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How do depth, duration and frequency of flooding influence the establishment of wetland plant communities?

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Abstract

In many temporary wetlands such as those on the Northern Tablelands of New South Wales Australia, the development of plant communities is largely the result of germination and establishment from a long-lived, dormant seed bank, and vegetative propagules that survive drought. In these wetlands the pattern of plant zonation can differ from year to year and season to season, and depth is not always a good indicator of the plant community composition in different zones. In order to determine which aspects of water regime (depth, duration or frequency of flooding) were important in the development of plant communities an experiment using seed bank material from two wetlands was undertaken over a 16 week period in late spring–early summer 1995–1996. Seed bank samples were exposed to 17 different water-level treatments with different depths, durations and frequencies of flooding. Species richness and biomass of the communities that established from the seed bank were assessed at the end of the experiment and the data were examined to determine which aspects of water regime were important in the development of the different communities. It was found that depth, duration and frequency of inundation influenced plant community composition, but depth was least important, and also that the duration of individual flooding events was important in segregating the plant communities. Species were grouped according to their ability to tolerate or respond to fluctuations in flooding and drying. The highest biomass and species richness developed in pots that were never flooded. Least biomass and species richness developed in pots that were continuously flooded. Short frequent floods promoted high species richness and biomass especially of Amphibious fluctuation-tolerator species and Amphibious fluctuation-responder species that have heterophylly. Terrestrial species were able to establish during dry phases between short floods. Depth was important in determining whether Amphibious fluctuation-tolerator or Amphibious fluctuation-responder species had greater biomass. Longer durations of flooding lowered species richness and the biomass of terrestrial species. Experiments of this kind can assist in predicting vegetation response to water-level variation in natural and modified wetlands.

Introduction

Water regime is a major determinant of plant community development and patterns of plant zonation in wetlands. It can be described by the depth, duration, frequency, rate of filling and drying, timing and predictability of flooded and dry phases in a wetland (Bunn et al. 1997). Wetlands on the Northern Tablelands of New South Wales, Australia have a range of different catchment, soil, rainfall and temperature characteristics and so experience a variety of water regimes (Brock et al. 1994). The region receives precipitation from southern frontal weather systems which dominate in the winter and spring, and from northern low-pressure systems which dominate in the summer and autumn, so the wetlands can experience floods or droughts in any season. The range of wetlands, and the large inter-annual variation in water regime produce a variety of plant communities. The patterns of plant zonation in these wetlands can change from year to year and season to season as water levels fluctuate in space and time making it difficult to predict the composition of the littoral plant communities in relation to depth. Since European settlement of Australia there has been a decline in wetland abundance and health, with a general trend to increasing the stability of water regimes, creating wetlands that are more continuously wet or dry (Brock et al. 1999). Water regime variation is increasingly seen as important in maintaining wetland functioning and diversity in Australia (Mitchell & Rogers 1985; Brock 1986; Chesterfield 1986; Brock 1991; Roberts 1994; Rea & Ganf 1994; Bunn et al. 1997; Brock et al. 1999) so understanding how water regime affects plant communities can assist in managing wetlands more predictively (Brock & Britton 1995).

Alternating wet and dry periods affect plant establishment from the seed bank by stimulating or inhibiting germination (Brock & Britton 1995), by modifying oxygen availability in the soil, and subsequent concentrations of nutrients and toxic substances, by desiccating aquatic plants or inundating terrestrial plants, and by changing the light climate with depth changes (Mitchell & Rogers 1985). Numerous studies on individual species show different responses to these effects (e.g., van den Brink et al. 1995; Rea & Ganf 1994; Denton & Ganf 1994; Smith 1998), and competitive interactions among species are modified by water regime (Keddy & Reznicek 1986). Where wetlands are managed for particular outcomes (e.g., increased abundance of particular plant or animal species; high biodiversity) it is important to know which aspects of water regime are important and which are less crucial.

Components of water regime have been examined to determine their effect on plant processes. Season of inundation affected germination of wetland species, with highest germination and the greatest species richness in the autumn and spring, and least germination in the summer (Britton & Brock 1994). Tolerance of dry periods governed growth of emergent species, whereas reproduction is affected by both frequency and depth of fluctuations (Smith 1998). Roberts (1994) found that species richness on river banks was highest where drawdown had occurred, and where there was low within year variation in water level. The duration and depth of flooding affected individual emergent species distribution on European floodplains due to species tolerance of anoxia (van den Brink et al. 1995), and the frequency of flood disturbances can affect species richness when an intermediate frequency of flooding events creates establishment opportunities for species and prevents competitive exclusion (Bornette & Amoros 1996) consistent with the Intermediate Disturbance Hypothesis (Connell 1978). Prolonged flooding eliminates some species while favoring others (van der Valk 1994) and the depth of flooding can have a significant effect on species composition and biomass of establishing plants (Seabloom et al. 1999). Plant communities are more likely to respond to the history of water levels than the water level at the time of survey (Roberts 1994; Tabacchi 1995) and exotic species can be more sensitive to changes in hydrology than native species (Tabacchi 1995).

Many previous studies have been based on field surveys, individual species rather than communities, or riparian zones rather than wetlands, and have looked at vegetation patterns resulting from several years of changed water regimes. Plant community composition and zonation are a result of establishment of individual plants in the short term, and competitive interactions become more important in the established phase of community development. Much of the variation in water-level in wetlands can occur in a short time frame, especially when there are storm events and high rates of evaporation, or when a wetland is purposely drained or filled for other reasons. In this study the establishment of species germinating from a seed bank was examined to determine whether short term variation in depth, duration and frequency of flooding were important alone or in combination for the species composition and development of different wetland plant communities.

Methods

Experimental design

The experiment was set up as a randomised block design, with 17 water-regime treatments in each of six replicate tanks for two seed banks (204 pots in 12 tanks).

