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Seed-bank dynamics of *Eleocharis*: can spatial and temporal variability explain habitat segregation?

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Abstract. Four *Eleocharis* species exhibit habitat partitioning in both extant vegetation and in the soil seed bank of upland temporary wetlands on the Northern Tablelands of New South Wales. Explanations for this partitioning were sought in seed-bank dynamics at three shore levels in two wetlands. Habitat partitioning (zonation) was explained in part by seedling recruitment but not by either persistence of seeds in the soil or by dormancy patterns. All four species recruited at wetland edges but only the deepwater species, *Eleocharis sphacelata*, recruited in deeper water. Viability of buried seeds was consistently high and species had very low decay rates and half-lives greater than 50 years. Two types of dormancy patterns with burial were shown. Most seeds of *Eleocharis sphacelata* and *E. pusilla* were non-dormant after a 3-month burial, whereas for *E. acuta* and *E. dietrichiana* seed germination percentages gradually increased over a number of years. These two dormancy patterns may contribute to coexistence, since coexistence is enhanced by a long-lived resistant phase in the life history of species and by temporal variability in germination. There were also spatial inconsistencies in patterns of dormant fractions. Burial in the deeper zones of the marsh-like Billybung Lagoon had an inhibitory effect both on germinability and on germination rates of *E. acuta* and *E. dietrichiana* seeds. All but *E. acuta* showed some degree of seasonal dormancy, but this pattern was also not consistent in space. Explanations for zonation should concentrate on other life-history phases, such as dispersal and seedling survival.

Introduction

Wetland vegetation is characterised by changes in species composition and life form along water-level gradients (Sculthorpe 1967; Spence 1982) and these changes can be expressed as the sorting of vegetation into distinct bands along a gradient. Sorting may be due to one or more of the following factors: (i) sorting at dispersal, (ii) zonation in a persistent seed bank, (iii) distinct responses of seeds to patterns of water-level fluctuations in zones, or (iv) differential establishment of seedlings and/or post recruitment processes.

Information on pre-germination processes in plant species of non-tidal wetlands is limited (Leck 1989). Densities of seeds of terrestrial species are usually highest next to the parent plant (Harper 1977). However, in wetlands where flotation, currents and water birds disperse seeds, it is likely that dispersal is not limited to the zone in which plants occur (Bell 2000). In wetlands where changes in water level are unpredictable, zones of adult plants (and thus seed rain) may not be static and a more homogeneous seed bank might be predicted. This unpredictability in water level partly explains why not all wetland seed banks reach maximum densities at the water depth at which adult plants are encountered.

Many seed-bank communities are broadly similar floristically to the extant vegetation of wetlands, but studies of zonation in wetland seed banks and comparisons of zonation in extant and seed-bank communities are limited (Leck 1989; Bell 2000). Persistence in the seed bank is common for aquatic and lake-edge plants (Baskin *et al.* 1989; Leck 1989; Britton and Brock 1994; Leck and Brock 2000). Of four seed-bank types (Thompson and Grime 1979), the two persistent types are those found in wetlands. In a review of wetland species from lakeshores, tidal freshwater marshes, salt marshes and intermittent ponds, Leck (1989) found that 94 of 97 species could be assigned to one of these two types of persistent seed banks.

Wetland species can be placed into response types on the basis of the response of their seeds to water level (Salisbury 1970; van der Valk and Davis 1978; Coops and Vandervelde 1995; Brock and Casanova 1997). For example, some species germinate only on exposed mudflats when there is no standing water, others germinate on exposed mudflats or in

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very shallow water, and some submerged and free-floating species require standing water for germination, although their propagules may survive on mudflats. Germination triggers therefore cover a spectrum of conditions, from a requirement for temperature fluctuations and oxygen to the damping down of air temperature fluctuations that occur at depth and anoxia (Pons 1982; Pons and Schröder 1986; Frankland *et al*. 1987; Leck 1996).

Studies of seedling recruitment from wetland seed banks have generally stressed the role of micro-environmental variations in temperature, salinity and depth of burial rather than seed density (van der Valk and Davis 1979; Galinato and Van der Valk 1986; Welling *et al*. 1988; Leck 1996). Micro-environmental conditions vary as water levels fluctuate; thus patterns of water-level fluctuations are thought to play a major role in establishment of vegetation from seed banks (van der Valk and Davis 1979; Keddy and Reznicek 1982; Keddy and Constabel 1986; Britton and Brock 1994).

Despite evidence of the importance of germination cues, post-recruitment processes play a major role in developing zonation patterns (Welling *et al*. 1988). Zonation in extant species may be due in part to differential physiological responses to water level at later stages of plant life cycles (van der Valk and Davis 1978; Smith and Kadlec 1983; Brock and Rogers 1998). Coops and Vandervelde (1995) found that early life-history characteristics, such as greater leaf or stem elongation of seedlings at depth, better predicted locations of emergent species of riparian-zone vegetation. However, in other wetlands many species have broad depth tolerances (Keddy and Ellis 1984; Brock 1991).

Closely related taxa are valuable for comparative studies of life-history strategies (Araki and Washitani 2000; Schütz 2000; Van Assche *et al*. 2002), especially if they share habitats or show spatial and temporal segregation. Six species of *Eleocharis* (spikerushes) occur in temporary wetlands on the Northern Tablelands of New South Wales; of these, four, *Eleocharis sphacelata* R.Br., *E. acuta* R.Br., *E. dietrichiana* Boeck. and *E. pusilla* R.Br., are common to most sites. Seeds are small (1.8–3.9 mg), and the numbers of seeds (from 208 m^{-2} for *E. sphacelata* to 52 000 m^{-2} for *E. dietrichiana*) in the soil (Bell 2000) suggest persistent seed banks. Recruitment of all four species occurred in seed-bank germination studies (Brock 1998), although recruitment of *E. sphacelata* seedlings was rare experimentally.

A long-term vegetation survey of six wetlands revealed habitat partitioning (zonation) in *Eleocharis* species, in both the standing vegetation and in the soil seed bank sampled at the beginning of the survey (Bell 2000). However, few seedlings were observed, and these only on mudflats.

This study addresses the issue that the seed bank and its dynamics may be critical for the pattern we see in emergent *Eleocharis* communities and examines the potential for sorting both in the seed bank and at recruitment. The question addressed was whether zonation in the seed bank and extant vegetation is related to patterns of recruitment and/or to differential persistence of seeds entering the soil? We predict that, for deepwater species, recruitment is limited to deeper water and post-dispersal seed persistence is poor in shallow water at lake edges, and conversely, for lake-edge species, that recruitment is confined to lake edges and that buried seeds survive less well in deeper water. We assessed the germinability of *Eleocharis* seed-rain seeds and then tested whether there was zonation in (1) recruitment of freshly dispersed seeds, and (2) dormancy and viability patterns of buried seeds.

