Are flood plain–wetland plant communities determined by seed bank composition or inundation periods?

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Abstract Vegetation zonation patterns are a common feature in flood plain–wetland complexes and are important to the biodiversity and functioning of such systems. The purpose of this paper is to identify links between water regime, seed bank and the establishment of zoned vegetation communities in a series of small distributary channels within the Narran Lakes flood plain–wetland complex, eastern Australia. Seed bank material from three distinct plant community zones within three distributary channels were collected and subjected to five inundation treatments over a period of 12 weeks to test the effects of location and inundation regime on the abundance of seedlings, species richness and species assemblages. The results of this study indicate that the water regime determines which species germinate and the seed bank influences the abundance of plants to emerge. This study provides insight into the implications of changing flooding regimes on plant community composition in flood plain–wetland systems.

Key words community composition; flood plain; inundation regime; vegetation patterns

INTRODUCTION

A floristic feature of flood plain–wetlands is the distribution of plant species in well-defined zones (Spence, 1982). These patterns occur at a variety of spatial scales and are thought to be driven by spatial variations in water regime (Brock & Casanova, 1997). Water regime has been defined by Rea & Ganf (1994) as continually changing water depth over time, including dry periods, and encompasses the duration, frequency, rate, magnitude, timing and predictability of inundation. In flood plain–wetlands, all these variables are influenced by the flow regime of the parent river (Thoms & Parsons, 2003).

In ephemeral systems, extended dry periods mean that the persistence of aquatic and semi-aquatic vegetation communities is dependent upon the presence of a viable seed bank (Leck & Brock, 2000). Previous studies on ephemeral and temporary wetland systems indicate that seed banks are relatively homogeneously distributed across elevation gradients (e.g. Haukos & Smith, 1993). Accordingly, spatial variation in plant species distributions would need to arise as a result of germination responses

to spatially variable water regimes. However, some studies suggest that the seed banks themselves are spatially variable (Bonis *et al.*, 1995), in which case spatial variation in species composition could arise regardless of a spatially variable germination response to inundation.

The response of flood plain–wetland plant communities to alterations in water regime brought about by water resource development will depend on whether vegetation zones are a product of a spatially variable seed bank or a germination response to the wetting regime. Therefore, understanding ecological responses to variations in flow (water regime) are paramount for improved flow management (Reid & Quinn, 2004). For flood plain–wetland plant communities, this knowledge requires an understanding of the mechanisms that underlie existing species distributions.

This study aims to elucidate the links between water regime (wetting and drying periods), germination and the establishment of zoned vegetation communities across an elevation gradient. A mesocosm experiment was undertaken to determine if vegetation zonation patterns seen in the distributary channels of the Narran Lakes flood plain–wetland complex, Australia, are a product of spatial differences in the seed bank or a response to differing periods of inundation, or a combination of the two.

METHODS

Study area

The Narran Lakes is a large (46 km^2) terminal flood plain–wetland of the Narran River situated in eastern Australia. The Narran Lakes complex incorporates several lakes (Clear Lake, Back Lake, Long Arm and Narran Lake) and large intervening flood plains that are dissected by an extensive network of smaller distributary channels. The climate is semiarid and the complex is subject to a highly variable and unpredictable hydrological regime. On average, the Narran Lakes fill about once in every two to five years following heavy rainfall in the upstream catchment.

The main vegetation communities of the area include riparian open forests and woodlands, predominately River Red Gum (*Eucalyptus camaldulensis*), Coolibah (*Eucalyptus coolabah*), Black Box (*Eucalyptus largiflorens*) and River Cooba (*Acacia stenophylla*), which occur in higher elevation areas around the lakes and along distributary channels. Areas of dense Lignum (*Muehlenbeckia florulenta*) and small patches of Common Reed (*Phragmites australis*) occur in and around the lakes. Following the recession of floodwaters a diverse mix of sedges and ephemeral herb fields occupy the lakebeds and distributary channels (Thoms *et al.*, 2002).

