Plant Ecol (2007) 188:145–164
DOI 10.1007/s11258-006-9153-0

ORIGINAL PAPER

Plant establishment from the seed bank of a degraded floodplain wetland: a comparison of two alternative management scenarios

Hugh A. Robertson · Kimberley R. James

Received: 19 April 2005 / Accepted: 12 April 2006 / Published online: 6 June 2006

Abstract There has been little research examining the soil seed banks of degraded floodplain wetlands and their contribution to wetland rehabilitation in Australia. Our aim was to assess the establishment of plants from the seed bank that may occur following the delivery of an environmental water allocation to Kanyapella Basin, a 2950 ha wetland located on the floodplain of the Goulburn and Murray Rivers in northern Victoria, Australia. Two hypothetical water regimes were investigated (flooded and dry) in a glasshouse experiment, where plants were left to establish from the seed bank over a period of 124 days. Differences in the establishment of plants from the seed bank indicated that the return of a flooding regime is likely to have a significant effect on the composition of the wetland vegetation. Mapping of the distribution of plant species indicated that propagules were highly dispersed across the wetland for the majority of taxa, in contrast to the localised distribution of many of the plant species represented in the extant vegetation. Inundation favoured the establishment of native wetland and floodplain plants, although many areas of Kanyapella Basin that are currently 'weed-free' have the potential to become colonised and potentially dominated by introduced plants if the wetland is not managed appropriately. Overall, results supported the aim of management to reestablish a wetting and drying regime through use of an environmental water allocation. This study presents a significant example of the application of seed bank investigations in wetland ecology and management.

Keywords Wetland vegetation · Elevation gradient · Plant community · Water regime · Water depth

Introduction

Conservation and rehabilitation of floodplain wetland ecosystems in the Murray–Darling Basin, Australia, is becoming increasingly reliant on the provision of environmental water allocations to reinstate the water regime that has been altered due to river regulation and other human activities. A lack of knowledge of the ecological water requirements of different wetland vegetation communities, however, remains a limiting factor in the implementation of environmental water allocations (Roberts et al. 2000; Schofield et al.

H. A. Robertson · K. R. James
School of Life and Environmental Sciences, Deakin University, 221 Burwood Highway, Burwood, VIC 3125, Australia

H. A. Robertson (✉)
Riverland Local Action Planning Committees, PO Box 427, Berri, SA 5343, Australia
e-mail: harobert@deakin.edu.au

2003). Without an understanding of how vegetation communities respond to different wetting and drying regimes, and under what conditions, it is difficult to determine how best to utilise the environmental water available for wetland conservation.

Floodplain wetlands in the semi-arid Murray–Darling Basin have an irregular wetting and drying regime, which is associated with the unpredictable flooding of the lowland river systems (Young 2001). During periods of prolonged dry conditions, or where flooding is impeded due to anthropogenic structures such as levee banks, floodplain wetland vegetation often becomes depleted, both in terms of biomass and species richness (Roberts and Ludwig 1991; Bunn and Arthington 2002). In these ecosystems, soil seed banks play an important role in the regeneration of plant communities following flood events. The presence of a diverse and abundant seed bank is also often related to the potential to rehabilitate wetland vegetation (Leck 1989; Brown and Bedford 1997). Assessment of the benefit of an environmental water allocation for degraded floodplain wetlands, or wetlands that have been dry for an extended period, is likely to benefit from information on the potential of the soil seed bank to contribute to the rehabilitation of the system. However, there have been relatively few studies of the seed bank potential of degraded floodplain wetlands and their contribution to wetland rehabilitation.

This paper specifically investigates the establishment of wetland plants from the soil seed bank of Kanyapella Basin, a degraded 2950 ha wetland located on floodplain of the Goulburn and Murray Rivers in northern Victoria, Australia (36°09′ S, 144°54′ E) (Fig. 1). River Red Gum (*Eucalyptus camaldulensis*) and Black Box (*Eucalyptus largiflorens*) are the dominant tree species represented at the site. A number of other floodplain vegetation communities also occur within the wetland, including areas dominated by rushes (*Juncus* spp.), *Typha* spp., and sedges (*Carex* spp.) (Robertson and James 2005). The wetland, including its vegetation, is degraded due to the effects of river regulation, tree clearing and agriculture, and a protracted period of low rainfall (since 1993) (Robertson and McGee 2003), which means that following inundation much of the plant biomass will regenerate from the soil seed bank.