Methods

Study area

On the Northern Tablelands of New South Wales about 56 shallow deflation lakes (known locally as lagoons) occur on landscapes associated with Tertiary basalt flows (Haworth *et al*. 1999). The wetland communities of these lakes (Upland Wetlands of the Drainage Divide of the New England Tableland Bioregion) are listed as Endangered Ecological Communities under the 1997 New South Wales Threatened Species Conservation Act. The study sites Little Llangothlin Lagoon (30°05′S, 151°47′E) and Billybung Lagoon (30°05′S, 151°46′E) lie 17 km north–north-east of Guyra, at an altitude of 1355 m and 1360 m, respectively. Both of these wetlands are in Little Llangothlin Nature Reserve; this reserve is included on the Ramsar List of Wetlands of International Importance. Little Llangothlin Lagoon covers 100 ha and has a maximum water depth of ~2 m; Billybung Lagoon covers 15 ha and is 80 cm deep in its deepest parts. Average monthly temperature maximum and minimum for Guyra are 24.6/10.8°C in summer and 10.3/–0.6°C in winter. Average annual rainfall at nearby Llangothlin Lagoon (30°04′S, 151°46′E) is 980 mm (White 1986), with summer maxima and smaller secondary peaks in June (Haworth *et al*. 1999). The vegetation of these lakes is described by Benson and Ashby (2000) as closed to mid-dense sedgeland and grassland.

Species

The four study species are rhizomatous plants: *E. sphacelata* and *E. dietrichiana* with a ‘phalanx’ growth form (thick rhizome with short internodes) and *E. acuta* and *E. pusilla* with a ‘guerilla’ growth form (narrower rhizomes with long internodes) (Lovett Doust 1981). Dispersal units are one-seeded nuts, hereafter referred to as seeds. Seedlings emerge mostly in spring or autumn (Britton and Brock 1994), and mature seeds are shed in early autumn. *Eleocharis acuta*, *E. dietrichiana* and *E. pusilla* occur mostly at the edges of lagoons and *E. sphacelata* in the deepest parts. *E. acuta* also sometimes occurs in intermediate positions along the water-level gradient.

Seed collection

For each experiment, inflorescences collected in early autumn were air-dried in the laboratory. Seed was rubbed from inflorescences, cleaned in an air blower/seed cleaner and stored in glass jars under nylon mesh. Seeds were pooled from several patches in Llangothlin, Little Llangothlin and Billybung Lagoons since previous work has shown that germinability varies among and within sites (Bell 2000).

Germinability in fresh seeds

Preliminary work had shown that mature fresh *E. sphacelata* and *E. pusilla* seeds were not germinable. In common with other marsh seeds, alternating temperatures produced the highest germination percentages (Galinato and Van der Valk 1986; Baskin *et al*. 1989), and light was a requirement for germination of both fresh and treated *Eleocharis* seeds. The germinability of fresh seeds was assessed in autumn 1996 with week-old seeds, except for *E. sphacelata* where pooled seeds from 5-day and 2-month collections were used.

In all germination tests, seeds were submerged in 30 mL of tap water in 6.5-cm-diameter Petri dishes and incubated in germination cabinets set to 12 h of light at 25°C and 12 h of darkness at 15°C. Light was provided by fluorescent tubes emitting an intensity of 35 μE m^{-2} s^{-1} over the diurnal cycle. Seedlings were removed from the dishes every 4–7 days for 6 weeks. The remaining seeds were submitted to the 'squeeze' test to determine whether they were rotten.

The tetrazolium test was used to check for viability. Cut seeds were covered with tetrazolium chloride (0.1% 2,3,5-triphenyltetrazolium chloride in a phosphate buffer) and left in darkness overnight. Intact seeds with pink or red embryos were deemed to be viable; those that were empty or did not stain, were inviable (Mackay 1972).

Seedling recruitment

Seedling recruitment was assessed in a factorial field germination experiment at Billybung Lagoon. Factors were species (four), seed burial depths (surface sown, 1 cm deep) shore level (three zones) and patch (two, chosen at random). The wetland was arbitrarily divided into three zones: the deep zone, which corresponded to *E. sphacelata* habitat, an intermediate zone (occasionally *E. acuta* habitat) and the edge zone (*E. dietrichiana*, *E. acuta* and *E. pusilla* habitat). Ninety-six replicate plastic vials 4 cm in diameter were prepared with small holes in the base. Vials were partially filled with river sand–lake soil mix topped with 2–3 cm of sterile lake soil that had been passed through a 2-mm sieve. Vials were covered with nylon mesh to prevent seed loss.

Eleocharis sphacelata, *E. acuta* and *E. dietrichiana* seeds used in this experiment were from autumn 1997 collections (3 months old at planting). Since seed production of *E. pusilla* was very low in 1997, those from an autumn 1996 Llangothlin Lagoon collection were used. The germinability and viability of each batch of seeds was tested at the time of planting.

Twenty-five seeds of each species were moistened by shaking in water then sown on or under dampened soil. Vials were sunk to soil level in Billybung Lagoon in randomly allocated positions in 30 × 30-cm patches. Standing vegetation was removed from within and around plots and plots caged with 5 × 5-cm rigid plastic mesh.

Water depth and maximum and minimum temperatures were periodically measured in patches at each shore level and floating algal mats frequently removed from flooded patches. Vials in edge zones only were checked for germinants every 2–3 weeks from late spring 1997 until late summer 1998, then every 2 months until winter 1998 and seedlings were counted and removed. Vials in deeper zones were left undisturbed. In winter 1998, vials were retrieved and all seedlings counted and removed. Vials were then placed in trays of water in a glasshouse for an additional year and allowed to dry out periodically. Temperatures in the glasshouse varied from 8°C to 32°C in winter and 8.5°C to 33°C in summer.

A one-factor ANOVA was used to detect differences among species in (1) germination percentages of edge surface-sown seeds, and (2) germinability and viability of stored seeds. Stored seed germination data were tested with Cochran's Test and arcsine-transformed to minimise heterogeneity of variances (C = 0.56, k = 4, v = 3). Glasshouse data were expressed as percentages of the remaining ungerminated seeds. A two-factor ANOVA was performed on both glasshouse and total germination percentages to detect the effects of zones on surface-sown seeds of different species.

Persistence of buried seeds

In situ studies of buried-seed persistence in wetlands are few (Araki and Washitani 2000), and none have assessed persistence along a gradient. The effect of shore level of burial was examined in a factorial field experiment with five factors: species (four), time (eight retrieval occasions), site (two), zone (three) and patch (two). Sites were Little Llangothlin and Billybung Lagoons.