Three distinct zones of vegetation communities occur within channels of the distributary network along an elevation gradient. The first zone, which extends from the edge of the channel to halfway down the bank is dominated by a bright yellow vine, *Cuscuta campestris* Yucker, and is termed the "Yellow zone". The second zone, termed the "Green zone", is dominated by *Polygonum plebieum* R. Br. and extends from mid-bank to the edge of the channel bed. These first two zones are replicated on both sides of the channel. The final zone, which is dominated by Creeping Heliotrope (*Helitropium supinum* L.), covers the channel bed (lowest elevation) and is termed the "Mint zone".

Study design

Soil samples were collected from each of the three vegetation assemblage zones at three distributary channel sites within a 1 km radius of each other. Samples from each collection point were subjected to five inundation treatments in a fully crossed two-factor (zone × treatment) randomized block design with treatments blocked across elevations at each site, totaling 45 samples. Thus, the study was designed to investigate the effects of inundation and elevation on germination and growth of plants. Dependent variables tested were species richness, seedling abundance and species assemblage.

Treatments were based on the range of possible inundation durations that could be experienced within the distributary channels (Thoms *et al.*, 2002). The experiment was conducted over 12 weeks since this period gives sufficient time for plants to establish and be identifiable (Casanova & Brock, 2000). The treatments applied were:

(1) submerged 12 weeks;
(2) waterlogged 12 weeks;
(3) submerged 4 weeks, waterlogged 8 weeks;
(4) submerged 4 weeks, waterlogged 4 weeks, dry 4 weeks;
(5) waterlogged 6 weeks, dry 6 weeks.

In this experiment the term "submerged" refers to a water depth of 2.5 cm, "waterlogged" refers to soil that is completely saturated but with no surface water, and "dry" indicates that no watering was done and the pots were left to dry out naturally.

Field

Transects extending from the lignum-herb field boundary (highest elevation) to the centre of the channel were established at three distributary channel sites. Vegetation assemblage zone boundaries along each transect were estimated by visual survey and the elevation of the midpoints of each zone was recorded. A 30 cm^2 square quadrat was placed on each midpoint and the species present and their percentage cover were recorded. Following the vegetation survey, the above-ground vegetation was cleared and the top 5 cm of soil was collected.

Laboratory

The experiment used two pots for each soil sample. The inner pot (2.8 L) contained the soil and the prescribed amount of water (the treatment), while the outer pot (5 L) held extra water to prevent the water level of the inner pot dropping through evaporation and absorption by developing plants. Inner pots were three quarters filled with a 50/50 mixture of sand and potting mix to provide a base for the developing root system. Three hundred millilitres (layer approximately 40 mm thick) of soil from the Narran study area (containing the seed bank) was placed on top. Inner pots were placed inside outer pots, filled with water and left for 16 h to saturate the soil to ensure that soil moisture was the same for all pots before beginning the treatments (Casanova &

Brock, 2000). One control pot per treatment containing potting mix only was used in the experiment.

After draining off excess water, each pot was filled to its prescribed treatment. Three sub samples from each zone–site combination were randomly placed throughout the glasshouse. At the end of the experimental period plants were identified using Harden (1990) to the highest taxonomic resolution possible (genus/species) and counted.

Data analysis

The effects of zone and treatment, as well any interaction effects on species richness and seedling abundance, were tested in a two-way Analysis of Variance (ANOVA) using the SAS program. The Tukey-Kramer multiple comparison analysis was then applied to determine where the differences lay. Comparison of assemblages across treatments and zones was made using a two-way Analysis of Similarities (ANOSIM) based on Bray-Curtis dissimilarity matrices calculated using both abundance and presence-absence data. Non-Metric Multidimensional Scaling (NMDS) was used to plot the data in multi-dimensional space.

