or a few days. *Typha* seeds floated as long as the long hairs lifted the pericarp above the water surface; once wetted, seeds were released from the capsules and sank soon after. No seeds of *I. pseudacorus* sank during the experiment, owing to their hard seed coat and gas space inside. When seed coats were removed, the seeds sank almost immediately.

Before applying ANOVA, the results on the buoyancy of *I. pseudacorus* seeds were excluded because no seeds were found to sink. The differences in floating capacity between the remaining species were significant for Ft_{50} ($F = 22.772$, $P < 0.01$) and Ft_{90} ($F = 4.899$, $P < 0.05$). Contrasts between means revealed that *Phragmites australis* and *T. latifolia* had relatively high Ft_{50} and Ft_{90} values, and *T. angustifolia*, *Phalaris arundinacea* and *S. lacustris* demonstrated brief buoyancy (Table 2).

Seeds did not germinate during the experiment, neither while floating nor after sinking to the bottom of the container, with the exception of *I. pseudacorus* seeds from which the seed coat had been removed. The latter group germinated within 7 days.

Germination experiment

The germination percentages of the investigated species showed a significant species × moisture interaction effect ($F = 38.749$, $P < 0.001$); thus, the optimum moisture classes of the species vary. *Phragmites australis* and *Phalaris arundinacea* seeds germinated well on drained soil, while very few *Phragmites australis* seeds germinated under flooded conditions (Fig. 2). In contrast, seeds of both *Typha* species germinated poorly on drained sediment, but germinated well on the saturated and flooded ones. Seeds of *Scirpus lacustris* did not show any germination response to the moisture conditions offered. Seeds of *I. pseudacorus* germinated exclusively on drained soil.

The effect of moisture on Gt_{50} was non-significant, implying neither delay nor acceleration of germination within the range of treatments. There were, however, significant differences between the species: *T. angustifolia* and *T. latifolia* germinated rapidly (average Gt_{50} 4.4 and 5.6 days, respectively), while *Phragmites australis*, *Scirpus lacustris* and *Phalaris arundinacea* germinated relatively slowly (average Gt_{50} 10.4, 12.4, and 15.3 days, respectively).

Seedling growth

Clear differences in the capacities of the various species to continue growth whether the sediment was flooded or drained were demonstrated by the development of shoot length in the flooding treatments (Fig. 3). Leaf extension in *S. lacustris* and *Typha* spp. was very rapid in submerged conditions. The long submerged leaves, which were very fragile and became desiccated when exposed, did not survive drainage. On exposed, moist soil the seedlings produced erect, slowly growing aerial shoots which were absent from submerged plants. *S. lacustris* seedlings that were drained after a period of submergence became desiccated. No net increase in length of seedlings of *Phalaris arundinacea* and *Phragmites australis* occurred under submerged conditions; growth stopped during flooding and restarted after drainage. Submersed growth of *I. pseudacorus* seedlings was poor, but these seedlings also regained their emersed growth rate when the plants were drained.

The final biomasses differed between the flooded and the drained soil conditions. In *T. angustifolia* the above-ground seedling biomass under flooded conditions (0.0011 ± 0.0003 g) was significantly higher than under exposed conditions (0.0006 ± 0.0002 g), while no significant difference was present in *S. lacustris* seedlings (0.0019 ± 0.0005 g and 0.0018 ± 0.0002 g, respectively). In contrast, biomasses were significantly lower under flooded than under exposed conditions in *T. latifolia* (0.0009 ± 0.0005 g and 0.0015 ± 0.0008 g), *Phragmites australis* (0.0008 ± 0.0005 g and 0.0044 ± 0.0015 g), *Phalaris arundinacea* (0.0039 ± 0.0017 g and 0.0254 ± 0.0118 g) and *I. pseudacorus* (0.0364 ± 0.01434 g and 0.0849 ± 0.0328 g). The shoot : root biomass ratios of these seedlings also responded differently to submergence (Fig. 4). S : R