Seeds were collected from several patches in one to two sites (Llangothlin, Little Llangothlin and Billybung Lagoons) in autumn 1995. Fifty seeds of each species separately were enclosed in a nylon-mesh bag (aperture size 0.8 by 0.3 mm). Nylon mesh allowed passage of water, small invertebrates and fine plant roots. In winter 1995, a randomly located position was allocated to each species in randomly placed patches in each zone. Thirty-two (plus two extra) bags of 3-month-old seeds were buried under ~10 cm of soil in each plot and the soil plug replaced. Bags were secured to small stakes with a length of nylon tape. Plots in intermediate and deep zones were caged with 5 by 5 cm nylon mesh to discourage removal of stakes by birds.

This burial study is concerned not with germination cues or with types of dormancy [see, for example, Baskin and Baskin (1998)] but with germinability after burial. Retrieved *Eleocharis* seeds were therefore exposed to conditions known to maximise germinability and seeds were classed as either rotten, intact and germinable or intact and dormant. The exact dormancy state of some seeds may not have been detected since the experimental condition was limited to only one temperature combination (25/15°C). Therefore, in this study, the dormant fraction refers to that fraction of seeds that do not have the ability to germinate at 25/15°C in light.

Four replicate bags of each species were retrieved from each patch in each season for 2 years, except for winter 1996, when water in Little Llangothlin Lagoon was too deep for access. Thirty-three months after burial, plots were dismantled and any remaining seed bags retrieved. Bags were rinsed on site and placed in film canisters filled with lake water. Next day, seeds were removed and placed in Petri dishes. After each retrieval, the germinability of four replicates of dry-stored seeds of each species was also tested. Viability of all remaining ungerminated seeds was tested after 18, 24 and 33 months of burial.

Germination percentages (percentages of total seeds) and percentage rotted (included empty) seeds from October 1995 to July 1997 retrievals were analysed initially in a five-factor ANOVA. There was a significant species × times × patch interaction but this was minor (F_{108} = 3.54) compared to other effects (e.g. for species F_3 = 1334.4) so patches were pooled within zones and data analysed in a four-factor ANOVA. Data for the 33-month retrieval were incomplete because of missing seed bags, and so were analysed in a three-factor ANOVA, factors being species (four), site (two) and zone (three). All data were checked for normality and tested with Cochran's test for homogeneity of variances.

Regression curves

Decay of seeds in soil over time was estimated by fitting exponential decay curves to the intact-seed fraction (total less rotted seeds). For each replicate bag, the natural logarithm of intact-seed numbers was plotted against time to produce a curve of the form:

$$\mathrm{Ln}y = \ln a - bt$$

where y is the percentage of whole seeds remaining in the seed bank, a, the initial percentage of whole seeds, b, the decay rate and t, time in years. Half-lives were calculated by setting y at 0.5 and solving for t. A four-factor ANOVA (species, site, zone, patch) was performed on decay rates and half-lives. For the purpose of analysis, negative half-lives and decay rates were adjusted i.e. set at 1000 years and zero, respectively.

Results

Germinability of fresh seeds and seedling recruitment

All species exhibited initial dormancy. Only a few *Eleocharis acuta* (0.9%), *E. dietrichiana* (3.4%), and

Table 1. Characteristics of *Eleocharis* seeds at harvest, after storage and after long-term burial in the soil
Each batch of seeds is from different pooled collections. Means followed by the same small letters are not significantly different

Species	Germinability of fresh seeds ($n = 4$)	Dry-stored for 3 months (recruitment experiment, $n = 4$)		Viability after a 33-month burial ($n = 24$)
		Germinability	Viability	
E. sphacelata	^{A}29.14 (± 6.50)a	35.42 (± 8.64)a	98.08 (± 1.92)a	93.9 (± 0.64)a
E. acuta	0.95 (± 0.94)b	14.35 (± 1.39)a	98.00 (± 1.16)a	91.4 (± 0.69)a
E. dietrichiana	3.46 (± 0.92)b	2.04 (± 1.17)b	95.00 (± 2.52)ab	83.1 (± 1.32)b
E. pusilla	2.63 (± 1.57)b	^{B}38.19 (± 5.31)a	84.23 (± 3.96)a	90.4 (± 1.14)a

^{A}*E. sphacelata* seeds 5–78 days after harvest. ^{B}*E. pusilla* seeds storied dry for 15 months.

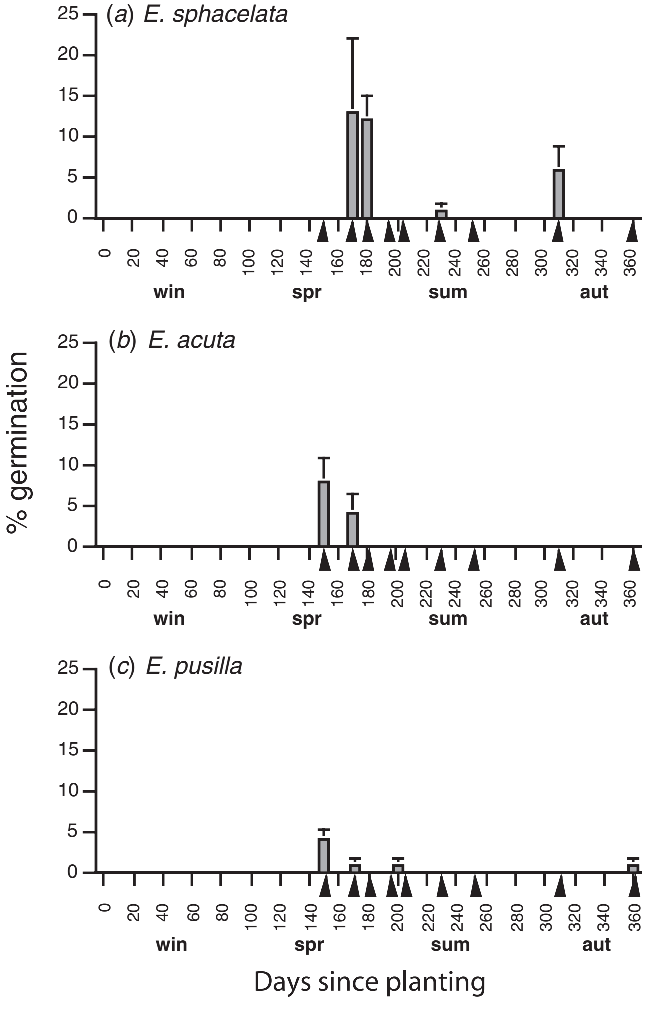


Fig. 1. Recruitment (germination) seedlings of three *Eleocharis* species at Billybung Lagoon. Seeds were sown on the surface of soil in vials in winter 1997. Error bars show s.e. Arrows show sampling times. Win, winter; spr, spring; sum, summer; aut, autumn.

E. pusilla (2.6%) and less than one-third of *E. sphacelata* (29.1%) fresh seeds germinated at harvest (Table 1).

Seeds of two of the edge species (*E. acuta* and *E. pusilla*) germinated as predicted at the edge but not in deeper water. However, seeds of the deep-water species *E. sphacelata* germinated both at the edge and in deeper water. A single *E. sphacelata* seedling emerged in an intermediate-zone vial (water depth ~30 cm). Only surface-sown seeds germinated between spring 1997 and winter 1998, although relatively few seedlings emerged (Fig. 1). No buried seeds germinated either in the field or in the glasshouse. *E. dietrichiana* seeds germinated only after removal to the glasshouse.

