Plant reproduction in temporary wetlands: the effects of seasonal timing, depth, and duration of flooding

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Abstract

In less predictable, drier climates depth, duration and season (month) of flooding influence not only germination and establishment of wetland plants but also completion of the life cycle through to sexual or asexual reproduction. A tank trial was carried out to investigate the effects of season (summer, autumn), duration (0–16 weeks) and depth of flooding (0–60 cm) and their interactions on sexual reproduction of a range of aquatic plant species. Seed bank material was collected from four New England wetlands in New South Wales, Australia. The majority of species germinating and establishing in the summer experiment were able to flower and set seed. In contrast, few of the plants growing during autumn had flowered after 16 weeks and biomass production was significantly reduced. For obligate submerged species flooding duration must be long enough to allow reproductive organs to form and for fertilisation and seed maturation to occur. Amphibious plants, in contrast, in particular those that respond morphologically to water presence or absence, had inflorescences emerging under a wide range of conditions, i.e. out of the water column when submerged, damp or spending only a portion of the life cycle submerged. Terrestrials established in autumn only in the damp treatments. A significant correlation was found for the dominant species from the amphibious and submerged groups between plant biomass and the number of reproductive units produced. Hence, diaspore production of wetland species is often a function of biomass production.
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1. Introduction

In Australia and other parts of the world where rainfall is unpredictable and infrequent, wetlands are characterised by the frequency, depth, duration and timing of flooding and these factors strongly influence plant species composition (Keddy and Reznicek, 1986; Poiani and Johnson, 1988; Brownlow et al., 1994; Rea and Ganf, 1994; Nielsen and Chick, 1997). In a dry continent, such as Australia, wetlands can become dry for long periods of time, but can also experience long periods of inundation. A similar unpredictability is found for the vernal pools of California (Zedler, 1987), the Mediterranean coastal wetlands (Britton and Crivelli, 1993) and in South Africa (Brock and Rogers, 1998). The plant species present in temporary wetlands must therefore be able to endure either long periods of desiccation or flooding with depths of submergence ranging from deep to shallow (Brock, 1986, 1994; Boulton and Brock, 1999). Survival during long dry periods as vegetative propagules is not feasible for the majority of species and seeds provide the main means for re-establishment of such wetland vegetation (Thompson, 1992). Many of these plant species survive during dry periods by building up a large seed bank in the soil during periods of water availability. Maintenance of a seed bank is a major factor in the survival of many Australian temporary wetland plants. Therefore, it is essential for floral initiation, fertilisation and seed set to occur during favourable flooding events to ensure the maintenance of the seed bank. Some species may be excluded because of a too brief hydroperiod. This study used a seed bank collected from three shallow wetlands and a reservoir on the New England Tablelands of New South Wales. Rainfall averages 790 mm annually on the New England Tablelands (Anon, 1988) but has considerable variability (Hobbs and Jackson, 1977). This leads to wide variation in all aspects of water regime in New England lagoons. These lagoons can be dry for long periods (months to years) and recolonisation following rewetting is dependent on a seed bank. Different longer-term local hydroclimates may well select for suites of different traits and lead to contrasts in species presence in the seed banks. While studies have been made on the influence of water regime on germination and establishment in these wetlands it is also important to understand the influence that the components of water regime have on their capacity to reproduce (Britton and Brock, 1994; Casanova and Brock, 2000; Crosslé and Brock, 2002).

Previous studies on these New England wetlands have found a large number of wetland species (>100) present in their respective seed banks (Casanova and Brock, 2000). Wetland plant species establishing from seed have been classified by Brock and Casanova (1997) into four major functional groups on the basis of germination, establishment and reproduction responses to water presence or absence: amphibious fluctuation tolerators, amphibious fluctuation responders, submerged species and terrestrial species. This classification has been tested in other wetland systems and found to work satisfactorily (Leck and Brock, 2000).

This study investigates the effect of depth, duration and seasonal timing of flooding on growth and sexual reproduction for a range of wetland plants from the major functional groups found in four New England wetlands.

2. Materials and methods

The seed bank material used in this study was composed of a mixture of substrates collected from the edge zone of four wetlands on the New England Tablelands (altitude

1000–1325 m) of New South Wales (30°39′S, 151°30′E). Two wetlands were on tertiary basalt, a near-permanent wetland, Llangothlin Lagoon, and an intermittent wetland, Barley Fields Lagoon, and two on granite, an intermittent wetland, Racecourse Lagoon and a constructed reservoir, Dumaresq Dam. The four substrates were collected during August and September 1997, air-dried and pooled. Extant vegetative material was removed before mixing.