Rehabilitation of Kanyapella Basin is planned in the near future with the delivery of an environmental water allocation (Robertson and James 2002). Due to the limited amount of environmental water available in the region, and impediments to water delivery imposed by surface water

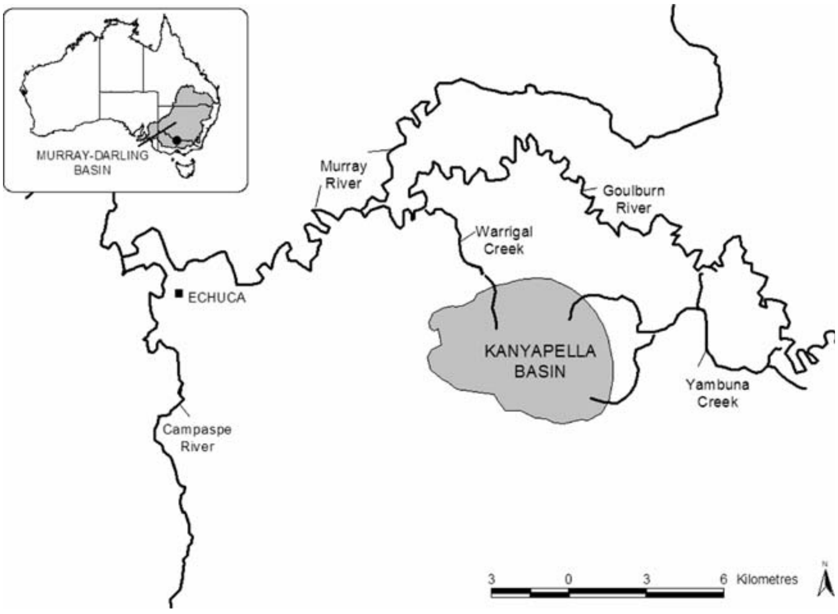


Fig. 1 Location of Kanyapella Basin, Murray-Darling Basin, Australia

drainage infrastructure, there is only a small range of water regime scenarios that can be implemented at Kanyapella Basin (Robertson and McGee 2003). These limitations influence which areas of the wetland, and which vegetation communities, will receive water from an environmental water allocation.

A number of wetland seed bank studies have investigated the response of soil seed banks to different watering strategies (e.g. Coops and van der Velde 1995; Galatowitsch and van der Valk 1996; Casanova and Brock 2000; Nicol et al. 2003). These studies typically involved removing soil cores from a wetland, applying different water regimes to the cores in a glasshouse experiment, and then monitoring the emergence or establishment of seedlings. In Australia, temporary wetlands have been examined on a number of occasions (e.g. Britton and Brock 1994; Brock and Casanova 1997; Nicol et al. 2003), but there has been little research examining the soil seed banks of degraded floodplain wetlands.

While most seed bank studies are explicit about how the water or salinity levels varied between treatments, few studies take into consideration how the seed bank responds differently from soil cores taken at different sites in a wetland. Wilson et al. (1993) noted that consideration of the seed bank response at different sites in a wetland is important in attempts to predict the response of wetland vegetation to different water management scenarios. For instance, the elevation at the site where the seed bank is sampled will affect the range of water depths that can occur at that particular site in future flood events. Yet few seed bank studies account for this in their experimental design. For example, instead of applying a water regime based on future water management scenarios, experimental designs have often used a fixed water depth for all samples (e.g. Brock et al. 1994; Brown 1998; Abernethy and Willby 1999). Where the elevation changes between sites, application of a constant water depth to all soil cores in a glasshouse will not reflect one single water regime scenario, but a continuum of different size flood events. These issues may significantly impact on the interpretation and application of results from seed bank investigations in wetland management.

Geospatial (GIS) models of the depth and distribution of flooding under different water management scenarios are valuable to wetland plant management (e.g. Jensen et al. 1992; Poiani and Johnson 1993; Lehmann and Lachavanne 1997; Narumalani et al. 1997; Williams and Lyon 1997), but have not often been applied to seed bank studies. Availability of a high-resolution Digital Elevation Model (DEM) for Kanyapella Basin (Department of Natural Resources and Environment 2002) provided the opportunity to apply this technology to this seed bank study, particularly for evaluating the differences in the establishment of plants from the seed bank along an elevation gradient.

Aim

The aim of this study was to investigate the seed bank response at Kanyapella Basin to two hypothetical water regimes (flooded and dry). Differences in the establishment of wetland plants from the seed bank under the different water regimes, and the spatial variation in the establishment of plant communities are examined. By using a study design based on future water management scenarios we also aimed to evaluate the use of soil seed bank investigations in guiding management decisions in wetland rehabilitation projects.

Methods

The seed bank response to two hypothetical water management scenarios was investigated in a glasshouse experiment. The two hypothetical management scenarios examined were, (i) a flood to the 93.5 mAHD contour in Kanyapella Basin (flooded), and (ii) dry conditions, receiving average rainfall only (dry). Inundation to 93.5 mAHD represents the water regime if an environmental water allocation of approximately 3000 ML of water (excluding the amount of water required to saturate the soil) is delivered. The dry condition scenario represents the situation if no environmental water allocation is obtained.

The methodological approach employed for this study was based on Brock et al. (1994) for study of the soil seed banks of Australian wetlands. Broadly, the method involves collecting soil cores from a number of sites in a wetland and then applying a variety of water regime treatments to the soil cores in a glasshouse. Plants that germinate from seed, spores and vegetative propagules in response to the different water regimes are then identified and their abundance recorded.