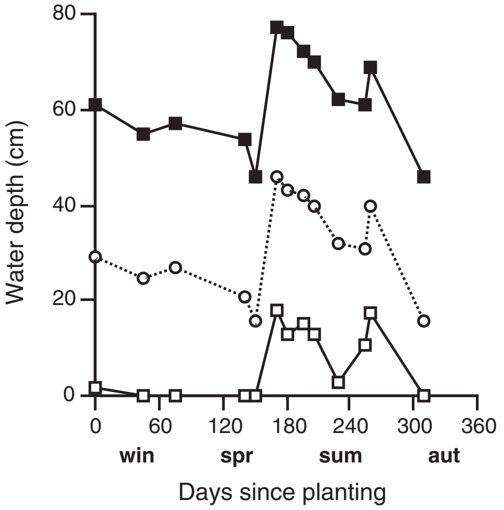


Fig. 2. Water depths in three zones in Billybung Lagoon during seedling recruitment (1997–1998). ☐ edge; ○ intermediate; ■ deep zones.

One-third of *E. sphacelata* seeds and 12 and 6% of seeds of *E. acuta* and *E. pusilla*, respectively, germinated. However, no significant differences among species were detected. Most recruitment was in spring, with additional emergence of *E. sphacelata* and *E. pusilla* seedlings in autumn and one *E. sphacelata* seedling in summer (Fig. 1). *E. acuta* and *E. pusilla* seedlings appeared on damp soil with little or no free water but *E. sphacelata* germinated only after days to weeks of inundation (Fig. 2). The majority of seeds were viable at the time of sowing, but only a few were germinable (Table 1). Patterns of germinability of dry-stored seeds were similar to those of fresh seeds, except for the 15-month-old *E. pusilla* seeds (Table 1).

Table 2. Species differences in total germinations of surface-sown *Eleocharis* seeds in the field and in the glasshouse

Glasshouse percentages of remaining ungerminated seeds and totals for field and glasshouse are given. Species means followed by the same small letters are not significantly different. $n = 4$

Species	% germination	
	Glasshouse	Field plus glasshouse
E. sphacelata	36.3 (± 5.58)a	44.7 (± 4.45)a
E. acuta	15.6 (± 2.99)b	19.0 (± 3.30)b
E. dietrichiana	7.7 (± 3.31)b	8.0 (± 3.11)b
E. pusilla	16.4 (± 3.37)b	18.3 (± 4.50)b

Water levels during this experiment varied between 0 and 18 cm in the edge zone, between 15 and 46 cm in the intermediate zone and between 45 and 78 cm in the deep zone, with a peak in summer (Fig. 2). There was no free water in edge-zone plots from winter to spring 1997 and again in winter 1998. The highest diurnal variations in temperature, the highest maxima (38°C) and the lowest minima (–10°C) were in edge-zone plots (Fig. 3*a*), with below-zero temperatures in spring 1997. Diurnal temperature variation was least in the deep zone, and neither of the flooded zones had below-zero temperatures (Fig. 3*b*, *c*).

Subsequent transfer of vials to a glasshouse for 1 year increased germination percentages to a maximum of 44.7% for *E. sphacelata* but to less than 20% for the other three species (Table 2). Many more surface-sown seeds germinated in the glasshouse, and there were significant species (F_3 = 9.2, $P < 0.005$) and shore-level (F_2 = 12.7, $P < 0.001$) storage effects. For all species, nearly three times as many of the remaining seeds germinated from deep samples (31.8%) as from edge (11.9%) and intermediate

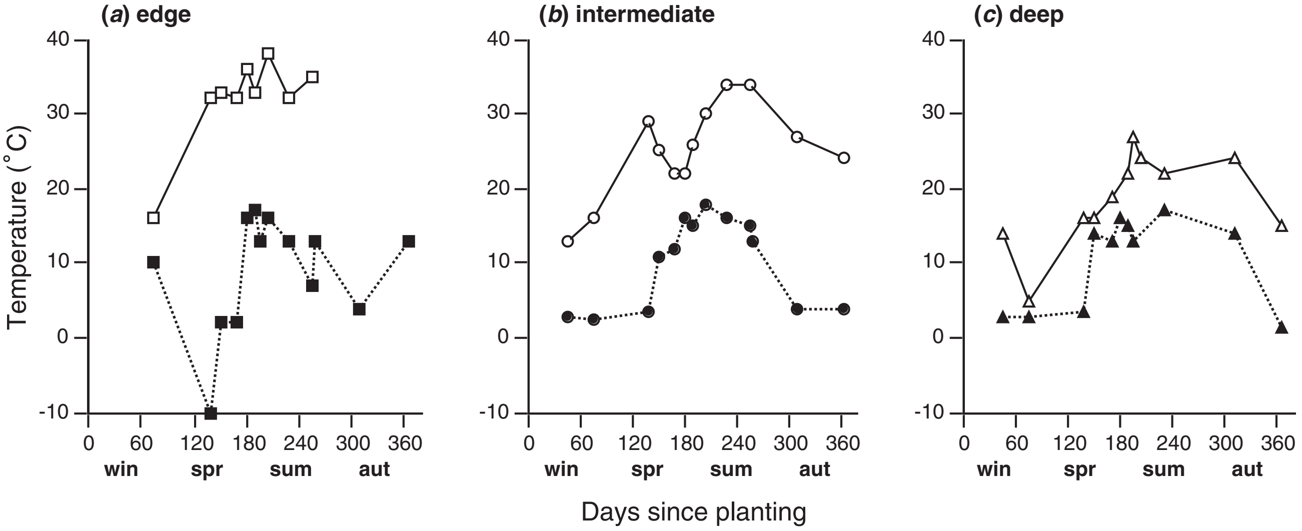


Fig. 3. Water temperature at soil surface in the three zones of (*a*) edge, (*b*) intermediate and (*c*) deep in Billybung Lagoon during seedling recruitment (1997–1998). Open symbols show maxima, filled symbols minima.

(13.3%) samples. Germination percentages of *E. sphacelata* seeds were approximately two times those of seeds of other species (Table 2).

Persistence of seeds in the soil

Persistence of species in the soil seed bank was not related to patterns of adult distribution and buried seeds of all species were persistent in all zones. The majority of seeds were still viable after a 33-month burial and relatively few seeds became rotten (Fig. 4, Table 1). *E. sphacelata*, *E. dietrichiana* and *E. pusilla* intact-seed regressions with time were significant ($P < 0.05$) and showed a very slow decline in the intact-seed fraction (Table 3). Regression for *E. acuta* was not significant ($P > 0.05$). Although there was a slight site × zone interaction for both half-lives ($F_2 = 3.6$, $P = 0.03$) and decay rates ($F_2 = 6.6$, $P = 0.002$), the major effect was species (half-lives $F_3 = 21.2$, $P < 0.0001$, decay rates $F_3 = 47.8$, $P < 0.0001$). Half-lives of *E. sphacelata* and *E. acuta* averaged over all zones were an order of magnitude greater than those of *E. dietrichiana* and *E. pusilla* (Table 3).