Water regimes were imposed in twelve round fibreglass tanks (1 m diameter × 60 cm deep). The experiment was set up as a randomised complete block design. A metal mesh frame fixed above each tank allowed individual plastic pots filled with substrate to be raised or lowered within each tank to simulate water level fluctuations. This allows a larger number of water regimes to be applied within one block (two tanks) (Casanova and Brock, 2000). Each tank held 16 pots with each water regime replicated four times within each pair of tanks and there were six pairs of tanks. The eight experimental water regimes were chosen to simulate flooded, damp and fluctuating water levels as given further.

- A: flood (pots permanently at bottom of tank 60 cm depth).
- B: damp (pots permanently at water surface).
- C: rapid flood to dry (pots moved from bottom of tank to dry over 4 weeks).
- D: slow flood to dry (pots moved from bottom of tank to dry over 16 weeks).
- E: rapid flood to damp (pots moved bottom of tank to water surface over 4 weeks).
- F: slow flood to damp (pots moved from bottom of tank to water surface over 12 weeks).
- G: rapid damp to flood (pots moved from water surface to bottom of tank over 12 weeks).
- H: slow damp to flood (pots moved from water surface to half depth of tank (30 cm) over 16 weeks).

Plastic pots (10 cm diameter × 10 cm deep) were filled to within 5 cm of the lip with Llangothlin Lagoon substrate: garden loam blend (50:50). The Llangothlin Lagoon substrate had been stored for a number of years and previous studies had shown that germination occurs predominantly from the top 2.5 cm of the substrate and therefore potentially confounding germinations from the Llangothlin substrate would not occur (Brock and Britton, 1995). The seed bank substrate mix was then placed in each pot to fill the remaining top 5 cm. For the first day all pots were held with the lip of the pot at the water surface. The water regimes were then initiated the following day. The water level for each pot was adjusted weekly for treatments with changing depth of submergence.

To investigate the effect of season of flooding the experiment was carried out during summer and autumn. The first experiment ran for 16 weeks from December 1997 to March 1998 and will be referred to as the summer experiment and the second, referred to as the autumn experiment, ran for 16 weeks from April 1998 to July 1998. Maximum and minimum daily air temperature was measured in a Stevenson screen next to the tanks and maximum and minimum daily water temperatures at 10 cm depth in the tanks. The average air and water maximum/minimum temperatures were 32 °C/12 °C and 24 °C/19 °C over the summer experiment and 17 °C/3 °C and 10 °C/8 °C during autumn experiment. Rainfall during both experiments was intermittent and highly variable. During the summer experiment total rainfall was 172 mm but the majority fell in the first 7 weeks and the remainder was ineffective. The plants in the two flood to dry treatments during summer (C and D), wilted and died after a few weeks out of the water column. In the autumn

experiment rainfall was similar to that of summer and totalled 165 mm. However, evaporative demand was much less during autumn and rain fell in large amounts in the latter half of the experiment. Thus, in contrast to the summer experiment plant growth was maintained in the two flood to dry treatments.

During each experiment pots were scored after 13 weeks for the presence/absence of plant species and these data were then used to calculate species abundance and reproductive abundance. Similarity in the number of species present or reproducing between treatments was

Table 1
Dominant species present (○) and reproducing (●) in the summer experiment after 13 weeks under eight experimental water regimes