Sample site selection and soil core sampling

All sample sites were located within the area bound by the 93.5 mAHD contour in Kanyapella Basin (Fig. 2). The vegetation type within this area was dominated by River Red Gum (*E. camaldulensis*) forest. To investigate differences in the seed bank response along an elevation (water depth) gradient under a flood to 93.5 mAHD, the study area was stratified into three elevation zones, < 93.3 m, 93.3–93.4 m and 93.4–93.5 m, which correspond to water depths (mid point) of 30 cm, 15 cm and 5 cm respectively. The three elevation zones were delineated from a high-resolution Digital Elevation Model (DEM) of Kanyapella Basin obtained from Airborne Laser Sensing (1 m GIS grid layer, with elevation in mAHD (*z*-value) accurate to approximately 10 cm[1]) (Department of Natural Resources and Environment 2002). Fifteen sites were sampled within each elevation zone (Fig. 2). The location of each site was randomly selected using a random number generator to select cells from a grid (cell size equivalent to 50 m × 50 m) placed over the DEM.

Sites were located in the field using a Geographic Positioning System (GPS). At each site a 5 m × 5 m quadrat was established. Twenty-four soil cores were collected from random locations within the quadrat, 12 cores for the 'flooded' treatment and 12 cores for the 'dry' treatment. Soil cores were 5 cm in diameter × 5 cm deep. Cores were removed from the soil intact using a soil corer and randomly placed in plastic trays for transportation (6 cores per tray). The number of sites (15 per elevation zone) and the area sampled per treatment at each site (0.024 m^2) was well above that recommended by Brock et al. (1994) for wetland seed bank studies (5 sites; 0.016 m^2).

[1] Although each grid cell in the DEM has an error of approximately 10 cm, this did not have a significant impact on delineating the three elevation zones due to the large number of data points reducing the overall error.

Experimental procedure

Twelve soil cores from each site (i.e. two plastic trays) were allocated to each experimental treatment. There were 90 samples in total, with 15 replicate samples for each elevation zone and treatment (3 elevation zones × 15 sites × 2 treatments). For each sample the soil cores in plastic trays were placed in a large, clear plastic tub (410 × 240 × 360 mm). Five control tubs were also established (3 flooded, 2 dry). Control tubs contained two trays of sterilized potting mix and were used to monitor whether propagules were transferred between samples or entered from an external source (which would invalidate results). Two glasshouses located at Monash University, Clayton, Victoria (37°55′ S, 145°07′ E), were used to conduct the experiment. The glasshouses were located 15 m away from each other, orientated in the same direction and subjected to the same light environment. The 95 tubs were randomly distributed between the two glasshouses.

The experiment started on 23 September 2002 and finished on 24 January 2003 (124 days). Prior to flooding, the soil cores were saturated with water for three days to limit the amount of floating organic matter following inundation. Samples for the flooded treatment were then inundated to 5 cm, 15 cm or 30 cm above the soil surface as determined by their elevation zone. Ocean Nature Sea Salt was added to each sample to increase the salinity of the tap water (50–70μS/cm) to 300–350μS/cm, the average recorded at Kanyapella Basin. Water was not changed during the experiment due to the large number of submerged and floating plants. However, filamentous algae were removed from samples experiencing excessive algal growth so as not to affect the establishment of other plants. Constant water levels were maintained for the duration of the experiment by topping-up as required. Salinity (electrical conductivity in μS/cm), pH, dissolved oxygen (mg/l), turbidity (NTU), water

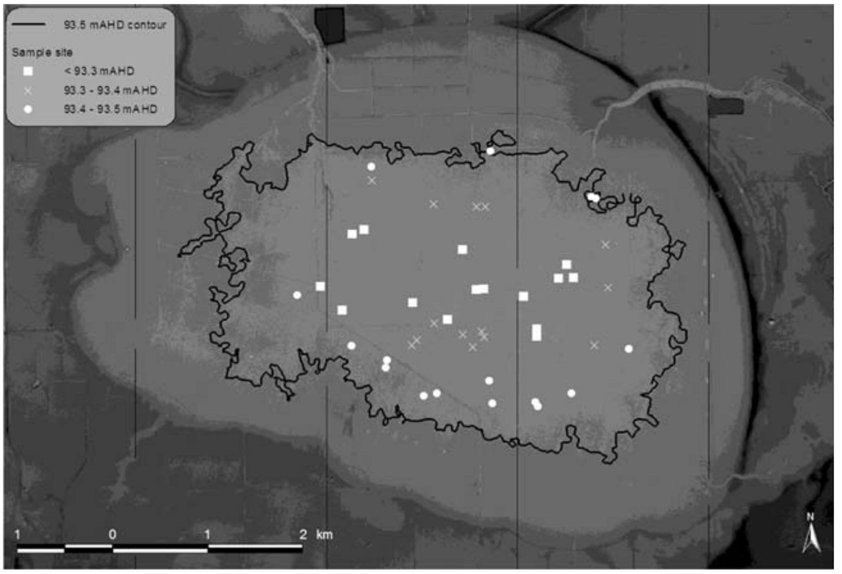


Fig. 2 Location of sample sites for seed bank experiment. Fifteen sites selected within each elevation category, < 93.3 m, 93.3–93.4 m and 93.4–93.5 mAHD. The 93.5 m AHD contour (black line) delineated from the digital elevation model (DEM) of Kanyapella Basin. DEM captured in 2002