Each water-regime treatment was labeled with a code describing the treatment, and each treatment consisted of a combination of depth, duration and frequency of flooding, such that the depth treatments were 5 cm (shallow), 14 cm (medium) and 60 cm (deep); the duration treatments were 0 weeks, 4 weeks, 8 weeks, 12 weeks and 16 weeks; and the frequency treatments were never, once, twice and four times flooded. These treatments were modified from those of Smith (1998). A complete factorial design (45 treatments) was not attempted. Instead relatively realistic

Table 1. Water-regime treatments. Each treatment was labeled with a code (*x/y/z*), the first number (*x*) indicating depth, second number (*y*) indicating total duration and the third number (*z*) indicating frequency of flooding. Individual flooding durations are the length of time the treatment was flooded on any one occasion (i.e., $y \div z$)

Treatment label	Depth of flooding (cm)	Total duration of flooding (weeks)	Frequency of flooding (times)	Individual flood durations (weeks)
5/4/2	5	4	2	2
14/4/2	14	4	2	2
60/4/2	60	4	2	2
5/8/2	5	8	2	4
14/8/2	14	8	2	4
60/8/2	60	8	2	4
5/12/2	5	12	2	6
14/12/2	14	12	2	6
60/12/2	60	12	2	6
5/8/1	5	8	1	8
14/8/1	14	8	1	8
60/8/1	60	8	1	8
5/8/4	5	8	4	2
14/8/4	14	8	4	2
60/8/4	60	8	4	2
14/16/1	14	16	1	16
0/0/0	Not flooded	0	Never	0

combinations of these water-regime variables were selected (Table 1). Treatment combinations equate to a number of possible field conditions, except for the most frequent fluctuations and deepest depths (e.g., 60/4/2, 60/8/4), as natural rates of drawdown are likely to be slower. These treatments were included to allow comparison of frequencies and durations at different depths. All treatments (except treatment 0/0/0 – never flooded) were started under water, and finished out of water and the depth changes were implemented incrementally. Three of these water regimes are illustrated (Figure 1). Depths given refer to the maximum depth reached for that treatment. Water level treatments were originally designed to allow isolation of the effects of depth, frequency and duration of inundation such that treatments 5/8/2, 14/8/2 and 60/8/2 differed only in depth of flooding, treatments 5/4/2, 5/8/2 and 5/12/2 differed only in total duration of flooding and treatments 5/8/1, 5/8/2 and 5/8/4 differed only in frequency of flooding. The experiment was conducted over 16 weeks because this time period encompassed a large proportion of the growing season and there was sufficient time for plants to establish whereas competitive effects would be minimised.

Sites and seed banks

Seed bank material was collected from two shallow freshwater wetlands on the Northern Tablelands of New South Wales Australia: A near-permanent wetland: Llangothlin Lagoon (30°04′ S, 151°46′ E) and an intermittent wetland: Racecourse Lagoon (30°39′ S, 151°30′ E). Both are found above 1000 m above sea level, and have relatively unmodified water regimes (Casanova & Brock 1990; Brock 1991; Brock *et al.* 1994). Wetlands such as these are scattered along the top of the Great Dividing Range in Northern New South Wales. They are characteristically found on basalt derived soil and are thought to be Pleistocene deflation basins (Haworth et al. 1999). A variety of depths, catchment sizes and soil conditions has produced a range of water regimes within the wetlands. The two wetlands selected (near-permanent and intermittent (Boulton & Brock 1999)) represent two extremes of natural water regime and both possess diverse, species-rich seed banks (Brock 1998). The near-permanent wetland dries only during extreme droughts although the edges of the wetland experience water level fluctuations several times in a season, whereas the intermittent wetland is more temporary

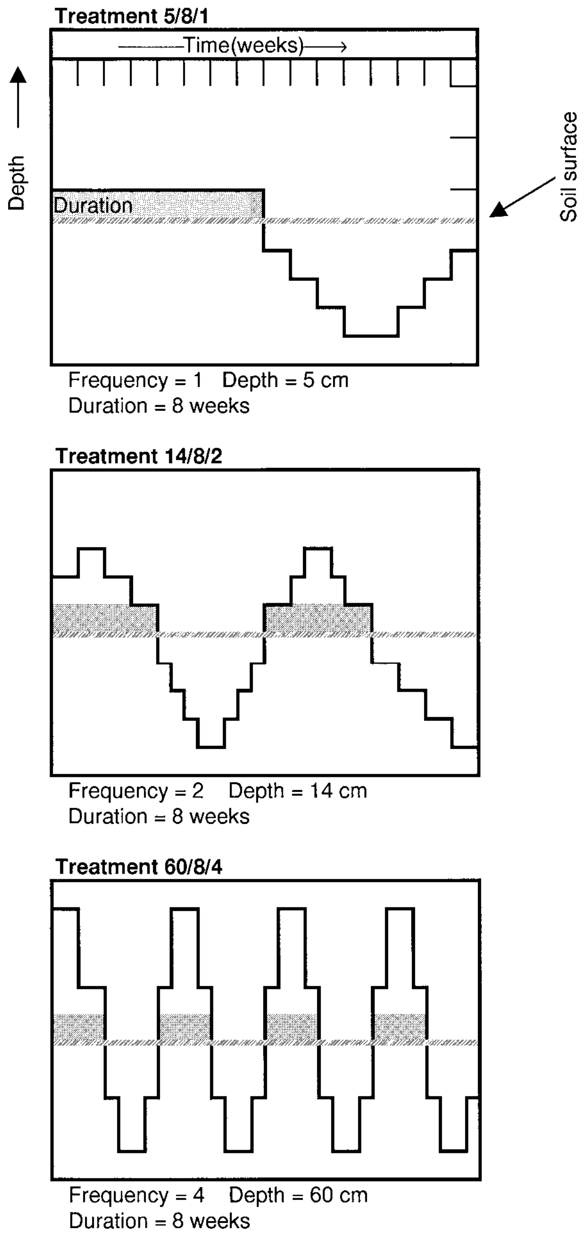

Figure 1. Three examples of the 17 water-regime treatments illustrated diagrammatically. Time (in weeks) is represented along the *x*-axis, so that total duration of flooding is illustrated by the shaded portion of the figure, depth is represented along the y-axis so that depth increases with distance above the line representing soil surface, and height out of the water increases with distance below the line representing the soil surface.