No seeds germinated in the bags during burial, except for one *E. sphacelata* seed in a bag retrieved after 3 months that had become dislodged and was found floating in the water column. Germination percentages were inconsistent among species, sites, zones and time ($F_{36} = 1.84$, $P < 0.005$) but the strongest effects were for species ($F_3 = 1229.94$, $P < 0.0001$), time ($F_6 = 196.09$, $P < 0.0001$) and site ($F_1 = 169.12$, $P < 0.0001$). Species exhibited one of two general patterns of dormancy. In *E. sphacelata* and *E. pusilla*, there was a pattern of large intact non-dormant fractions and small intact dormant fractions, and this pattern was generally consistent through time in all zones (Fig. 4*a*, *b*). In *E. acuta* and *E. dietrichiana*, most seeds in the soil were dormant initially, the fraction of intact non-dormant seeds gradually increasing over time (Fig. 4*c*, *d*).

Release from dormancy in the deeper zones of Billybung Lagoon was slower than in all other zones, and dormant intact fractions remained higher after 2-year burial (Fig. 4*c*, *d*). *E. pusilla* seeds were slower to come out of dormancy in the edge of Little Llangothlin Lagoon than in the deeper zones of this wetland (Fig. 4*b*).

In the deeper zones of Billybung Lagoon, the germination rate in an incubator was lower for seeds of species normally found in shallower water (*E. acuta*, *E. dietrichiana* and *E. pusilla*) (Fig. 5). The shape of cumulative germination curves for these three species in Billybung deeper zones was almost linear (Fig. 5*d*, *f*, *h*). In contrast, all other curves more or less reached a plateau after 2–3 weeks in the incubator.

Water levels in seed burial/retrieval patches at the edge of lakes were initially zero for the first 3 months after burial, reached a peak at ~15 months and dropped to zero again 33 months after burial (Fig. 6).

Seasonal dormancy

All species except *E. acuta* exhibited some degree of seasonal dormancy, i.e. changes in dormant fractions related to season, but these changes were inconsistent among species, sites and zones. The dormant fraction of *E. sphacelata* seeds increased by 20% in the second summer (after an 18-month burial) in the edge of Little Llangothlin Lagoon, with a similar but less marked pattern in the first summer and in Little Llangothlin intermediate and Billybung Lagoon edge zones (Fig. 4*a*). The dormant fraction of both *E. dietrichiana* and *E. pusilla* seeds increased by between 4 and 8% in autumn in both deeper zones of Billybung Lagoon (Fig. 4*b*, *d*).

Discussion

Field germination and buried-seed survival/dormancy did not fully explain zonation of adult plants. However, this study demonstrated that there is prolonged viability in *Eleocharis* seeds in the seed bank, with estimated buried-seed longevities of 50 to >100 years. Seed persistence was not related to dormancy level and species with mostly non-dormant seeds had equally high levels of viability as those with large dormant fractions (Table 1). Dormant-seed fractions and rates of germination in buried seeds were different for different species and were also inconsistent within and among wetlands.

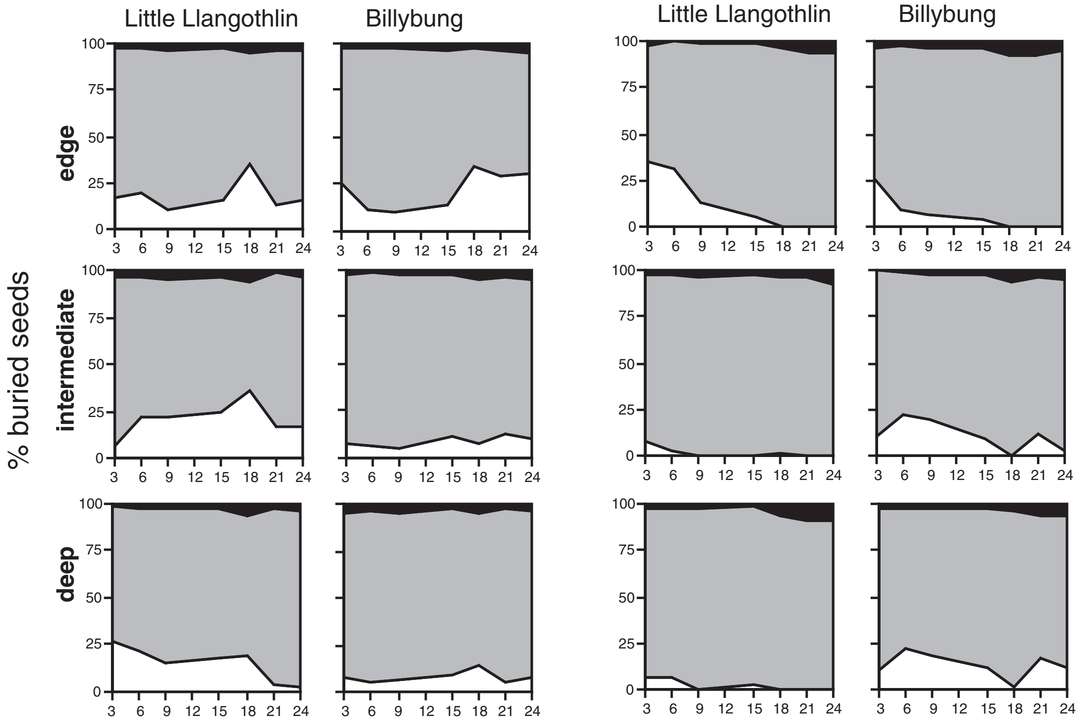
Recruitment in freshly dispersed seeds

The issue of habitat segregation in *Eleocharis* communities is complex, and inconsistencies in patterns of extant vegetation reflect these complexities (Bell 2000). Zonation was explained in part by seedling recruitment, despite low numbers of germinants, but not by persistence of seeds in the soil (Table 4). Seedlings of two shallower-water species, *E. acuta* and *E. pusilla*, germinated on damp soil or at shallow depths, but not in deeper water. Seeds of many wetland species germinate only after drawdown, i.e. when soils are damp but free water is largely absent, and *E. acuta* and *E. pusilla* fit this pattern. The absence of these edge species in deeper water is therefore due either to zonation of the seed bank or to post-recruitment processes.

The deep-water species, *E. sphacelata*, showed a wider range of tolerance to water level and recruited in both shallow and deeper water. A range of tolerances is an advantage to a deep-water species in temporary wetlands since recruitment is possible either at depth or when re-flooding begins after prolonged drought. The absence of *E. sphacelata* plants at lake edges must again be due to strict zonation of the seed bank or to post-recruitment processes such as predation.