temperature (°C), and maximum and minimum air temperature (°C) were monitored at approximately fortnightly intervals throughout the course of the experiment. All samples in the dry treatment were watered every three days during the course of the experiment with 80 ml of water, though sometimes more frequently during hot weather (e.g. >32°C) to maintain the plants that had germinated. The 80 ml represents the mean rainfall for September to January[2].

Plant surveys

Plants that established from the seed bank were identified and harvested at the end of the experiment. While other seed bank studies continually harvest plants as they germinate, the 'emergence method' (e.g. van der Valk and Davis 1978; Britton and Brock 1994; Brock et al. 1994; Brown 1998), plants were left to establish to provide an indication of the plant community that may establish at Kanyapella Basin following an environmental water allocation. This method of leaving plants to establish has been applied in wetland seed bank studies elsewhere (e.g. Smith et al. 2002).

[2] Mean rainfall per month for September–January at Echuca aerodrome weather station is 34 mm (Commonwealth Bureau of Meteorology 2001). 80 ml is the equivalent volume of water required applied to the two trays (12 cores) every 3 days.

As it was not possible to process the 95 tubs concurrently, the experiment continued longer for some samples than for others, and plants continued to grow until they were harvested. Plant surveys and harvesting was initiated on 7 January 2003 and completed by 24 January 2003. To reduce the effect of processing date on results the samples were processed in random order. All plant material (shoots, leaves and roots) was harvested and sorted by taxa into pre-weighed paper bags, dried in an oven at 70°C for a minimum of 48 h when weight loss had ceased, and weighed. Dry-weight was recorded in grams to two decimal places.

Identification of plants to species level was possible for the majority of individuals. The remaining plants were identified to genus level. Species identification and species names follow Walsh and Entwisle (1994, 1996, 1999) and Ross and Walsh (2003). Sainty and Jacobs (2003) was used to discriminate between Charophytes (i.e. *Chara* spp. and *Nitella* spp.). Taxa were classified as 'aquatic', 'amphibious' or 'terrestrial' based on the plant functional type classification developed by Brock and Casanova (1997) and Leck and Brock (2000). These groupings were further validated using descriptions of the plants' ecological requirements and habitat in Walsh and Entwisle (1994, 1996, 1999) and other wetland plant and general botanical texts (Cunningham et al. 1992;

Romanowski 1998; Roberts and Marston 2000; Sainty and Jacobs 2003). These botanical references were also used to categorize the taxa as native or introduced, and annual or perennial. In instances where taxa were identified only to genus, and the species in the group included both native and introduced species, or annual and perennial species, the species most likely to be observed in the seed bank at Kanyapella Basin was considered (typically only a few species had been recorded in the region and from previous surveys, and this information was used to limit the number of possibilities, which allowed the provenance and life history attributes for each taxa to be estimated).

Statistical and spatial analysis

The response of the soil seed bank to the two water regime treatments were analysed using a number of univariate and multivariate statistical procedures. For each sample the species richness and the total biomass (dry weight) were calculated. The total biomass per sample of native/introduced plants, aquatic/amphibious/terrestrial plants and other plant assemblages were also calculated. Differences in species richness and biomass between the flooded and dry treatments for each of these indices were examined using Chi-square analysis and ANOVA. Differences in the response of the seed bank between elevation zones, for example between samples inundated to 5 cm, 15 cm and 30 cm (for the flooded treatment only) were also analysed using these indices. Variation in water quality between samples (flooded treatment only) and over time was evaluated using Repeated Measures ANOVA. Linear assumptions were checked with residual plots (Quinn and Keough 2002).

Differences in plant community composition between treatments and elevation zones were analysed using a number of multivariate statistical routines within PRIMER v.5 (Clarke and Gorley 2000). PRIMER uses relatively robust non-parametric methods that are not constrained by sample distribution and variability assumptions (Clarke 1993). A samples versus species similarity matrix (Bray–Curtis similarity, square root transformed) was calculated in PRIMER based on the biomass (dry weight) of each taxon. Biomass data was square root transformed to add more weight to rare taxa that were not as abundant, and consequently, less weight to the dominant taxa (Legendre and Legendre 1998). Non-metric multidimensional scaling (NMDS) ordination was performed to compare the similarity of the plant communities that established between treatments and elevation zones (i.e. different water depths). Analysis of Similarities (ANOSIM, Clarke 1993), a Mantel (1967) type permutation test using the rank order of similarities, was used to test for differences in species composition and abundance between the flooded and dry treatments, and between elevation zones for the flooded treatment. SIMPER analysis (Clarke and Warwick 2001) was subsequently performed to examine which taxa were contributing most to the dissimilarity in species composition between treatments and at different water depths.