Table 2. Species occurrence (×) in the seed bank of each wetland (the intermittent wetland and the near-permanent wetland) and classification into groups defined in Table 3 (Brock & Casanova 1997).

Species name	Near-permanent	Intermittent	Classification
Agrostis avenacea	×	×	ATe
Alternanthera nana	×	×	Tda
Amphibromus sp	–	×	ATe
Bidens pilosa	–	×	Tdr
Bromus catharticus	–	×	Tdr
Carex spp	–	×	ATe
Centaurium erythraea	–	×	Tda
Centipeda minima	×	–	ATl
Chara fibrosa	–	×	S
Chara muelleri	×	×	S
Chenopodium pumilio	×	×	Tdr
Cirsium vulgare	–	×	Tdr
Conyza bonariensis	×	×	Tda
Crassula helmsii	×	–	ARp
Cynodon dactylon	–	×	Tdr
Cyperus eragrostis	–	×	ATe
Cyperus sanguinolentus	×	×	ATe
Cyperus sp	–	×	ATe
Echinochloa crus-galli	×	–	Tda
Elatine gratioloides	×	×	ARp
Eleocharis acuta	–	×	ATe
Eleocharis deitrichiana	–	×	ATe
Eleocharis pusilla	×	×	ATe
Eleusine tristachia	×	×	Tdr
Eragrostis trachycarpha	×	×	Tda
Geranium sp	–	×	Tdr
Glossostigma cleistanthum	×	–	ARp
Glyceria australis	×	×	ATe
Gnapthalium spp	×	×	Tdr
Holcus lanatus	–	×	Tda
Hydrocotyle tripartita	×	×	ATl
Hyperchoerus radicata	–	×	Tdr
Hypericum japonicum	×	×	Tda
Isoetes muelleri	×	–	S
Isolepis sp	–	×	ARp
Isotoma fluviatilis	×	–	ATl
Juncus articulatus	×	×	ATe
Juncus bufonius	×	×	Tda
Juncus pin	×	×	Tda
Lilaeopsis polyantha	–	×	ATe
Limosella australis	×	×	ARp
Lipocarpha microcephala	–	×	ATe
Lythrum salisarcia	–	×	ATe
Marsilea mutica	–	×	ARp
Medicago spp	×	×	Tda
Mimulus peruviana	–	×	ATe
Modiola caroliniana	–	×	Tdr
Myriophyllum variifolium	×	×	ARp
Myriophyllum verrucosum	–	×	ARp

Table 2 continued.

Species name	Near-permanent	Intermittent	Classification
Najas tenuifolia	–	×	S
Nitella cristata	×	×	S
Nitella sonderi	×	–	S
Nitella subtilissima	×	–	S
Oxalis sp	×	×	Tdr
Panicum gilvum	×	×	Tda
Paronychia brasiliana	–	×	Tdr
Persicaria decipiens	–	×	ATe
Persicaria hydropiper	–	×	ATe
Persicaria prostrata	–	×	Tda
Plantago lanceolata	–	×	Tdr
Polygonum arviculare	×	–	Tdr
Polygonum plebium	×	–	Tdr
Portulaca oleracea	–	×	Tdr
Potamogeton tricarinatus	–	×	ARp
Ricciocarpus natans	×	×	ARf
Rorippa palustris	×	–	Tda
Rumex crispus	×	×	Tda
Schoenoplectus validus	–	×	ATe
Schoenus apogon	–	×	ATe
Sonchus oleraceus	×	×	Tdr
Trifolium spp	×	×	Tda
Typha orientalis	–	×	ATe

and is dry approximately three years in five. Water level data has been collected on a regular basis for these wetlands over more than a decade.

Seed bank material was chosen as a starting point for examination of plant community responses to water regime because the species representation in each seed bank was well-known (Britton & Brock 1994); each well mixed seed bank contained a larger suite of species than could be feasibly obtained by harvesting the seeds or spores; the ease or difficulty of obtaining seedlings or sporelings did not bias the selection of species for the experiment; and we could compare our experimental results directly with the results of field surveys. As well, few species in these wetlands rely on vegetative propagules for reproduction or regeneration following drought. Species that germinated from each seed bank in this experiment are listed in Table 2.

Experimental procedure

The experiment was run in a set of 12 outdoor tanks (800 l capacity) at the University of New England, Armidale, New South Wales, Australia from 15 December 1995 to April 9 1996. Tanks were uncovered and exposed to rainfall which was an average of 25 mm per week over that period. Temperatures varied from 4 to 40 °C in the air and 13 to 31 °C in the water. Tanks were filled with tap water (average pH 7.2 to 9.6; conductivity 250 to 360 μS cm^{-1}) and flushed regularly by draining and overflowing to maintain clarity. Tap water characteristics were similar to the pH and conductivity found in Llangothlin and Racecourse Lagoons (Casanova 1993).

Seed bank material was collected from the near-permanent wetland in October 1995 and the intermittent wetland in November 1995. Soil was collected by removing the top 0.02 to 0.05 m of soil in 0.01 m^2 patches over a 20 m wide transect running from the shore of the lagoon into the water to a depth of 0.2 m (approximately 0.25 m^3 for each soil). Each sample was mixed well, sieved through a 2 mm sieve to remove plant vegetative material, dried in the sun and stored dry until it was used in the experiment. Drying has been shown to enhance germination of many species from the seed bank of these wetlands (Brock 1991; Brock et al. 1999).

Experimental pots (170 mm diameter × 170 mm deep) were partly filled with clean river sand and topped with a 2.5 cm layer of seed bank material leveled at the top of each pot. No germination was recorded from the river sand during the experiment. Each pot was suspended by a chain and hook from a steel frame above the tanks, and the water-level for each pot was independently adjusted by raising or lowering the pot on its chain. Each tank had pots containing one soil type to prevent cross contamination of seed banks and each tank had all 17 water level treatments imposed concurrently within it. At the start of the experiment all pots were hung with the surface of the pot 1–2 cm above the surface of the water for 16 hours so that the soil could saturate before the pots were flooded. Treatments were then implemented and the position of pots in the water adjusted twice a week. This design meant that the water level treatments could be randomised within the tanks, which enabled statistical comparison of water regime and the interactions among the treatments.