Few *Eleocharis* plants recruited at the edge of a wetland over 12 months, reinforcing the idea that very few seeds of any species are exposed to the right conditions (safe sites) for

(a) ***E. sphacelata*** **(b)** ***E. pusilla***



(c) ***E. acuta*** **(d)** ***E. dietrichiana***

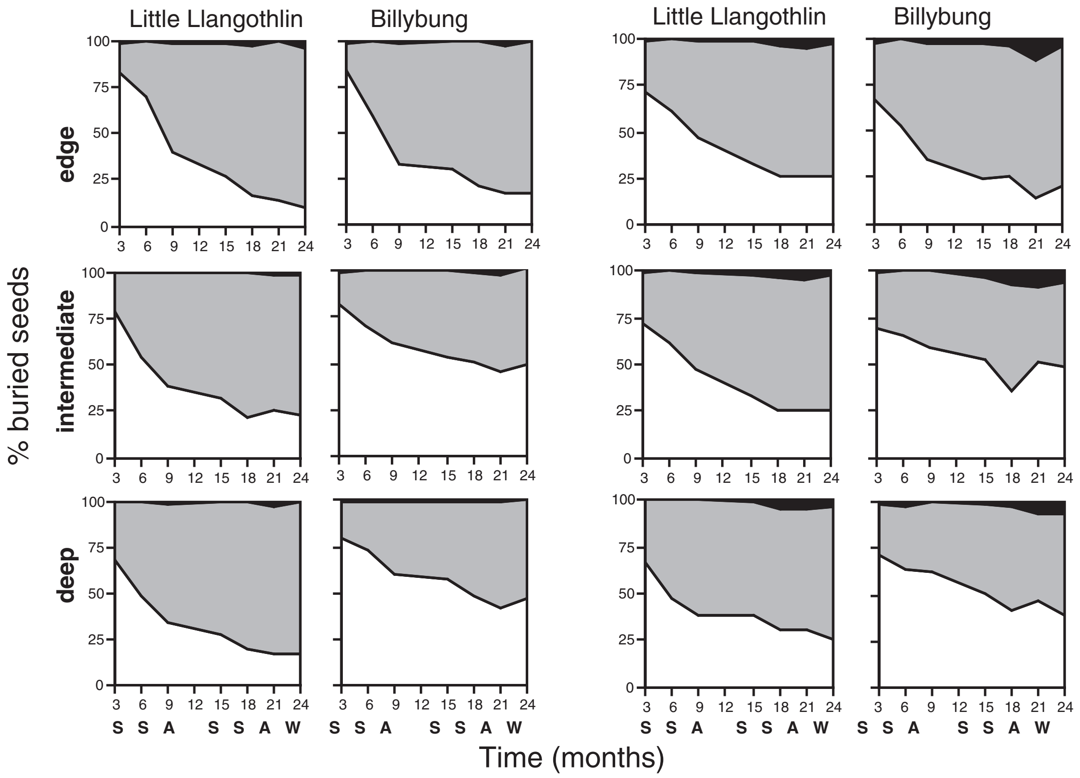


Fig. 4. Germinability and decay of buried seeds of four *Eleocharis* species in three zones of two sites (Llangothlin and Billybung Lagoons) over time (1995–1997). Black area, rotted seeds; shaded area, intact non-dormant seeds; open area, intact dormant seeds. l.s.d. = 4.34–10.56.

Table 3. Estimated longevity of *Eleocharis* seeds in the soil

Decay rate and half-life data are calculated from adjusted data; R^2 from pooled data. Regression significance: $^*P < 0.05$; $^{***}P < 0.001$; n.s., not significant. Species means followed by the same small letters are not significantly different

Species	Predicted decay rate (± s.e.)	R^2-value	Estimated half-life (years) (± s.e.)	Significance
E. sphacelata	0.011 (± 0.0002)a	0.015	400 (± 65)a	*
E. acuta	0.0008 (± 0.0001)a	0.011	448 (± 63)a	n.s.
E. dietrichiana	0.037 (± 0.0002)b	0.25	49 (± 21)b	***
E. pusilla	0.031 (± 0.0002)b	0.22	54 (± 21)b	***

optimal germination (Harper 1977). Buried seeds become non-dormant after a 3- (most *E. sphacelata* and *E. pusilla* seeds) to 9-month burial (*E. acuta* and *E. dietrichiana*) (Fig. 4); however, conditions to which seeds on the surface are exposed are different from those of buried seeds. Surface seeds may have re-entered dormancy as a result of high irradiance or desiccation during the period when the soil surface was dry between 60 and 150 days after planting (Fig. 2), or they may have become non-viable.

Eleocharis sphacelata recruitment has been recorded in clear water down to 45 cm (M. Casanova, pers. comm.); however, in this study only one seedling recruited in deeper water ~30 cm deep). Lack of recruitment of *E. sphacelata* in deeper water was probably due to lack of light; the absence of recruitment in the other three species may be the result of low light intensity, of anoxic soils or of the damping down of water-temperature fluctuations. However, 12 months spent in deeper water resulted in higher germination percentages in the glasshouse for all *Eleocharis* species. The lower (minimum 1.5°C, maximum 17°C) and less variable temperatures (Fig. 3*c*) may have had the effect of breaking dormancy in seeds in deep-water vials as a result of chilling (stratification).

Rapid burial is one explanation for low levels of recruitment in surface-sown light-requiring seeds at the lake edge. Burial results from material being deposited on seed or from vertical movement of seeds into the soil or into soil cracks. Burial agents include rainwater, water birds or earthworms (Grace 1984), structures on seed or fruit coats, e.g. the perianth on *Eleocharis* fruits, currents and small invertebrates such as ostracods which re-suspend fine sediments and debris. Since persistence is enhanced by storage in the soil, sinking rapidly (for seeds dispersed into water) or rapid burial is therefore an advantage for freshly dispersed *Eleocharis* seeds.

Seed banks and changes in dormant fractions

As predicted for species of disturbance-prone habitats, including many wetland habitats, these four *Eleocharis* species form persistent seed banks (Thompson and Grime 1979; Baskin and Baskin 1988; Leck 1989). The potential to form persistent seed banks was also predicted by the small size of *Eleocharis* seeds (Thompson and Grime 1979), by their high viability (Wesson and Wareing 1967; Villiers 1973) and by their lack of germination when buried. After 33 months in the soil, most seeds were viable but not all were germinable (Table 1, Fig. 4).