Spatial analysis of differences in the distribution and abundance of plants that established from the soil seed bank was undertaken within a GIS. For each of the 45 sites sampled, the distribution and abundance of selected plant indices and plant taxa were mapped according to the location of the sample site, and then correlated with a number of environmental variables within the wetland. This included geographically referenced data on the extant vegetation (e.g. average cover abundance of introduced plants) obtained from field surveys conducted between 2000 and 2002 at Kanyapella Basin (Robertson 2006). Spearman rank correlation was applied to test for relationships (c.f. Linear (Pearson) correlation, because the data were not normally distributed, even after transformation, and as the change of X on Y was not necessarily linear). BIOENV analysis within PRIMER was used to investigate multivariate patterns between plant community composition and multiple environmental variables. The BIOENV procedure searches for combinations of environmental variables that best explain the similarity in the plant communities determined by the NMDS ordination, calculating a *Rho* value between 0 and 1 (Clarke and Warwick 2001).

Results

Establishment of plants from the seed bank

Plants rapidly established from the soil cores following inundation and for the dry treatment in response to regular watering. A total of 59 taxa were recorded during the seed bank experiment. Thirty-seven of these were native taxa and 22 introduced taxa, representing a variety of different plant growth forms (Table 1). The number of taxa per sample ranged from a minimum of 1 to a maximum of 15, with an average of 8.8 (±0.3 SE) taxa emerging from each sample. A significant

Table 1 Plant taxa that established from the soil seed bank in the flooded and dry experimental treatments, from the samples collected from low, medium and high elevation. Number in parentheses is maximum possible number of observations

Plant taxa	Traits			Frequency of Occurrence							
	Origin	Life-history	Habitat	Flooded treatment (elevation)			Flood Total (45)	Dry treatment (elevation)			Dry Total (45)
				Low 30 cm	Medium 15 cm	High 5 cm		Low	Medium	High	
Alisma lanceolata	I	P	Aq	7	9	7	23			1	1
Alopecurus geniculatus	I	P	Am						1		1
Alternanthera denticulata	N	P	Am					3		1	4
Amphibromus spp.*	N	P	Am			5	5	4	3	5	12
Avena barbata	I	A	T							2	2
Azolla filiculoides	N	P	Aq	12	10	12	34	1	2		3
Callitriche hamulata	I	A	Am	13	14	12	39	10	9	11	29
Callitriche umbonata	N	A	Am			2	2		2		2
Cardamine moirensis	N	A	Am	5	7	5	17	11	14	11	36
Centipeda cunninghamii	N	P	Am					1	1		2
Cerastium glomeratum	I	A	T					2	1	2	5
Chara spp.**	N	P	Aq	6	7	2	15				
Chenopodium album	I	A	T							1	1
Cirsium vulgare	I	A	T						1		1
Cotula australis	N	A	Am					1	1		2
Cotula bipinnata	I	A	Am					2			2
Cotula coronopifolia	I	P	Am					1			1
Crassula peduncularis	N	A	Am		1	3	4			1	1
Cyperus eragrostis	I	P	Am	1	1	2	4	2	1		3
Damasonium minus	N	A	Aq	2	3	2	7				
Elatine gratioloides	N	A	Aq	14	14	14	42			1	1
Eleocharis acuta	N	P	Am	10	11	12	33	10	10	7	27
Eleocharis pusilla	N	P	Am	2	1	1	4			1	1
Epilobium hirtigerum	N	P	Am						3	4	7
Eucalyptus camaldulensis	N	P	Am							1	1
Euchiton spp.***	N	A	T					2	1	2	5
Gratiola pumilo	N	P	Am	5	7	6	18	1	4	3	8
Hordeum murinum	I	A	T							1	1
Juncus bufonius	N	A	Am					1	2	1	4
Juncus gp1.****	N	P	Am	3	1	3	7	13	11	6	30
Juncus holoschoenus	N	P	Am	9	9	8	26	11	14	5	30
Lachnagrostis filiformis	N	P	Am		1	2	3	5	10	8	23
Lacuta serriola	I	A	T							1	1
Lemna disperma	N	P	Aq	12	8	5	25				
Limosella australis	N	P	Am	1	4	9	14		2	1	3
Lobelia pratioides	N	P	Am							2	2
Lolium spp. #	I	A	T					2		3	5
Lythrum hyssopifolia	N	A	Am	2	3	5	10	2	2	4	8