The experiment was harvested from April 9–19 1996. The number of individual plants was counted where possible and the reproductive status of each species was assessed. The above-ground plant material was removed at the soil surface and separated by species into paper bags. Plants were dried at 80 °C in

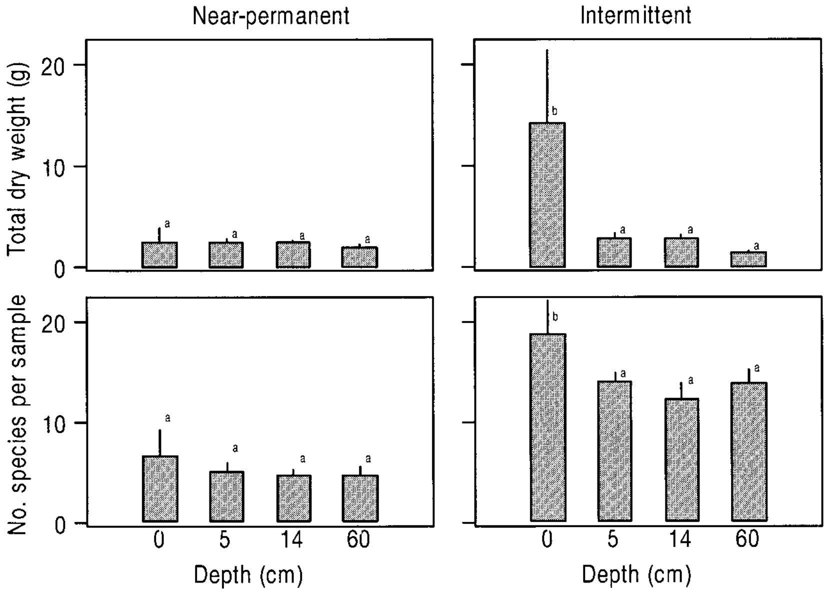

Figure 2. Total dry weight and species richness for the near-permanent and the intermittent wetlands in relation to maximum depth of flooding. Values are the averages of all pots that were exposed to each depth, error bars indicate the standard error of the mean. Different lower case letters indicate significant differences among the treatments.

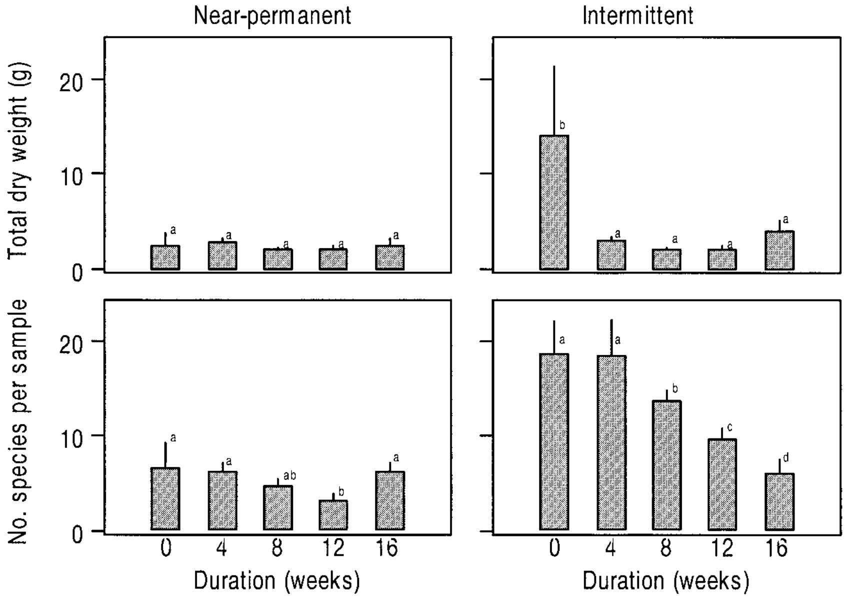

Figure 3. Total dry weight and species richness for the near-permanent and the intermittent wetlands in relation to total duration of flooding. Values are the averages of all pots that were exposed to each depth, error bars indicate the standard error of the mean. Different lower case letters indicate significant differences among the treatments.

an oven for at least 24 hours, cooled in a desiccator then weighed. Any plants that had died and remained in the pots were also identified and weighed and their reproductive status determined. Only species with dry weights greater than 0.01 g were used in subsequent analyses. This excluded newly germinated individuals that had not yet established. *Medicago* spp and *Trifolium* spp were grouped for analysis as 'terrestrial pasture legumes'. The other plant species were identified to species for the analysis except where similarity of congeners prevented identification (e.g., *Gnapthalium* spp).

Analysis

Differences among the means of treatments were detected using univariate analyses (analysis of variance, generalised linear model analysis of variance for unbalanced designs, least significant difference) with Minitab (Anon. 1993). Species biomass' were analysed with multivariate analyses to detect whether different plant communities developed under different treatments. Relationships among treatments for both the near-permanent wetland seed bank and the intermittent wetland seed bank were detected using hierarchical cluster analysis (association using the Gower metric, and fusion using flexible unweighted pair-group method with arithmetic means (UPGMA) with $\beta = -0.1$). The characteristics of the treatments were further investigated by discriminant analysis with BMDP 7M (Dixon et al. 1990) which determined significantly different treatments and the species that best separated the treatment groups. Species were assigned to species groups (Table 3) following the criteria of Brock & Casanova (1997).

Results

Species richness and biomass for depth, duration and frequency

The main effects of depth, duration and frequency of inundation were averaged over other effects for direct comparison of their influence on the number of species that established from the seed bank and the total above-ground biomass of all species.

There was no significant difference among the different depth treatments (average of treatment 0/0/0 compared to the average of treatments 5/4/2, 5/8/2, 5/12/2, 5/8/1 and 5/8/4 (5 cm), treatments 14/4/2, 14/8/2, 14/12/2, 14/8/1 and 14/8/4, (14 cm) and treatments 60/4/2, 60/8/2, 60/12/2, 60/8/1 and 60/8/4 (60 cm)) for either biomass or species richness for the near-permanent wetland seed bank, whereas there were significantly more species and greater biomass in the damp treatment (treatment 0/0/0), than in any other treatment for the intermittent wetland seed bank (Figure 2).