RESULTS

The abundance of seedlings was significantly affected by both zone ($F = 7.12$; d.f. = 2, 38; $p = 0.0024$) and treatment ($F = 7.22$; d.f. = 4, 38; $p = 0.0002$). A Tukey-Kramer multiple comparison found that the Yellow zone (highest elevation) and Green zone (mid-elevation) yielded higher abundances of individual plants compared to the Mint zone (channel bed), but they were not significantly different to each other (Fig. 1). Treatment 1 (T1) (submerged for 12 weeks) produced significantly lower plant abundance compared to all other treatments (Fig. 1).
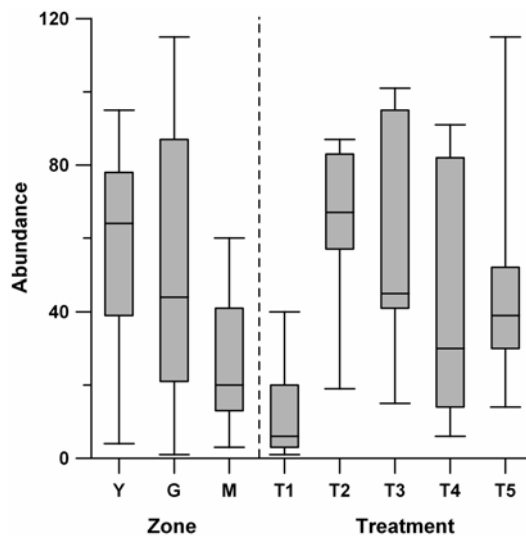
Fig. 1 Abundance of species of each sample across zone (Y = yellow zone, G = green zone, M = mint zone) and treatment (T1–T5 indicates treatment: see text for detailed explanation). Includes median, maximum, minimum, range, 75th and 25th quartiles.
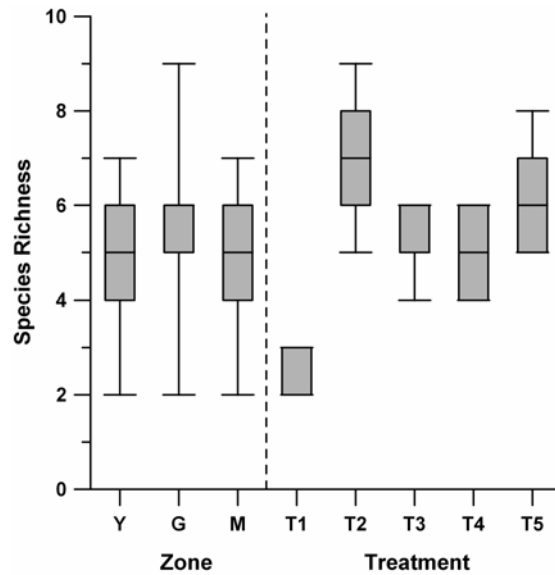
Fig. 2 Number of different species (species richness) that germinated and established across zone (Y = yellow zone, G = green zone, M = mint zone) and treatment (T1–T5 indicates treatment: see text for detailed explanation). Includes median, maximum, minimum, range, 75th and 25th quartiles.

Table 1 Summary of ANOSIM pairwise tests on zone and treatment groups based on species abundance and presence/absence data.

| Groups	Species abundance		Presence/absence	
	R statistic	*p* value	*R* statistic	*p* value
Green, mint	0.115	0.170	–0.056	0.726
Green, yellow	0.281	0.006	–0.074	0.765
Mint, yellow	0.43	0.009	–0.007	0.499
T1, T2	0.580	0.004	0.704	0.004
T1, T3	0.580	0.003	0.654	0.001
T1, T4	0.272	0.077	0.481	0.002
T1, T5	0.537	0.005	0.685	0.002
T2, T3	–0.185	0.860	0.012	0.469
T2, T4	0.333	0.030	0.302	0.053
T2, T5	–0.012	0.520	0.049	0.384
T3, T4	0.148	0.174	0.142	0.215
T3, T5	0.210	0.097	0.284	0.072
T4, T5	0.309	0.051	0.093	0.266

Number of permutations: 999 (random sample from a large number). Sample statistic Global *R* and *R* statistic: >0.75, groups well separated; >0.50, groups overlapping but a clear difference; <0.25, groups not separable.