Table 1 continued

Plant taxa	Traits			Frequency of Occurrence							
	Origin	Life-history	Habitat	Flooded treatment (elevation)			Flood Total (45)	Dry treatment (elevation)			Dry Total (45)
				Low 30 cm	Medium 15 cm	High 5 cm		Low	Medium	High	
Marsilea drummondii	N	P	Am							1	1
Medicago polymorpha	I	A	T					1	3	1	5
Mimulus gracilis	N	P	Am					2			2
Myriophyllum spp. ##	N	P	Am	10	14	10	34	7	10	4	21
Nitella spp. ###	N	P	Aq	8	9	9	26		1		1
Paspalum distichum	I	P	Am			2	2			1	1
Polypogon monspeliensis	I	A	Am			2	2		1	2	3
Ranunculus scleratus	I	A	Am			2	2			1	1
Ranunculus spp. ####	N	A	Am		3	1	4		5	3	8
Riccia spp	N	P	Aq	8	10	12	30			1	1
Rumex brownii	N	P	Am			1	1		2	3	5
Rumex crispus	I	P	Am			1	1	2	1	1	4
Senecio quadridentatus	N	A	T	1			1	1	1	4	6
Sonchus oleraceus	I	A	T					1		2	3
Stellaria angustifolia	N	A	Am					2			2
Trifolium spp.+	I	A	T					3	4	4	11
Triglochin procerum++	N	P	Aq							1	1
Typha spp. +++	N	P	Aq	1			1				
Veronica peregrina	I	A	Am	1		2	3	1	2	4	7
Vulpia bromoides	I	A	T							1	1
Wahlenbergia spp. ++++	N	P	Am			1	1			1	1

Key: N (Native), I (Introduced), A (Annual), P (Perennial), Aq (Aquatic), Am (Amphibious), T (Terrestrial), New (New record for the wetland), Inf (Infrequently observed at the wetland). *Note*: 'Habitat' based on the plant functional type classification of Brock and Casanova (1997) and Leck and Brock (2000)

* All *Amphibromus* species common to the region are native (Walsh and Entwisle 1994). Species most frequently recorded was *A. nervosus*

** All *Chara* species in Australia are native (Michelle Casanova pers. comm. 2004)

*** All *Euchiton* species recorded in Victoria are native (Ross and Walsh 2003). Most common species recorded from extant vegetation *E. sphaericus*

**** This *Juncus* group includes *Juncus* species other than *J. holoschoenus* and *J. bufonius*, which were more readily identified

All *Lolium* species recorded in Victoria are introduced (or naturalized) (Ross and Walsh 2003). Species most frequently recorded was *L. rigidum*

Growing of 20 individuals of unidentified *Myriophyllum* identified two species *M. crispatum* and *M. variifolium*

All *Nitella* species in Australia are native (Michelle Casanova pers. comm. 2004)

This *Ranunculus* group includes all *Ranunculus* species other than *R. scleratus*. Species most frequently recorded was *R. pumilio* var. *pumilio*

+ All *Trifolium* species recorded in Victoria are introduced (or naturalized) (Ross and Walsh 2003)

++ *Triglochin procerum* has been revised and is now split a number of different species following Aston (1993, 1995)

+++ Only the native *Typha* species (*T. orientalis and T. domingensis*) have been recorded from extant vegetation surveys at Kanyapella Basin

++++ All *Wahlenbergia* species recorded in Victoria are native (Ross and Walsh 2003). Most common species recorded from extant vegetation *W. fluminalis* difference was observed in the average number of taxa per sample between the flooded ($\mu = 9.8$) and dry ($\mu = 7.8$) treatments ($F = 9.892$, df = 1, $P = 0.002$). The dry treatment had greater species richness overall, although this included a high number of introduced taxa (Fig. 3). No significant difference in the average number of taxa per sample was evident across the three elevation zones in the flooded treatment of the seed bank experiment ($F = 1.005$, df = 2, $P = 0.38$). Four species established from the soil seed bank had not been previously recorded at Kanyapella Basin (*Callitriche umbonata*, *Gratiola pumilo*, *Juncus holoschoenus*, *Nitella* spp.), and a number of others had only been infrequently recorded from previous surveys of the extant vegetation completed during 2000–2002 (Robertson 2006). While these less-common species established under both the flooded and dry conditions, only one (*Chenopodium album*) was classified as terrestrial, with all others capable of tolerating either complete or partial flooding for a period of time. No seedlings emerged from the control samples indicating there was no cross-contamination or input from external propagules during the experiment.

Many plants frequently established in both flooded and dry conditions (Table 1), although growth forms for some of these species (e.g. *Myriophyllum* spp.) differed considerably between treatments. There were a number of taxa that were not tolerant of inundation and only established under dry conditions (Table 1).

Different elevation zones in the flooded treatment (i.e. 5 cm, 15 cm and 30 cm water depths) favoured particular taxa. For example, *Limosella australis* became increasingly common as the water depth decreased, but was not common in the dry treatment. Wetland grasses including *Lachnagrostis filiformis*, *Amphibromus* spp. (predominantly *A. nervosus*), and *Polypogon monspeliensis* only typically established in shallow water (5 cm) and under dry conditions. Plants that were more common in deep inundation (30 cm) included the submerged charophyte *Chara* spp. However, other true aquatics such as *Nitella* spp. were also observed at shallower depths (Table 1).