When treatments were averaged over the duration of inundation there was no significant difference among different treatments in the biomass of species establishing from the near-permanent wetland seed bank, but significantly lower average species richness in pots that had been inundated for 12 weeks (treatments 5/12/2, 14/12/2, 60/12/2) than pots that were inundated for four weeks (treatments 5/4/2, 14/4/2, 60/4/2), never or always inundated (treatments 0/0/0 and 14/16/1). A similar trend was observed for the intermittent wetland seed bank, where (except for durations of four weeks or less) there was a general decline in species richness with longer flooding treatments, and the highest biomass was found in the treatment that was never flooded (Figure 3).

When treatments were averaged over frequency of flooding there was no significant difference for either species richness or biomass for the different flooding frequencies for the near-permanent wetland seed bank, but for the intermittent wetland seed bank the highest biomass and greatest species richness were found in pots that were never flooded (treatment 0/0/0). For the intermittent wetland seed bank the lowest species richness was found in the treatment that was always flooded (treatment 14/16/1) and intermediate species richness in the pots that experienced fluctuations (i.e., were flooded once, twice or four times) (Figure 4).

Community development in relation to water regime

Initial cluster analysis showed that the 17 different water regimes resulted in several different communities. The statistical significance of these results was examined using hierarchical discriminant analysis. The magnitude of the difference between treatments 14/16/1 and 0/0/0 for both soils had a strong influence on the clustering of the other treatments (Figures 5a, 5b), so the analysis was repeated with 14/16/1 and 0/0/0 excluded (Figures 5c, 5d). In these analyses for the near-permanent wetland seed bank there were significant differences among treatments 5/4/2 and 14/4/2 (shallow and medium flooding twice for two weeks each time), treatment 60/4/2 (deep flooding twice for

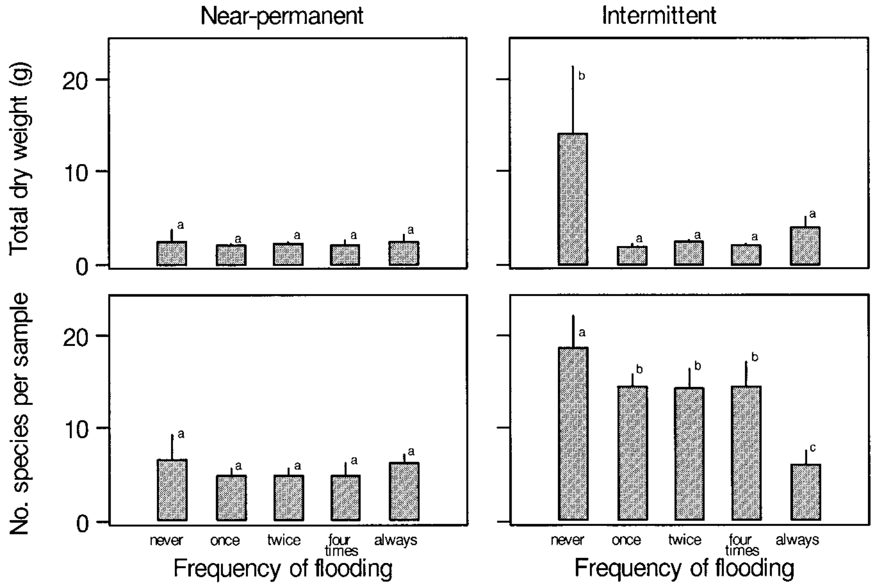

Figure 4. Total dry weight and species richness for the near-permanent and the intermittent wetlands in relation to frequency of flooding. Values are the averages of all pots that were exposed to each depth, error bars indicate the standard error of the mean. Different lower case letters indicate significant differences among the treatments.