Species	Water regime							
	A	B	C[a]	D[a]	E	F	G	H
Amphibious-responders								
E. gratioloides Cunn.	●	●	●	●	●	●	○	○
L. australis R. Br.	○	●	●	●	●	●	○	○
M. variifolium Hook. f.	●	●	○	●	●	●	●	●
M. verrucosum Lindley	○			●	●	●	●	●
N. geminata (R.Br.) Kuntze	○	●	○	○				
P tricarinatus F. Muell. & A. Benn. ex A. Benn.	●					●		
Amphibious-tolerators								
Centipeda minima (L.) A. Braun & Asch.		●	○	○	●			
Cyperus sanguinolentus Vahl		●	○	●	●			
Eleocharis acuta R. Br.		○		○	●	○	○	○
Eleocharis dietrichiana Boeck.	○	●	○	●	●	○	○	●
E. pusilla R.Br.	○	●	○	●	●	○	○	○
Hydrocotyle tripartite R. Br. ex A.Rich.		●		○	●			
Lipocarpha microcephala R. Br. (Kunth.)		●			●			
Lythrum salicaria L.	○	●	○	●	●	●	○	○
Typha orientalis C. Presl.		○	○		○			
Submerged								
Chara spp.	●	●				●	●	●
Najas tenuifolia R. Br.	●					●	●	●
Nitella spp.	●			○		●	●	●
Potamogeton ochreatus Raoul	●					●		
V. gigantea Graeb.	●					●	●	●
Terrestrial								
Eragrostis trachycarpha (Benth.)		●			●			
Gnaphhalium spp.			○					
Juncus spp.		●	○		●			
Panicum gilvum Launert	●	○						○
Polygonum aviculare L.		●			●			○
Portulaca oleracea L.		●	○		○			
Rorippa palustris (L.) Besser		●	○	○				○
Rumex crispus L.		○	○					

Treatments as indicated in Fig. 1.

[a] Indicates treatments where the pots had dried out after 13 weeks and information was used from 7 week score for these treatments.

calculated using the Czekanowski coefficient (S_c) (Kent and Coker, 1992). The coefficient is calculated as follows:

$$S_c = \frac{2\sum_{i=1}^{m}\min(X_i, Y_i)}{\sum_{i=1}^{m}X_i + \sum_{i=1}^{m}Y_i}$$

where X_i and Y_i are the abundances of species present or reproducing i, $\sum_{i=1}^{m}\min(X_i, Y_i)$ the sum of the lesser scores of species i where it occurs in both treatments, and m the number of species present. The coefficient values can range from 0 (complete dissimilarity) to 1 (total similarity).

The aquatic plant species that established during the experiment were classified into four functional groups according to Brock and Casanova (1997). Amphibious species, which tolerate or respond to water level fluctuations, were placed in two groups. Amphibious responders, that change in form (e.g. leaf shape, petiole length) as a result of altered flooding pattern, and amphibious tolerators that do not have a major change in form. The other two groups were submerged species, which cannot tolerate drying, and, terrestrial species, which cannot tolerate submersion.

After 16 weeks of growth six replicate pots of each water regime treatment were removed from the tanks. The plant biomass from each pot was sorted into individual species and the numbers of reproductive units counted. Plant material was dried at 70 °C for 24 h and then weighed.

All statistical tests were carried out using Minitab 13.0 and Statview 5.0. Data for number of species present, number of species reproducing and plant biomass was analysed using one- and two-way analysis of variance (ANOVA) and Tukey's HSD test was used to make pair-wise comparisons. Simple linear regression was used to test for correlation between biomass and number of reproductive units for particular species. Data were natural log-transformed to meet assumptions of normality and homogeneity of variances.

Table 2
Dominant species present (○) and reproducing (●) in the autumn experiment after 13 weeks under eight experimental water regimes

Species	Water regime							
	A	B	C	D	E	F	G	H
Amphibious-responders								
Elatine gratioloides Cunn.	○	●	●	○	○	○	○	○
Limosella australis R. Br.	○	○	●	○	○	○	○	○
M. variifolium Hook. f.	○	○	○	○	○	○	○	○
Amphibious-tolerators								
E. pusilla R. Br.	○	○	○	○	○	○	○	○
Hydrocotyle tripartite R. Br. ex A. Rich.		○	○					
Lythrum salicaria L.		○	○	○	○			
Terrestrial								
Gnaphhalium spp.		○	○		○			
Juncus bufonius L.		○	○	○	○			○
Rorippa palustris (L.) Besser		○	○					

Treatments as indicated in Fig. 1.