The proportion of the total biomass of aquatic ($F = 72.948$, df = 1, $P < 0.001$), amphibious ($F = 8.565$, df = 1, $P = 0.004$) and terrestrial plants ($F = 21.696$, df = 1, $P < 0.001$) that established in the seed bank differed significantly between the flooded and dry treatments (Figure 4). As expected, native and introduced aquatic plants generally only developed a substantial biomass when flooded. Amphibious taxa contributed most to the total biomass in both treatments, while terrestrial plants, which were predominantly introduced plants, germinated and established under dry conditions. Interestingly, of the 13 terrestrial species that emerged from the soil seed bank 12 were annual, and 10 were introduced, while seven of the ten aquatic plants that established during the experiment were native perennials. Differences in the biomass of

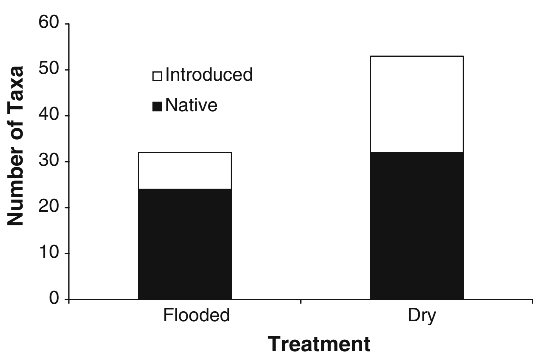


Fig. 3 Number of native and introduced taxa that established from the seed bank in the flooded and dry experimental treatments ($\chi^2 = 1.898$, df = 1, $P = 0.17$)

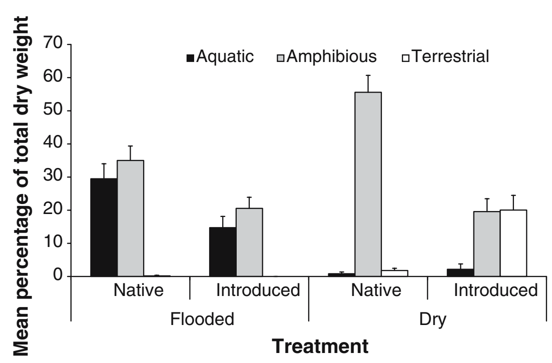


Fig. 4 Mean percentage of the total dry weight of native and introduced aquatic, amphibious, and terrestrial plants that established from the soil seed bank in the flooded and dry experimental treatments. Error bars represent standard error of the mean

plant species were also observed across the three elevation zones. For example, while *Alisma lanceolata* and *Eleocharis acuta* were frequently observed in all elevation zones, there were large differences in biomass with both species having greater biomass when flooded to 5 cm.

A high cover of the floating fern *Azolla filiculoides* occurred in some samples, which may have been an artifact of the experiment. A large biomass of filamentous algae also appeared in a number of flooded samples. Although the algae were removed, they may have had an impact on water quality and influenced the recruitment of wetland plants. *Azolla filiculoides* and filamentous algae were observed at aquatic refuge sites in the field, however their abundance in the seed bank experiment was much greater than was recorded during extant surveys (Robertson 2006).

Water quality of the flooded samples

Water quality observations were recorded for each of the flooded samples on seven occasions between October 2002 and January 2003, and immediately prior to plant harvesting. Mean turbidity during the experiment was significantly different between samples inundated to different water depths (Table 2), with the shallow-flooded (5 cm) samples having the highest mean turbidity. Mean turbidity increased as the experiment proceeded, with the rate of change in mean turbidity being significantly different for different depth treatments. Although soil types differed a little across sample sites (from observation, the proportion of clay–silt–sand, and organic matter), factors other than resuspended soil appeared to contribute to the increased turbidity. For example, the large biomass of *Azolla filiculoides* and other plants contributed organic matter in some samples flooded to 5 cm. However, the effect of dilution in the 15 cm and 30 cm samples on turbidity may also partly explain differences.

Mean salinity also varied depending on water depth with slightly higher salinity levels for the shallow samples (Table 2). Again, the effect of dilution may partly explain the differences between water depths. Salinity levels did not vary significantly during the course of the experiment. Dissolved oxygen, water temperature and pH were not significantly different between the water depths, or over time (Table 2). Air temperature in the glasshouses varied between 19°C and 48°C. The high air temperatures (>40°C) were above what is typical for River Red Gum forests near Kanyapella Basin, but these periods did not extend for prolonged periods (typically 1–2 days).