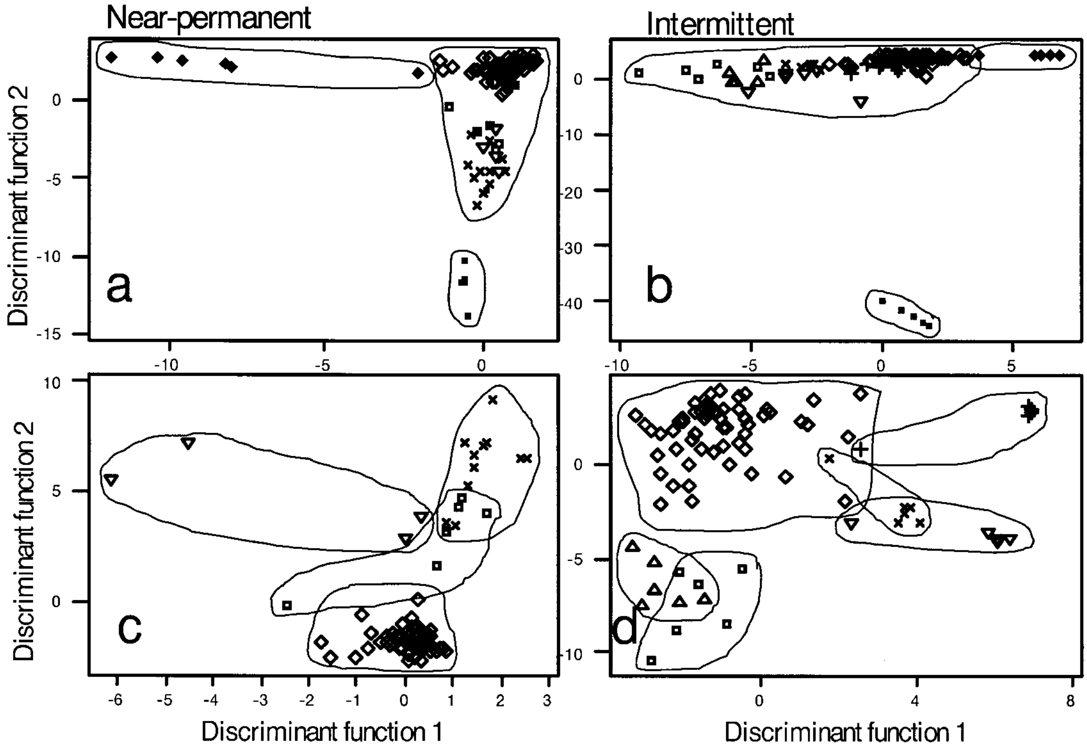

Figure 5. Scatter plots indicating separation among community groups as determined by Discriminant analysis. (a) and (c) the near-permanent wetland seed bank. Depth/duration/frequency treatment symbols: X, 5/4/2 & 14/4/2; ▽,60/4/2; □, 5/8/4; ●, 14/16/1; ■, 0/0/0; ◇, all other treatments. b) and d) the intermittent wetland seed bank. Depth/duration/frequency treatment symbols: X, 5/4/2; + 14/4/2; ▽,60/4/2; □, 5/8/4; △, 14/8/4, ●, 14/16/1; ■, 0/0/0; ◇, all other treatments. In figures (c) and (d) treatments 14/16/1 and 0/0/0 were excluded from the analysis.

Table 3. Classification of species that occurred in field surveys and established under experimental conditions into seven species groups after Brock & Casanova (1997).

Primary category	Secondary category	Description
Terrestrial	Dry species: Tdr	Species which germinate, grow and reproduce where there is no surface water and the water table is below the soil surface
Terrestrial	Damp species: Tda	Species which germinate, grow and reproduce on saturated soil
Amphibious fluctuation-tolerators	Emergent species: ATe	Species which germinate in damp or flooded conditions, which tolerate variation in water-level, and which grow with their basal portions under water and reproduce out of the water
Amphibious fluctuation-tolerators	Low-growing species: ATl	Species which germinate in damp or flooded conditions, which tolerate variation in water-level, which are low-growing and tolerate complete submersion when water-levels rise.
Amphibious fluctuation-responders	Morphologically plastic species: ARp	Species which germinate in flooded conditions, grow in both flooded and damp conditions, reproduce above the surface of the water, and which have morphological plasticity (e.g. heterophylly) in response to water-level variation.
Amphibious fluctuation-responders	Species with floating leaves: ARf	Species which germinate in flooded conditions, grow in both flooded and damp conditions, reproduce above the surface of the water, and which have floating leaves when inundated.
Submerged: S	–	Species which germinate, grow and reproduce underwater

two weeks each time) treatment 5/8/4 (shallow flooding four times for two weeks each time) and all the other treatments (Figure 5c).

For the intermittent wetland seed bank when treatments 14/16/1 and 0/0/0 were excluded from the analysis, treatments 5/4/2, 14/4/2 and 60/4/2 were significantly different from each other, as were treatments 14/8/4 and 60/8/4 (medium and deep flooding four times for two weeks each time), and they were all different from the treatments that received floods of greater than two weeks individual duration (Figure 5d).

Functional groups in plant communities

The contribution of different species functional groups (as defined in Table 3; Brock & Casanova 1997) to each plant community (as determined by discriminant analysis) was assessed (Figure 6). Overall the near-permanent wetland was dominated by the Amphibious fluctuation-responder group, most of which consisted of *Limmosella australis* and *Glossostigma cleistanthum,* and the Amphibious fluctuation-tolerator group, represented by *Cyperus sanguinolentus* and *Eleocharis* spp. The continuously damp treatment (0/0/0) was dominated by pasture legumes and terrestrial grass species (e.g., *Panicum*, *Eleusine*) and the continuously flooded treatment (14/16/1) was dominated by Submerged and Amphibious fluctuation-tolerator species. The treatments that received greater than two weeks individual flooding events were dominated by the Amphibious fluctuation-responder species and the treatments that received two weeks individual flooding durations (5/4/2 and 14/4/2, 60/4/2 and 5/8/4) were dominated almost equally by Amphibious fluctuation-responder and Amphibious fluctuation-tolerator species. A similar pattern existed for the intermittent wetland except that the dominant Amphibious fluctuation-responder species in all pots was *Myriophyllum variifolium,* and the Terrestrial-damp group of species made a contribution to most communities.

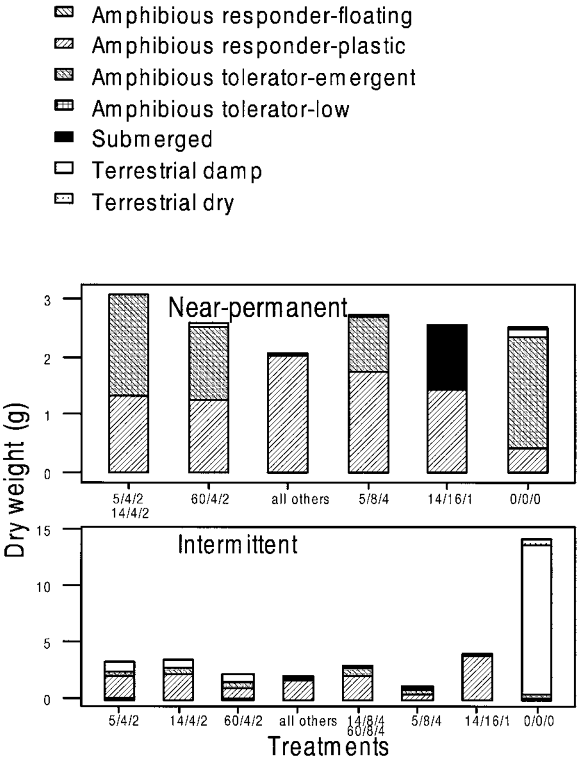

Figure 6. Dry weight per pot for each significant treatment group (based on discriminant analysis). Weights are divided into species functional groups (after Brock & Casanova 1997), see Table 3 for group definitions.