3. Results

In the summer experiment a total of 29 species established from the seed bank across all treatments and all but two of the species flowered in at least one treatment (Table 1). In autumn, nine species established but only two of these flowered (Table 2). In summer the number of species establishing was evenly distributed between the submerged, terrestrial, amphibious responder and amphibious tolerator groups as was the number of species reproducing. Amphibious species were spread over all the water treatments whereas the submerged plants grew only under water regimes with predominantly flooded conditions. The terrestrial species only appeared in the damp or drier treatments. In the autumn experiment
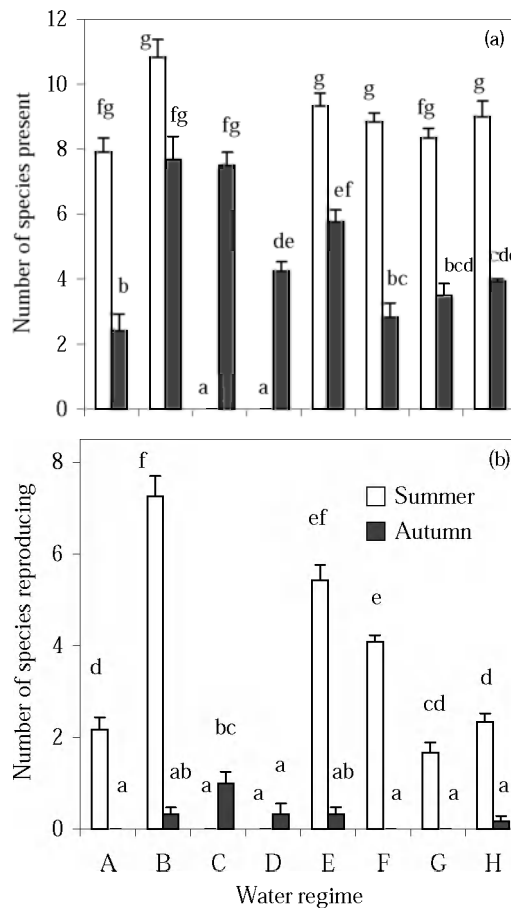

Fig. 1. Number of species present (a) and, number of species reproducing (b), in emerging seed bank material under eight experimental water regimes for the summer and autumn experiment at 13 weeks. Values are means±standard error ($n = 12$). Different letters indicate significant differences among means (Tukey's H.S.D.). Water regimes are: A, flood; B, damp; C, rapid flood to dry; D, slow flood to dry; E, rapid flood to damp; F, slow flood to damp; G, rapid damp to flood and H, slow damp to flood.

the flooded regimes were predominantly occupied by amphibious species. No submerged species established in autumn.

The number of species present after 13 weeks varied significantly between water regimes, between seasons and with a significant interaction (water regime d.f. $= 7$, $F = 96.7$, $P < 0.0001$; season d.f. $= 1$, $F = 3.95$, $P < 0.05$; water regime $\times$ season d.f. $= 7$, $F = 146.8$, $P < 0.0001$) (Fig. 1a). The significant interaction effect was most probably due to drying off in treatments C and D during summer. Greatest species numbers were found in summer particularly in damp treatments. Lowest species numbers were found in autumn in the flood treatments. The number of species reproducing varied significantly between water regime and season with a significant season and water regime interaction (water regime d.f. $= 7$, $F = 44.0$, $P < 0.0001$; season d.f. $= 1$, $F = 577.4$, $P < 0.0001$; water regime $\times$ season d.f. $= 7$, $F = 65.3$, $P < 0.0001$) (Fig. 1b). The flood treatments (A, G and H) had significantly lower numbers of species reproducing than the damp treatments (B, E and F) (Fig. 1b).

For the summer experiment the treatments that had the greatest species similarity (Czekanowski coefficient) to the flood treatment (A) were the slow flood to damp (F) and both damp to flood treatments (G and H); (Table 3a). The damp treatment (B) was most

Table 3

Czekanowski similarity coefficients for the number of species present and reproducing for the summer experiment, and number of species present for the autumn experiment

Season–state	Water regime	A	B	C*	D*	E	F	G	H
a. Summer–number of species	A	1.00							
	B	0.44	1.00						
	C	0.37	0.62	1.00					
	D	0.62	0.67	0.71	1.00				
	E	0.44	0.82	0.71	0.75	1.00			
	F	0.85	0.37	0.54	0.71	0.61	1.00		
	G	0.88	0.47	0.55	0.62	0.53	0.89	1.00	
	H	0.80	0.55	0.56	0.77	0.63	0.90	0.78	1.00
b. Summer–number of species reproducing	A	1.00							
	B	0.05	1.00						
	C	0.03	0.31	1.00					
	D	0.06	0.61	0.45	1.00				
	E	0.04	0.73	0.40	0.78	1.00			
	F	0.64	0.25	0.42	0.35	0.27	1.00		
	G	0.81	0.04	–	–	0.04	0.63	1.00	
	H	0.47	0.23	–	0.34	0.25	0.44	0.59	1.00
c. Autumn–number of species	A	1.00							
	B	0.52	1.00						
	C	0.47	0.55	1.00					
	D	0.59	0.77	0.79	1.00				
	E	0.53	0.69	0.71	0.93	1.00			
	F	0.73	0.88	0.67	0.76	0.62	1.00		
	G	0.66	0.80	0.67	0.74	0.87	0.97	1.00	
	H	0.71	0.76	0.62	0.81	0.72	0.88	0.78	1.00