There was no difference in species richness between zones (Fig. 2); however, treatment had a significant effect ($F = 32.11$; d.f. = 4, 38; $p < 0.0001$). The Tukey-Kramer multiple comparisons showed that T1 yielded lower species richness compared to the other treatments. Treatment 2 (T2) had higher species richness compared to treatments 1, 3 and 4 (Fig. 2).

Significant differences were detected between seedling assemblages according to zone when abundance data were used (ANOSIM Global *R*: 0.272; $p = 0.003$, Table 1).
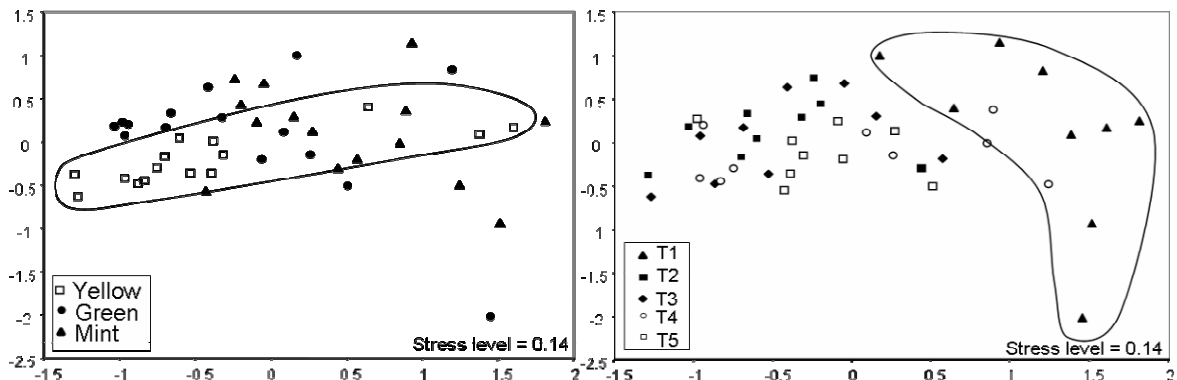
Fig. 3 Non-metric multi-dimensional scaling plot showing the difference in composition of: (a) the yellow zone (circled) compared to the green and mint zones and (b) the composition of Treatment 1 (circled) compared to the communities that established under treatments 2, 3 and 5.
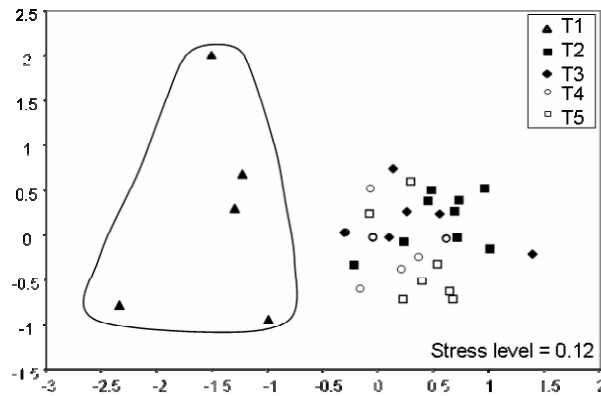
Fig. 4 Non-metric multi-dimensional scaling plot based on presence/absence of species by treatment. Treatment 1 is clearly separated from the other groups (circled).