The overall pattern of results has been summarised in Figure 7. When the seed bank was dampened seeds were stimulated to germinate (Figure 7a). If the seed bank remained damp without drying or flooding the vegetation that developed was dominated by Terrestrial-damp and Terrestrial-dry species (Figure 7b). This treatment had the highest species richness and biomass, although individual species typically had low individual biomass. If the seed bank was flooded the seeds of submerged species were stimulated to germinate, and if it remained flooded these species ended up dominating the vegetation, although some Amphibious fluctuation-responder species survived (Figure 7c). Seed bank that was subject to slow fluctuations in water-level with periods of inundation exceeding two weeks had a low species richness (Figure 7d). Although Terrestrial-damp species were present in these pots Amphibious fluctuation-responder species dominated. Seed bank that was subject to fluctuations in water-level of less than two weeks duration in any one flooding event were dominated by Amphibious fluctuation-responder, Amphibious fluctuation-tolerator and Terrestrial-damp species (Figure 7e). If there were more than two fluctuations then the biomass of Terrestrial-damp species was lower (Figure 7f). Depth was important in determining the characteristics of the plant community when there were many short fluctuations. At shallower depths (5 cm, 14 cm) Amphibious fluctuation-tolerator species were most abundant, at deeper depths (60 cm) Amphibious fluctuation-responder species were favored.

Discussion

Depth, duration and frequency of flooding all affected plant community development in some way, although for the near-permanent wetland seed bank only different durations of flooding were significant when the main effects of each aspect of water regime were examined. Segregation of plant communities in the near-permanent wetland was apparent following multivariate analysis of the individual species contributions to the total biomass in each of the treatments. The plant communities in the intermittent wetland responded to each main factor alone. Aquatic seed banks can be diverse, allowing temporal as well as spatial segregation of plant communities (van der Valk & Davis 1976; Schneider 1994). Under stable water levels there is the development of zonation of plant communities in relation to depth, a pattern which can be maintained through development of a zoned seed bank (van der Valk & Davis 1978). The development of plant communities in this sort of experiment is primarily dependent on the composition and viability of the seed bank present in the soil. Different water regimes can select for different plant communities only if the seed bank contains the potential for different plant communities to develop. The seed bank of a very stable or species-poor site might allow only a single plant community to develop, whereas the seed bank of the two sites selected for this experiment allowed several different communities develop, depending on the water regime imposed.

A large proportion (60%) of the terrestrial species establishing from the intermittent wetland seed bank were exotic species. Invasion of exotic terrestrial species may be a consequence of the longer dry periods that are part of the natural water regime of this wetland. Exotic species were found to be more sensitive to changes in hydrology than native species in Europe (Tabacchi 1995), and this is likely to be so

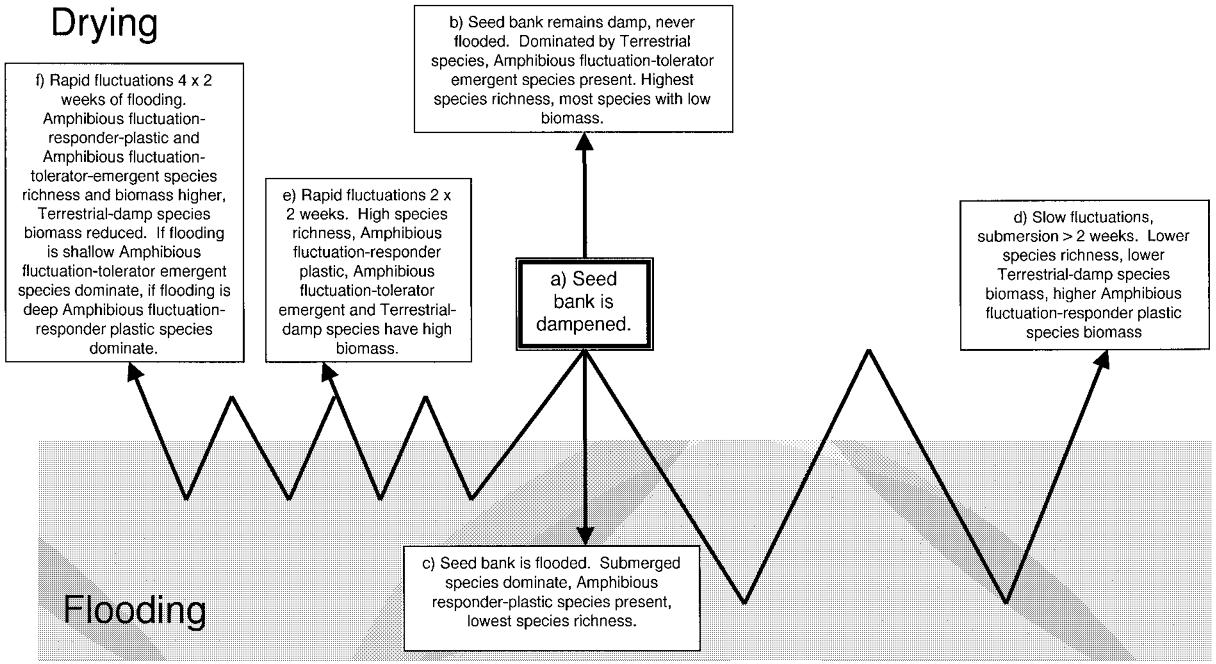

Figure 7. Diagrammatic outline of how different wetland communities established in response to water-level fluctuations. Only treatment combinations that produced significantly different communities are illustrated. (a) Initially the seed bank was flooded then (b) kept damp, (c) flooded for 16 weeks, (d) exposed to fluctuations of greater than two weeks individual flooding durations, (e) exposed to two fluctuations of individual durations of two weeks, (f) exposed to four fluctuations of individual durations of two weeks.

here, for few exotic species established well in anything but the damp treatment. The near-permanent wetland, in contrast, is rarely dry for long periods (only approximately 10 times in the last 100 years; Brock et al. 1994), although the littoral zone from which the seed bank sample was collected floods and dries more frequently. This wetland seed bank had a much smaller contribution from both terrestrial and exotic species to the biomass of the damp treatment.