Treatments as indicated in Fig. 1.

similar to the rapid flood to damp treatment (E). Reproductive similarity for the summer experiment was not as strong as that found for the similarity in number of species present but there was a similar pattern (Table 3b). Similarities were less distinctly related to flood or damp treatments in the autumn experiment as fewer species established and those that did were found in all treatments (Table 3c).

Total above ground biomass after 13 weeks growth was significantly affected by water regime, season and there was a significant interaction (water regime d.f. $= 7$, $F = 18.3$, $P < 0.0001$; season d.f. $= 1$, $F = 365.3$, $P < 0.05$; water regime $\times$ season d.f. $= 7$, $F = 26.2$, $P < 0.0001$) (Fig. 2). The interaction was again primarily due to the death of plants in the dry treatments (C and D) (Fig. 2a). Biomass production was reduced five-fold or greater in autumn compared with summer, and therefore the data for summer and autumn were analysed separately to investigate water regime effects (Fig. 2b). Summer biomass production was equally high in flood and damp treatments (A, B, E, G and H) and least in damp to flood (F). In contrast, autumn damp treatments (B and E) had significantly greater biomass production than the flooded treatments (A, F, G and H).
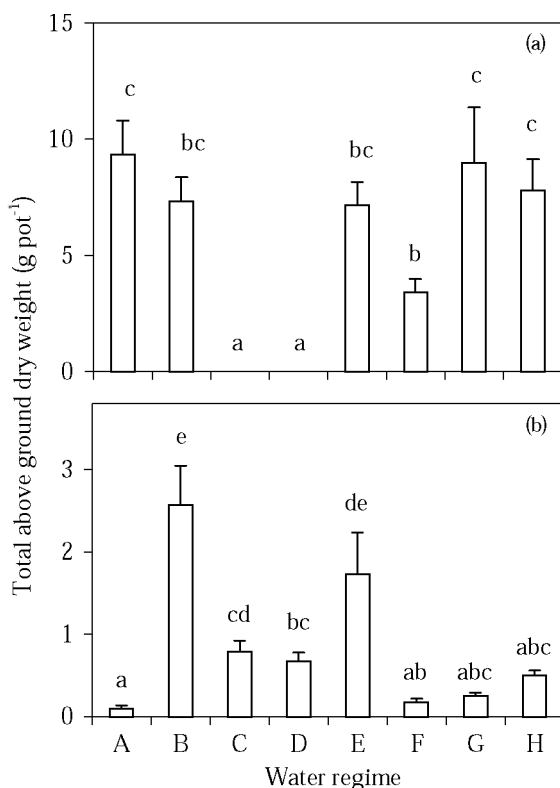

Fig. 2. Total above ground dry weight (g per pot) of the eight dominant species grown under eight experimental water regimes for 16 weeks for the summer and autumn experiments. Values are means ± standard errors ($n = 12$). Different letters indicate significant differences among means (Tukey's H.S.D.). Treatments as indicated in Fig. 1.