The pairwise comparison of the zone groups revealed differences between composition of the yellow zone and those of the green and mint zones (Fig. 3(a)). There was no difference between the assemblages of the green and mint zones. Significant differences were also found between the seedling assemblages of treatment groups using abundance data (Global *R*: 0.266; $p = 0.001$). The pairwise test showed that the composition of T1 was different to that of T2, 3 and 5 (Fig. 3(b)). When analysed based on species present (ignoring abundance) this difference increased (Global *R*: 0.315; $p = 0.001$) with T1 composition being different to all four treatments (Fig. 4). No differences were detected between the other treatments. No between-zone differences in assemblages were detected when presence–absence data were used (Global *R*: –0.052; $p = 0.758$). All ordinations had a stress level less than 0.2, suggesting the resultant pattern was not random (Williams, 2002).

DISCUSSION

The results of this study suggest that the distribution of flood plain–wetland plant communities in distributary channels of the Narran Lakes are influenced by both seed

bank composition and watering regime. Seed reserves in the soil substrate are the foundations for the germination of each species. Seeds must be present and viable in order to provide for different plant communities to potentially develop (van der Valk & Davis, 1978). However, the inundation regime is the mechanism that selects which species develop (Moore & Keddy, 1988).

Vegetation assemblages were not statistically different by zone based on species presence–absence alone, meaning that most species were present across all treatments regardless of which zone the soil came from. However, the abundance of each species that emerged did vary across zones, with soils taken from higher elevations producing a higher abundance of plants. This suggests that the seed bank may be zoned in terms of the total and relative abundance of seeds from each species, but not based on which species occur in each zone. The density of seeds in each zone may be linked to seed dispersal and flooding history. The decrease in seed bank density at lower elevations may result from longer periods of inundation, reducing the viability of seeds through decay (Schneider, 1994). Similarly, seed dispersal may be important. Most wetland seeds are distributed via floodwaters, with seeds floating on the water surface and subsequently deposited at the water's edge, resulting in an accumulation of seeds along the high-water mark (Smith & Kadlec, 1985). Alternatively, the apparent variation in seed abundance across zones may reflect variation in the seed production capacity of each community.

Of all the inundation treatments used in this study, only the 12-week submerged treatment produced a significantly different vegetation assemblage with regard to presence–absence or species abundance. This inundation regime suppressed germination for eight of the twelve species that emerged in the other treatments. Total seedling abundance was also markedly lower under this regime and, to a lesser extent, in the other two treatments that were submerged for the first four weeks of the regime (T3 and T4). In contrast, highest species richness was found in the treatment where soil was waterlogged for the entire period (T2). It would appear that the waterlogged soil treatment provided the niche requirements for the largest range of species to develop. These results are consistent with previous wetland vegetation studies, which showed that long periods of inundation produced assemblages of low abundance and low species richness (Nicol *et al.*, 2003) and that highest species richness occurs in waterlogged soil. Despite the patterns evident for species richness, there was no difference in the species assemblages of T2 and the remaining treatments (T3, T4 and T5) or between these remaining treatments.

Also, it is interesting to note that eight species that were not observed in the field surveys germinated in the glasshouse. Among these were some of the most abundant species, including *Ammania multiflora* Roxb, *Cyperus pygmaeus* Rottb and *Ranunculus* spp. This shows the diversity of the seed bank and the ability of seeds to remain dormant until triggered to germinate by a suitable inundation regime (Brock & Rogers, 1998).

These results have implications for the flow management of flood plain–wetlands, highlighting the importance of the nature and duration of flooding. Exposure and waterlogging are key factors for the development of species rich and abundant communities. Flow management strategies should consider these patterns and species responses if they aim to maintain or enhance current levels of biodiversity in flood plain–wetland vegetation communities.

CONCLUSIONS

Seed bank composition in the distributary channels of the Narran Lakes flood plain was the dominant factor controlling abundances of species to emerge from the meso-cosm experiment. However, the inundation regime determined which species would become established by stimulating or suppressing the germination of species and then providing niche requirements for development and establishment. The seed bank is important to flood plain–wetland systems and the inundation regime is vital in maintaining diverse vegetation communities. The results of this study show that changes in inundation regime have the potential to affect vegetation assemblages at small scales and increases our capacity to predict how these vegetation communities will respond to alterations in flow regime.

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