Of the three factors examined, depth alone was the least important in determining plant community development when water levels fluctuate. Once a site is flooded anoxic conditions may develop in the soil and plants respond to water as the medium of growth. These conditions vary little with depth. Variation in depth affects light quality and quantity and the ability of emergent plants to reach the surface. In this experiment variation in light is unlikely to have influenced plant community development because high water clarity was maintained. The only significant effect of depth in isolation of other effects was differentiation of treatments that experienced waterlogged soil (in which a combination of Amphibious and Submerged species established), and the treatment that did not flood at all (treatment 0/0/0), in which Terrestrial-dry and Terrestrial-damp species along with drought-tolerant Amphibious species established. It is clear from the literature that different species can be expected to have different depth tolerances under stable water regimes (e.g. Spence 1967; Seabloom et al. 1998), however, in this experiment when water levels fluctuated, absolute depth was less important than frequency of fluctuations and duration of flooding.

There was a gradual decline in species richness under longer durations of flooding for the intermittent wetland seed bank. Submerged species made up the greatest proportion of species in the pots flooded for the longest duration, and there is a particularly rich suite of species represented in the seed banks of the two lagoons, including charophytes (Britton & Brock 1994). With shorter durations of flooding there was time for Amphibious species to germinate and establish between flooding events, and shorter durations of anoxia during the flooding events for terrestrial species to tolerate. Survival at the intermediate durations requires tolerance of both emersion and immersion. Only the Amphibious groups of species have adaptations for both these conditions. For the intermediate durations of flooding there was survival of species that could tolerate both extremes as well as establishment of both terrestrial and submerged species during dry and flooded phases of the fluctuating water levels. Duration of flooding is often correlated with depth, longer durations being a consequence of deeper flooding.

Frequency of flooding had an effect on species richness and biomass for plants establishing from the intermittent wetland seed bank, but once again the response was dominated by the high biomass and species richness in the pots that were never flooded (treatment 0/0/0), and the low biomass and species richness in the pots that were always flooded (Treatment 14/16/1). There was no significant difference among pots that were flooded for different frequencies. This is comparable to a study by Bornette et al. (1994) in which it was found that a habitat templet based on flood frequency was not as useful in predicting species richness in Rhone River wetlands as other aspects of water-level fluctuations. Flood frequency in riparian wetlands is usually closely linked with flood depth and duration (high frequency of short shallow floods verses low frequency of long deep floods) and so the effects of frequency can be difficult to isolate. In this experiment we had floods of the same frequency but different depth and total durations of flooding. The lowest flooding frequency (never flooded) had the highest species richness but all other flooding frequencies (except permanently flooded 14/16/1) had low species richness.

When overall community response to individual water regime treatments was assessed using multivariate analysis it was found that several different plant communities developed from the seed banks, and that the segregation of communities in relation to treatments was similar for both the near-permanent and the intermittent wetland seed banks. Duration of flooding is of great predictive value in wetlands (van der Valk 1981), a concept supported by this study. However the major factor that determined separation of the plant communities was not the total duration, frequency or depth of flooding, rather it was the duration of individual flooding events that correlated best with the groupings of treatments. Flooding events of two weeks at a time produced one plant community, flooding events of longer than two weeks produced a different plant community. Both of these community types were secondarily segregated by flooding depth and frequency of flooding. Depth can be important for individual emergent species since these species can tolerate anoxic soils when culms or leaves remain in the air (van der Valk 1994). For low-growing species all depths are essentially equal, and for Amphibious fluctuation-responder species the duration of each flooding event will determine if there is time for plants to respond (by changing leaf morphology or elongation of stems) to flooded or dry conditions. Amphibious plant response times can however, be much shorter than two weeks, especially when the response involves stem elongation.

The dry phase of the fluctuations was also an important influence on the survival of different species under the different water regime treatments. Long dry phases (short flooding durations) gave an opportunity for terrestrial species to establish. It was the large contribution of Amphibious fluctuation-tolerator species (in the near-permanent wetland seed bank) and the Amphibious fluctuation-tolerator and Terrestrial-damp species (for the intermittent wetland seed bank) under the longer dry phases (shorter flooding durations) that caused the separation of these treatments from the group of treatments with longer individual flooding durations. The Amphibious fluctuation-tolerator species were largely species of *Eleocharis* and *Cyperus* for these two wetland seed banks, and while those species apparently prefer to grow under damp conditions, their emergent morphology allowed them to tolerate short periods of submergence.

The two wetland seed banks developed slightly different plant communities under the same regimes because of the different suites of species in the seed banks (Brock & Casanova 1997). The main effects of treatments were less marked for the near-permanent wetland seed bank than for the intermittent wetland seed bank, possibly because the latter soil was of lower fertility (having a higher sand content) than the near-permanent wetland soil. Weiher & Keddy (1995) found that there was higher species richness under low-fertility in combination with treatments, possibly because competition is reduced under those conditions. The major difference between the results for the near-permanent and the intermittent wetland seed banks was the high contribution of Terrestrial species to the intermittent wetland. This may be because the natural water regime (dry periods of 2–3 years, followed by wet periods of 2–3 years) of this wetland favors the invasion of terrestrial species and the development of a terrestrial species seed bank.

Our study was similar to the filter concept study of Weiher & Keddy (1995), but because we used natural seed banks the change in species richness was not only subtractive (i.e., removal of species that did not establish after the initial germination stimulus) but also additive (other species were stimulated to germinate under subsequent conditions). While we cannot interpret the results in terms of environmental filters (e.g., one fluctuation removes x species, two fluctuations remove $x + y$ species) the design of the experimental facilities could allow this sort of experiment. Completion of the experiment within 16 weeks prevented the maturation of perennial species, and possibly reduced the effects of competition in the pots (cf., Smith & Brock 1996). We were therefore restricted to examining the establishment of communities rather than long-term community development. However, because natural wetlands do experience water-level fluctuations on a similar time frame, and community development is largely from the seed bank, the results are useful for management decisions in wetlands.

The development of plant communities under natural, fluctuating water regimes is a consequence of many factors, including grazing by invertebrates and vertebrates, competition among species, pathogen activity and individual plant tolerance of or response to the stresses of flood and drought. Despite this, studies like this can allow us to cautiously interpret vegetation response to historical water regimes, as well as to develop hypotheses about the consequences of water regime modification.

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