Three of the dominant species were examined for their response to water regime in the summer experiment. The amphibious responder, *Myriophyllum variifolium*, was found in all treatments during summer, excluding the dry treatments (C and D). Dry weight and reproductive shoot number differed significantly between treatments (dry weight − water regime: d.f. = 7, F = 7.35, P < 0.0001; reproductive shoot number − water regime: d.f. = 7, F = 4.0, P < 0.01) (Fig. 3a). Only in the flood treatment (A) were no reproductive spikes produced, whereas large number of spikes were found in both damp and slow flood to damp treatments (B, E and F). In contrast, the amphibious tolerator, *Lythrum salicaria*, was
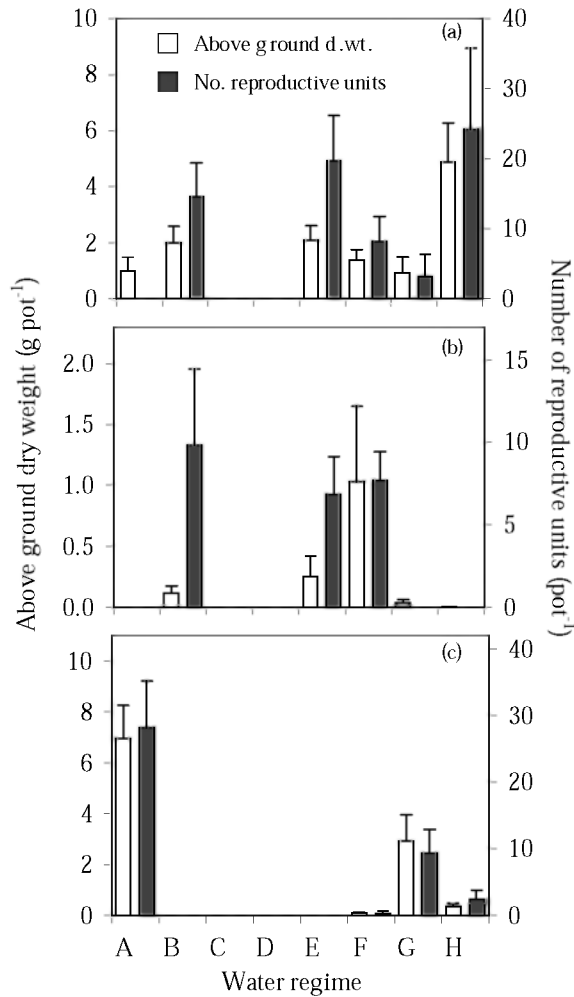
Fig. 3. Above ground dry weight (g per pot) and number of reproductive units (per pot) for the summer experiment after 16 weeks for the amphibious responder: (a) *M. variifolium* (reproductive shoots), the amphibious tolerator; (b) *Lythrum salicaria* (inflorescence spikes), and the submerged species; (c) *Vallisneria gigantea* (male inflorescences + female flowers). Values are means ± standard error ($n = 6$). Treatments as indicated in Fig. 1.

found exclusively in B, E and F with greatest dry weight in F. Inflorescence production was even across all three treatments (dry weight − water regime: d.f. = 7, F = 2.55, P < 0.05; reproductive shoot number–water regime: d.f. = 7, F = 10.2, P < 0.0001) (Fig. 3b). The depth of flooding in all other treatments prevented establishment and reproduction. The submerged species, *Vallisneria gigantea*, established and only produced significant biomass and reproduced in the flood treatments (A, G and H) (dry weight − water regime: d.f. = 7, F = 20.96, P < 0.0001; reproductive shoot number − water regime: d.f. = 7, F = 13.1, P < 0.0001) (Fig. 3c).

In contrast to the summer experiment, the plants establishing in the autumn experiment produced little reproductive material. Dry weight for *Myriophyllum variifolium* varied significantly, was reduced relative to summer, and was much more evenly spread across treatments, with greatest production in B, E and H (water regime: d.f. = 7, F = 9.19, P < 0.0001) (Fig. 4a). The amphibious tolerator, *Eleocharis pusilla*, followed a similar
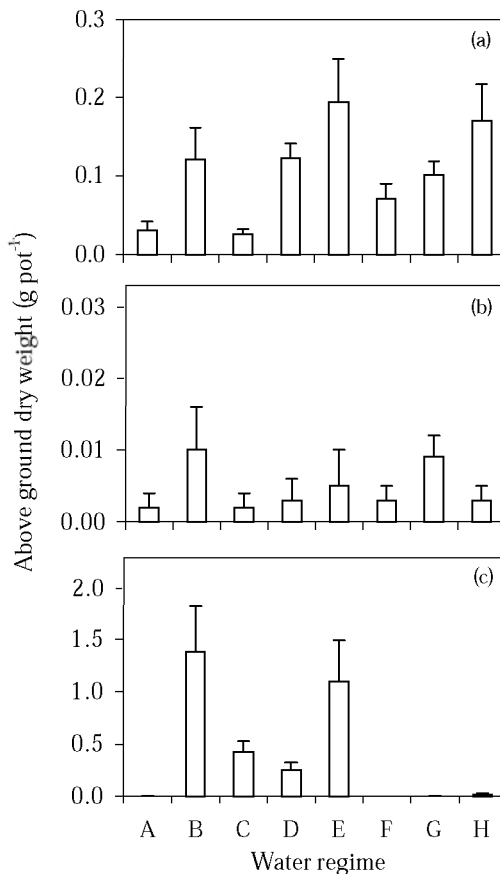