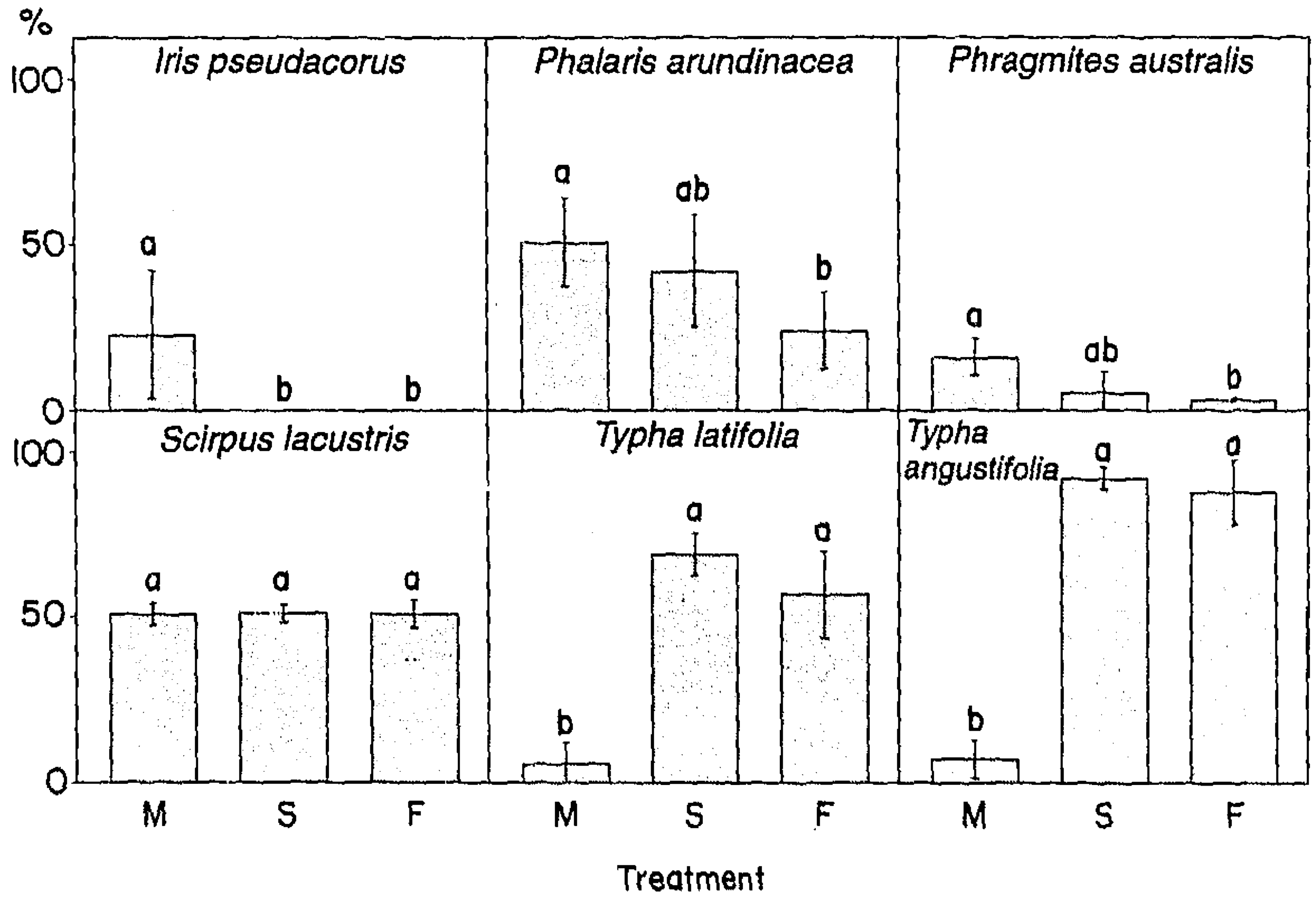

Fig. 2 Germination percentage of seeds of six helophyte species under laboratory conditions. Mean germination percentages ± 2 SE on moist (M), saturated (S) and flooded (F) substrate are presented (n=3); significant differences (LSD-test after angular transformation, $P < 0.05$) are indicated by different symbols.