Seeds of *E. dietrichiana* and *E. acuta* exhibited prolonged dormancy (Grime *et al.* 1981), i.e. these species form persistent seed banks in which, after 2 years, 25–50% of seeds are non-germinable. An increasing fraction of *E. dietrichiana* and *E. acuta* seeds gained the ability to germinate at 25/15°C in light after 1–2-year burial (Table 4). Gradual loss of dormancy has been found in other wetland perennials in glasshouse-based studies (Baskin *et al.* 1989), but not over a 33-month time period. A seed bank of mostly dormant seeds is an advantage for long-lived perennial species. Opportunistic recruitment can occur but the risk of seedling loss is countered by germination of only a small proportion of the seed bank. This bet-hedging promotes survival in an unpredictable habitat. *E. acuta* often occurs in patches similar in size to the bare ground associated with bird disturbance. The principal mode of establishment in this species could therefore be germination of only a few seeds followed by rapid 'guerilla'-type colonisation.

Most fresh seeds of *E. sphacelata* (a deep-water species) and *E. pusilla* (an edge species) were initially non-germinable, although this state was short-lived. Most seeds were germinable after a 3-month burial (Fig. 4). This pattern delays germination until spring, after which seeds are inhibited by darkness or other environmental restraints. Environmental inhibition of germination (Thompson *et al.* 2003) is a trait associated with opportunistic plants (Harper 1977) and with many annual wetland plants (Baskin *et al.* 1993*a*). *E. pusilla* is an early coloniser of exposed mud and in these wetlands functions as an opportunistic ruderal species. In contrast to *E. acuta*, loss of seeds from the seed bank is minimised by inhibition of germination rather than by a largely dormant seed bank.

In a habitat where drawdown and refilling are unpredictable, possession of this opportunistic seed-bank trait also confers a considerable advantage on a plant such as *E. sphacelata* that grows in deep water but can also germinate in shallow water. Recruitment opportunities are rare and include periods when water levels are rising after a severe drought or when water is deeper but clear. A seed

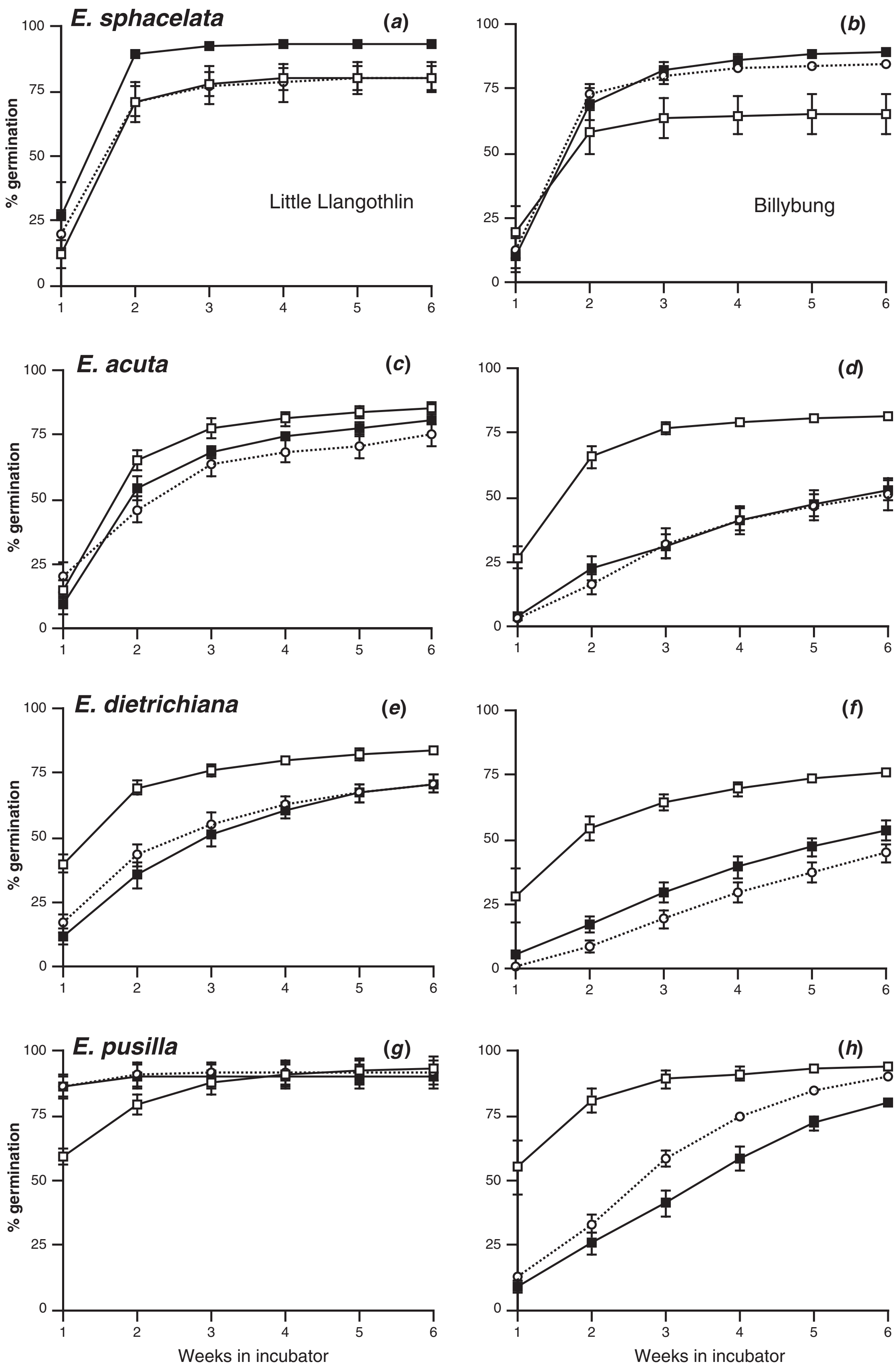


Fig. 5. Germination over 6 weeks of seeds of four *Eleocharis* species retrieved from Little Llangothlin and Billybung Lagoons after a 24-month burial. □, edge; ○, intermediate; ■, deep burial zones. Error bars show s.e. $n = 4$.

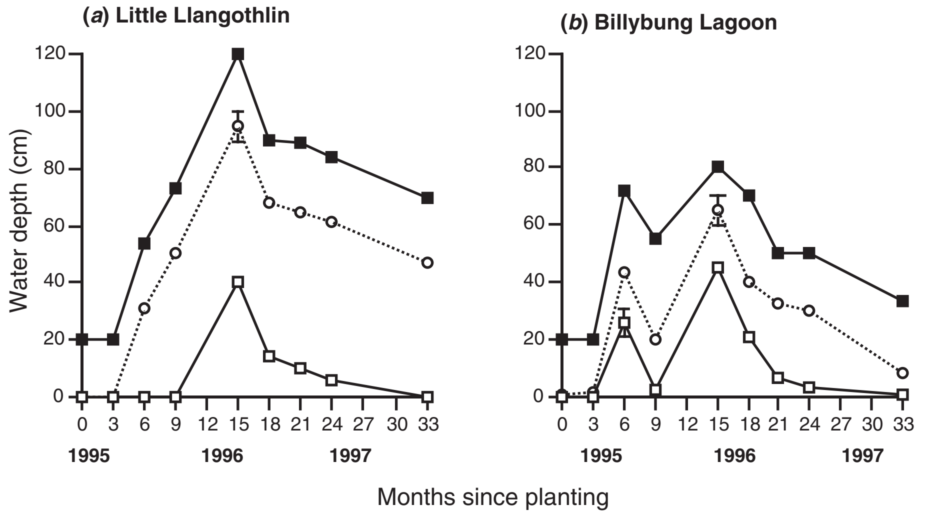


Fig. 6. Water depths in three zones of two sites (Llangothlin and Billybung Lagoons) during seed-persistence experiment (1995–1997). Error bars show s.e. □, edge; ○, intermediate; ■, deep.

bank of non-dormant seeds is more likely to provide a source of seeds able to respond to these brief recruitment windows.