Fig. 4. Above ground dry weight (g per pot) for the dominant species establishing in the autumn experiment after 16 weeks: (a) the amphibious responder *M. variifolium*, (b) the amphibious tolerator, *E. pusilla*, and (c) the terrestrial, *Juncus bufonius*. Values are means ± standard error (n = 6). Water regimes are as indicated in Fig. 1.

even pattern to *M. variifolium* and no significant treatment effect was found (Fig. 4b) (water regime: d.f. = 7, F = 1.50, P = 0.18) (Fig. 4b). No submerged species established, but the terrestrial, *Juncus bufonius*, was a dominant species in the damp and dry treatments (B–E) (water regime: d.f. = 7, F = 20.93, P < 0.0001) (Fig. 4c).

Regressions were made of the number of reproductive units against the biomass produced. A significant positive relationship was found between biomass and the number of reproductive units for the three dominant species (Fig. 5). The correlation held across three
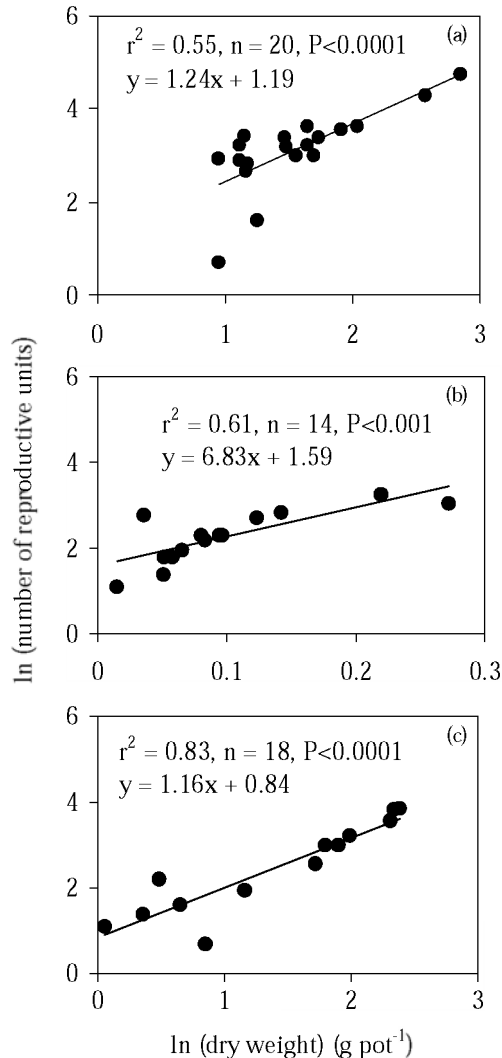
Fig. 5. Regressions of above ground dry weight (g per pot) and number of reproductive units (per pot) from the summer experiment for the amphibious responder, (a) *M. variifolium*, the amphibious tolerator, (b) *Lythrum salicaria*, and the submerged species, (c) *V. gigantea*.

functional groups, being significant for an amphibious responder, amphibious tolerator and a submerged species.

4. Discussion

Duration of flooding had a strong influence on species composition in the summer experiment. Treatments with periods of flooding of 12–16 weeks had similar species abundance and numbers of reproducing species. In contrast, treatments with only short flooding (4 weeks) were more like the damp treatment. Whereas species composition differed, long periods of submergence or of a damp treatment allowed reproduction to occur in those wetland plants that established. Terrestrial species were only able to establish in damp treatments or those that moved quickly out of the water column as long periods of submergence did not favour their germination, establishment and reproduction. Treatments moving out of the water column completely had only a few fast-growing ephemeral species reproducing in summer (e.g. *Elatine gratioloides* and *Limosella australis*). During summer these two species had the high growth rate and rapid formation of floral parts necessary for reproduction to be completed prior to drying. In the autumn experiment predominantly terrestrial species established following emergence from the water column.