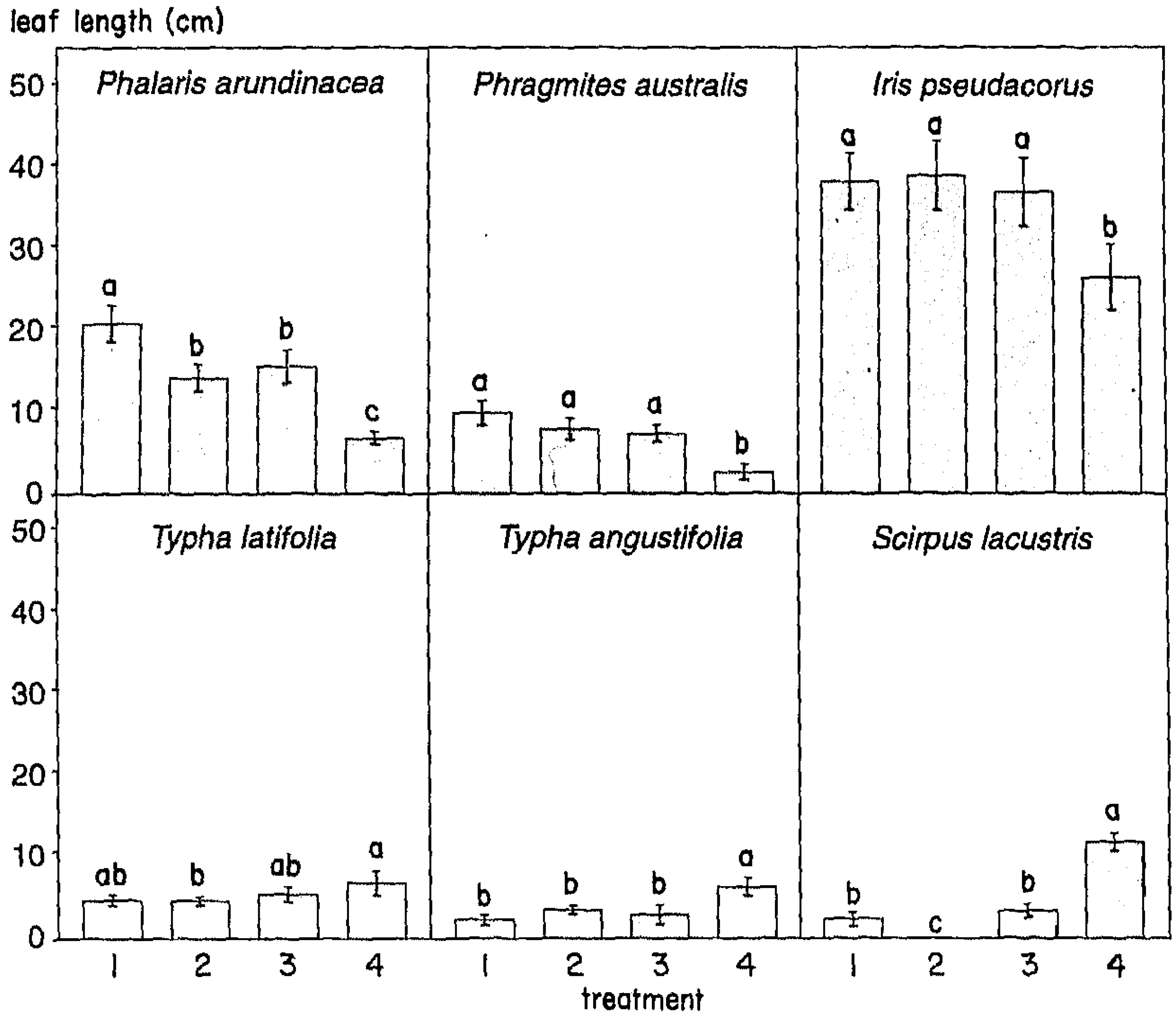

Fig. 3 Seedling growth of six helophyte species under varying exposed and inundated conditions: final length of the shoot ± 2 SE is shown for each treatment. The treatments shown are: (i) permanently drained during 6 weeks; (ii) 5 weeks drained, followed by 1 week flooded; (iii) 5 weeks flooded, followed by 1 week drained; (iv) permanently flooded during 6 weeks. Significant differences (LSD-test after logarithmic transformation, $P < 0.05$) are indicated by different symbols.

was least affected in low zonation species like *S. lacustris*, but was substantially affected in the species occurring at higher locations on the shore, including *Phragmites australis*.

Discussion

Each of the species showed a combination of characteristics probably related to their position in the zonation. No relationship between seed weight and buoyancy time was observed for the six species studied. However, there was an obvious trade-off between seed size and number of seeds produced by a single shoot. In addition to the floating capacity of the seeds, the efficiency of seed dispersal depends on the numbers of seeds produced, the distance of seed sources and alternative means of transport (Van der Pijl, 1982). While floating on the water surface, the propagules are transported to the shoreline by currents or wind drift (Koutstaal, Markusse & De Munck, 1987; Nilsson, Gardfjell & Grelsson, 1991). The sequence of floating times shown in Table 2 is comparable with those reported by Ridley (1930), who found seeds of *S. lacustris* to float for a few hours or not at all,