Seasonal dormancy

Seasonal dormancy of seed-bank seeds has been found in a number of species, including desert annuals (Baskin *et al.* 1993*b*), chalk grassland species (Pons 1991) and wetland perennials (Baskin *et al.* 1989; Schütz 1997; Van Assche *et al.* 2002). A period of initial dormancy (or a requirement for after-ripening) is typically followed by summer or winter dormancy (Harper 1977; Chesson and Warner 1981; Baskin *et al.* 1993*a*). For these four species, seasonal changes in dormancy fractions did not generally appear in the first year of burial, were not as marked as those of other studies and were clearly related to shore level (Fig. 4). The relatively long storage period in the laboratory before burial is the most likely explanation for the absence of seasonal patterns in the first year. One possible explanation for the relatively small peaks in the intact dormant seed fraction (Fig. 4*a*, *b*, *d*) is that the temperature regime used for germination testing may not have been optimal. A second explanation is that conditions for field-buried seeds are far more heterogenous than those for seeds buried in pots in a glasshouse. The reduced fraction of seeds responding to soil-temperature changes may thus reflect microhabitat variability.

The damping down of air-temperature fluctuations that occurs at depth is the most likely explanation for shore-level differences in seasonal responses of buried seeds. However, response patterns were different for different species at different sites. *E. sphacelata* buried seeds were generally less germinable at high temperatures (in summer) (Fig. 4*a*). This result was predicted since, in a seed-bank germination trial, seedlings of most Northern Tablelands lake species were most abundant in spring and autumn (D. Britton, pers. comm.) (Britton and Brock 1994).

However, some of both *E. dietrichiana* and *E. pusilla* seeds buried in deeper water also became non-germinable in autumn, but only in Billybung Lagoon (Fig. 4*b*). A non-dormant seed bank is typical of mudflat species; however, the phenomenon of seeds of these species re-entering dormancy in colder months in deeper water is more difficult to explain, as is the site specificity. These anomalies in seed-dormancy levels illustrate the need to replicate field experiments in the range of the habitats in which seed banks occur and at a number of spatial scales.

Table 4. Summary of recruitment and seed bank characteristics in four *Eleocharis* species

Characteristic	*E. sphacelata*	*E. acuta*	*E. dietrichiana*	*E. pusilla*
Initial germination percentage (%)	[A]30	<5	<5	<5
[B]Time to 50% germination percentage in buried seeds (months)	<3	6–8	6–9	<3
Season of peak recruitment	Spring, autumn	Spring	None observed	Spring
Recruitment zone	Edge to intermediate	Edge	Edge	Edge
Estimated half-life (years)	400	>400	50	50
Seasonal dormancy	Summer	Not present	Autumn	Autumn

[A]<5% in preliminary study. [B]Little Llangothlin Lagoon.

Zone × site interaction

Burial in Billybung Lagoon reduced germination rates of buried seeds, but only for *E. acuta*, *E. dietrichiana* and *E. pusilla* and only for seeds retrieved from deeper plots (Figs 4, 5). Conversely, changes in dormant fractions of *E. sphacelata* buried seeds were absent in deeper water in Billybung Lagoon.

The anomalies in the dormant-seed fractions and germination rates in Billybung Lagoon are clearly linked to differences in vegetation cover. In Billybung Lagoon, dense vegetation occurred across the whole of the lake, whereas in Llangothlin Lagoon deeper burial patches were placed in an extensive band of open water where vegetation was usually absent. An increased level of dormancy is one explanation for the slower germination rate. Changes in dormancy level have been related to temperature and soil gases such as O_2 (Baskin and Baskin 1998). Temperatures at or near the soil under vegetation in deep water are often lower than in comparable non-vegetated wetlands because there is little or no current-assisted vertical water exchange (Fig. 3*c*). Dense plant growth in wetlands increases the oxygen content of sediments by oxygenation of rhizospheres (Armstrong *et al.* 2000). Changes in soil O_2 levels do not explain, however, why most *E. sphacelata* buried seeds are non-dormant in the well vegetated deeper zones of Billybung Lagoon.

Myriophyllum variifolium is the dominant plant in the intermediate and deep zones of Billybung Lagoon and seed bags in these zones often contained fine roots of this species. The inhibitory effects of allelochemicals have been recorded in aquatic plants (Gopal and Goel 1993) but, although these chemicals inhibit germination in Petri dishes, there is no evidence for allelochemical-induced changes in the dormancy states of seeds (Baskin and Baskin 1998). However, absorption of *M. variifolium* root exudates by buried *Eleocharis* seeds may occur. The gradual leaching of such exudates would then explain the slower germination rate of seeds. Possible causes of changes in dormancy levels for buried seeds in well vegetated wetlands could be tested both in the laboratory and by experimental manipulation of vegetation cover in the field.

Implications—coexistence

Coexistence is favoured in species with long-lived, resistant life-history phases that allow persistence under unfavourable conditions (Chesson 1983; Chesson 1994). Temporal variation among species either within or among years then promotes co-occurrence (Chesson and Warner 1981; Chesson 1986); one example is the different proportion of seeds germinating each year in coexisting desert annuals (Pake and Venable 1995). *Eleocharis* partially fits this model; species have persistent seed banks but different patterns of dormancy (Table 4).

However, uniform survival of buried seeds of all species in all zones did not explain patterns of adult distribution. Although dispersal of seeds may be less homogeneous than expected, recruitment patterns indicate that the seedling phase of the life cycle is crucial to the development of zonation (Fig. 1). Further studies are needed on the dispersal in space of *Eleocharis* seeds, on the survival under field conditions of seedlings of this genus and on the effects of marsh vegetation on buried seeds of these and other wetland species.

Studies on zonal community establishment in wetlands usually involve subjecting wetland seed banks to different water-level fluctuations (Casanova and Brock 2000). Although such studies are useful for predicting community composition, they are confounded by lack of information on seed age (Thompson *et al.* 2003). This study provides unambiguous evidence of buried-seed longevity and of changes in dormancy levels in buried seeds.

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