Any differences between summer and autumn establishment and reproduction will be due to differences in temperature, day length and light quality rather than changing seed viability as most species from these wetlands have persistent seed banks (Leck and Brock, 2000). Storage of seed bank material before germination in autumn did not led to a reduction in seed viability in the seed bank (Britton and Brock, 1994). In similar seed bank material, even after 5 years of repeated wetting, dry storage and then re-wetting the numbers of species emerging had not declined significantly (Brock, 1998; Leck and Brock, 2000). The number of species establishing and the above ground biomass were reduced in autumn compared with summer and this may be predominantly due to lower temperatures. Seabloom et al. (1998) reported that for annual wetland plants a reduction in day/night temperatures from $30\,^{\circ}\text{C}/20\,^{\circ}\text{C}$ to $15\,^{\circ}\text{C}/5\,^{\circ}\text{C}$, halved the species richness in a damp treatment, and had a significant effect on biomass in annual wetland plants. More than 10-fold reduction in plant biomass was found in damp and flooded treatments. A seasonal contrast was the presence of large numbers of *Juncus bufonius* seedlings that were a significant component of the biomass in the damp or drying treatments in autumn. This species was able to germinate and establish better than other species at the lower temperatures in autumn.

The near absence of sexual reproduction in the autumn experiment was either a result of shortening day length or low temperatures. A study of the interaction of day length and temperature on the growth and reproduction of the submerged plant, *Ruppia drepanensis*, found that temperature was more important than day length in determining whether reproduction occurred (Santamaría and Hootsmans, 1998).

The amphibious fluctuation responder species were the most likely to grow and reproduce in all the water regime treatments. However, the amphibious fluctuation tolerator species while present in all treatments but were only capable of reproducing in damp rather than submerged treatments. Prolonged submergence or immersion slowed or prevented reproduction for the amphibious fluctuation tolerator species. As the amphibious tolerators are

not able to respond morphologically to inundation there will be limits set on the depth of inundation tolerated by each species which is a direct function of the final height of the plants following establishment. Periods of inundation greater than about 4 weeks will lead to a submerged and amphibious-responder dominated population. Under deep flooding reproduction will occur only in submerged and amphibious responders. A depth limit may be set on the amphibious responders as they have to reach the air–water interface to sexually reproduce (Farmer and Spence, 1987; Robe and Griffiths, 1998).

The significant correlation between the number of reproductive units and the biomass of the plant has also been reported for annual terrestrial species, in a range of environments (Samson and Werk, 1986; Lovett-Doust, 1989). Moreover, studies by Grillas and Battedou (1998) in seasonal marshes in the Camargue, France have also found significant correlations between diaspore numbers and plant biomass. This correlation suggests that once a wetland plant has received the environmental cues to reproduce the greater the biomass that can be produced the more reproductive units are formed. This relationship held across a number of water regimes. Although no significant reproductive output occurred in the autumn experiment by 16 weeks, those species with vegetative biomass already formed would be able to produce large numbers of reproductive units when temperatures increased in spring. It should be appreciated that in these ephemeral wetlands a single season and water regime that is favourable to seed production will allow the transfer into the seed bank of adequate numbers of diaspores that will persist for many years (Bonis et al., 1995; Leck and Brock, 2000).

The composition of a plant community in these wetlands is primarily a function of the species composition of the seed bank and secondly by selection based on water regime at germination. This paper demonstrates that a further filter occurs by selection of those species able to reproduce and therefore contribute to the "next generation" seed bank. Wetland reproductive dynamics is strongly influenced by depth, duration and season of inundation. A range of flooding patterns is important in wetlands to establish not only a diversity of plant species but also to allow a diversity of plant species to reproduce. The species growing in this study arose from seed bank material collected at the edge of the wetland, a zone of high emergent wetland plant species-richness (Brock and Casanova, 1997). The results indicate that should a particular regime be imposed on this diverse seed bank material selection will take place for a particular suite of species. Permanent flooding or long periods of inundation will result in a submergent-dominated wetland, whereas, long periods of damp will lead to an amphibious-dominated community. This has particular implications for the conservation of species-richness in wetlands in agricultural areas (Brock and Jarman, 2000). Many wetlands if not drained are now restricted to relatively uniform water regimes. The maintenance of long periods of deep inundation will ultimately lead to low species richness and dominance of submerged species. Only a relatively small area on the edges of these permanently flooded wetlands will provide a zone where reproduction of fluctuation-tolerating or responding species can occur.

Acknowledgements

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