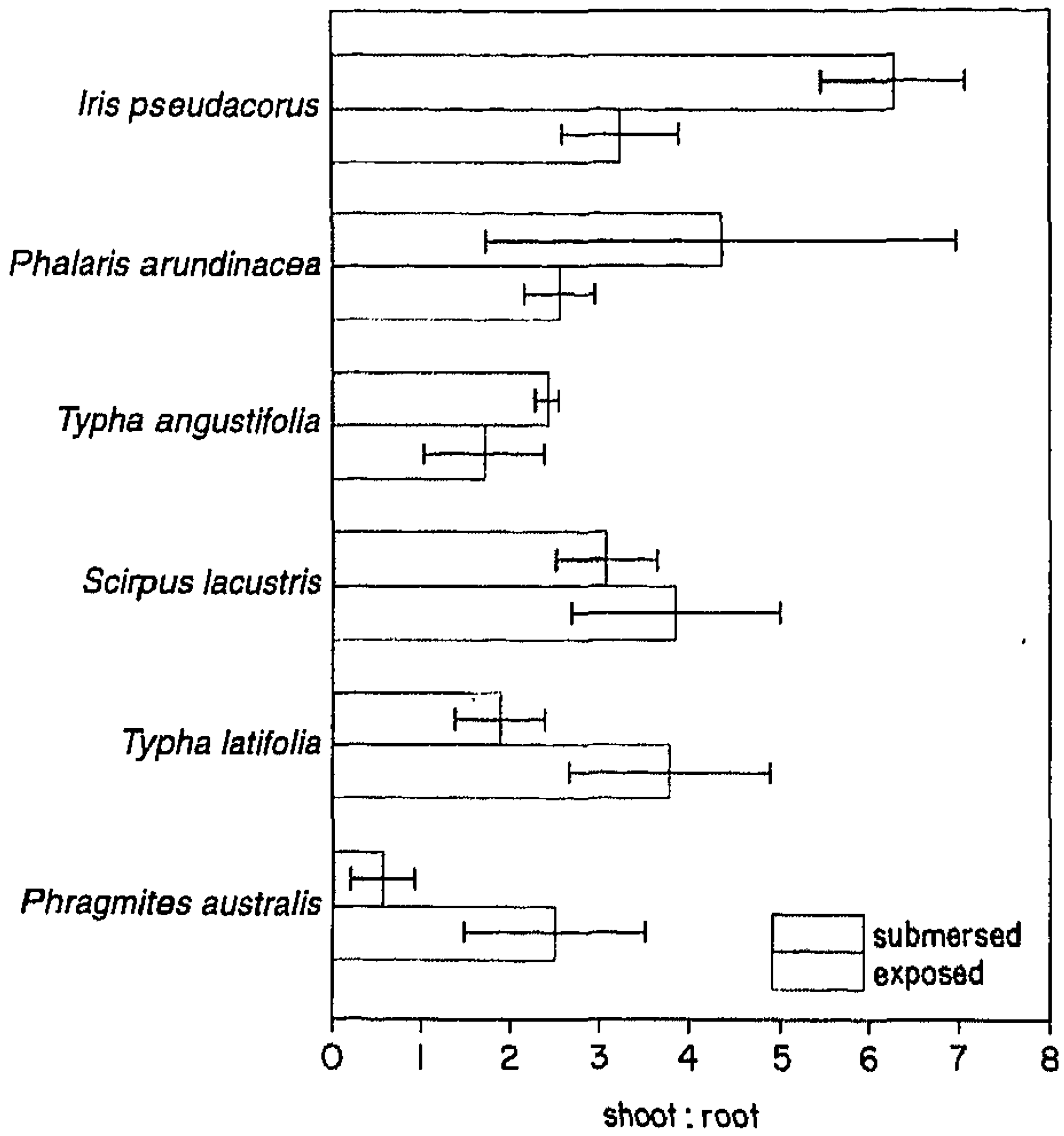

Fig. 4 Seedling shoot : root biomass ratios (dry weight ratio ± 2 SE) for six species of helophytes after 6 weeks of uninterrupted growth under submerged or exposed conditions.

T. angustifolia for about 4 days, *T. latifolia* for 4 weeks, and *I. pseudacorus* for 7 months after release on a calm water surface. In addition, dispersal through the air and on or in animals might be alternative mechanisms. Dispersal by air may be relevant for the lightweight, plumed propagules of *Typha* spp. and *Phragmites australis* (Ridley, 1930). However, after transport through the air, the probability that seeds land on the water surface is great and thereafter they are transported hydrochorously (Cook, 1987; Nilsson *et al.*, 1991). Transport of seeds by waterfowl may also have an impact, particularly in long-distance dispersal, but their role is hard to quantify (Van der Valk, 1987).

The ability of seeds to float and sink to the bottom after a period of time probably plays a role in directing seeds towards sites where germination and establishment may take place (Van der Pijl, 1982; Howe & Smallwood, 1982). The obviously different capacities of the species for dispersal by floating on the water surface imply that hydrochorous dispersal might be an important process underlying patterns of riparian plant zonation by structuring the seed bank (Poiani & Johnson, 1989; Grelsson & Nilsson, 1991). Long-floaters might arrive at higher elevations on the shoreline than short-floaters.

Germination and seedling survival are the next 'sieves' in the life history of plants by which hydrology might play a structuring role in vegetation development (Keddy & Ellis, 1985; Moore & Keddy, 1988). *I. pseudacorus* and *Phalaris arundinacea*, both species occurring at higher positions in the zonation, germinated well on exposed soil, while *S. lacustris* was indifferent and *Typha* spp. germinated poorly on dry soil. Comparable results have been reported in various studies demonstrating the range of water level or soil moisture conditions required for successful germination of *Phragmites australis* (Hürlimann, 1951; Van der Toorn, 1972; Haslam, 1973; Rodewald-Rudescu, 1974), *Phalaris arundinacea* (Junttila, Landgraff & Nilsen, 1978), *S. lacustris* (Seidel, 1955) and *Typha* spp. (Yeo, 1964; Bedish, 1967; Grace & Harrison, 1986; Frankland, Bartley & Spence, 1987; Evans & Etherington, 1990). On exposed soil surfaces, moisture availability in the germination period depends not only on the groundwater level, but is correlated with the particle size of the sediment as well (Keddy & Constabel, 1982).

The flooding regime of the seedling site might also determine the initial zonation of the vegetation. The seedlings of all helophyte species in the present study survived total inundation for 7 weeks, but their responses differed: *Phragmites australis* and *Phalaris arundinacea* seedlings showed hardly any growth when inundated, while *S. lacustris* and *Typha* spp. developed submerged leaves that did not survive subsequent drainage (Seidel, 1955; Weisner, Granéli & Ekstam, 1993). The latter species may benefit from flooding in early life stages in contrast to the species advantaged by periodic exposure. The probability of inundation or exposure during these stages is related to the elevational position of seedlings on the shoreline. Thus, differences between species in seedling performance might add to zonation patterns.

Dispersal, seed germination and seedling performance characteristics of a species might be interrelated. Of the six species studied, *I. pseudacorus* typically occurs on higher grounds on the shore and in wet meadows (Falinska, 1986). The seeds float for a very long time – even after having been shallowly buried in loose submerged sediment and having floated up to the water surface again – and will therefore be washed into existing vegetation on the higher shoreline during high-water levels. Flooding of the seed-bank site implies relocation of the seeds. Germination of *I. pseudacorus* is restricted to exposed soil conditions, and seedling growth is retarded after flooding of the plant. On the other hand, *S. lacustris* occurs at the deeper fringe of the riparian zonation, usually outside the reedbelt (Seidel, 1955; Weisner *et al.*, 1993). Its seeds sink shortly after their release on the water surface. Seeds of this species therefore have a good chance of being incorporated in the seed bank in the neighbourhood of the parent plant. Germination of *S. lacustris* seeds appears to occur both on shallowly flooded and exposed soil, while the seedlings overcome permanent flooding by forming specialized submerged leaves. Because chances of establishment and seedling survival on the higher shore are poor, these characteristics are suggested to be of adaptive significance. As a consequence, rapid spreading over large areas by dispersing seeds is unlikely for *S. lacustris*, while the seeds of *Typha* spp. and *P. australis*, which are produced in massive quantities, may travel over large distances and thus colonize large areas quickly. The dispersal of *S. lacustris* seeds over large distances probably depends on transport by seed-consuming birds; seeds of *Scirpus* spp. even show enhanced germination after being consumed and defaecated by ducks (De Vlaming & Proctor, 1968).

The responses to water level in the regenerative life phase of the species under study vary according to their position in the shoreline zonation. Many helophyte species depend almost exclusively on vegetative spreading (Shay & Shay, 1986). In riparian areas, reproduction by germinating seeds may be a rare event (Bartley & Spence, 1987), which is often related to prolonged water level drawdown (Gopal, 1986; Brock, Van der Velde & Van de Steeg, 1987).

The formation of riparian vegetation zonation under these circumstances appears to start during the early stages of development. This can be concluded from the 'sieves' in the life history of the species that were studied: directional dispersal, response of germination to flooding conditions and response of seedlings to flooding. It is not clear, however, to what extent species profit from an initial advantage by being dominant as seedlings (Wilson, 1988).

The contributions of other life-history stages to the forming of zonation will be considered in a separate paper.

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