Effect of water regime and elevation on plant community composition

Assessment of the response of individual taxa to different water regimes provides only a one-dimensional perspective of the plant communities that established from the soil seed bank. The impact of the two water management strategies (flooded and dry) on overall plant community composition was investigated through multivariate analyses. NMDS ordination based on the dry weight of taxa indicated the plant communities that established from the soil seed bank were significantly different between the flooded and dry treatments (ANOSIM Global $R = 0.53$, $P < 0.001$) (Fig. 5).

Table 2 Mean (±standard error of the mean) salinity, turbidity, pH, dissolved oxygen (DO) and water temperature of the flooded samples from different elevation zones inundated to 5 cm, 15 cm and 30 cm during the seed bank experiment

Water depth	Salinity[a,b] (μS/cm)	Turbidity[b] (NTU)	pH	DO (mg/l)	Water temperature (°C)
5 cm	0.36± 0.01	21.6± 8.5	7.3± 0.2	8.3± 0.4	21.1± 1.1
15 cm	0.31± 0.01	9.5± 3.3	7.4± 0.1	8.2± 0.4	20.8± 1.0
30 cm	0.29± 0.01	5.2± 2.1	7.3± 0.1	8.1± 0.4	20.7± 0.9

[a] $P < 0.01$ for within-subject ANOVA (time*elevation zone) from repeated measures analysis for the change in water quality over time between samples from different elevation zones, using the more conservative Greenhouse–Geisser *P*-value

[b] $P < 0.01$ for between-subjects ANOVA (elevation zone) describes the effect of elevation zone with all repeated measures combined, using the normal *P*-value

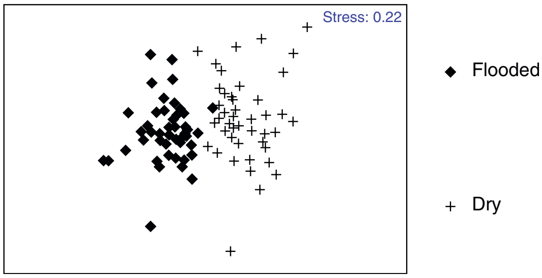


Fig. 5 NMDS ordination showing the relative similarity of plant community composition between samples from the flooded and dry treatments in the seed bank experiment. Based on Bray–Curtis similarity of the dry weight (square root transformed) of all taxa

SIMPER analysis identified the species that contributed most to the observed dissimilarity in plant community composition between the two treatments (Table 3). Many of the taxa contributing to the difference showed a preference for either flooded or dry conditions. These taxa may emerge as useful indicators to describe the response of the wetland vegetation to different water management scenarios, such as receiving an environmental water allocation. For example, *Azolla filiculoides* and *Alisma lanceolata*, which together explained approximately 16% of the difference in plant composition between the flooded and dry treatments, only typically established under flooded conditions. *Eleocharis acuta* and *Juncus holoschoenus*, which were also important in explaining differences in community composition, were common in both water regime treatments but established a greater biomass when in dry conditions. It should be noted the average dissimilarity/standard deviation ratio is relatively low for many of the taxa listed in Table 3, which highlights variability in the response of taxa within and between treatments.

In the flooded treatment, the position in the landscape along the elevation gradient from which the soil cores were collected, and therefore the water depth under the hypothetical flood to 93.5 mAHD, had a significant influence on plant community composition and structure. Different wetland plant communities established depending on whether the soil cores were shallow (5 cm) or deeply (30 cm) flooded (Fig. 6) (ANOSIM Global $R = 0.109$, $P = 0.01$) ANOSIM comparing the 5 cm and 15 cm replicates (Global $R = 0.102$, $P = 0.03$) also indicated significant differences in plant community. However, there was no evidence of a difference in the plant communities between areas of low (30 cm inundation) and medium elevation (15 cm) (Global $R = -0.002$,

Table 3 Species that contributed to 80% of the dissimilarity observed in plant community composition between the flooded and dry treatments (SIMPER analysis). Species are listed in order of their contribution to the dissimilarity between the two treatments. Based on Bray–Curtis similarity of the dry weight (square root transformed) of all taxa

Taxa	Avg. biomass (g) (Flooded)	Avg.biomass (g) (Dry)	Avg. dissimilarity/ SD ratio	Cumulative % contribution to dissimilarity
Callitriche hamulata	0.31	0.63	1.04	9.69
Azolla filiculoides	1.80	0.00	0.64	18.78
Alisma lanceolata	0.46	0.00	0.74	24.72
Cardamine moirensis	0.00	0.14	0.96	30.17
Eleocharis acuta	0.11	0.16	0.92	35.48
Juncus holoschoenus	0.06	0.17	0.78	40.76
Lachnagrostis filiformis	0.02	0.27	0.64	45.86
Elatine gratioloides	0.07	0.00	1.15	50.44
Juncus gp1	0.01	0.12	0.76	54.41
Amphibromus spp.	0.06	0.15	0.55	58.23
Myriophyllum spp.	0.08	0.01	1.05	62.03
Trifolium spp.	0.00	0.22	0.50	65.37
Lolium spp.	0.00	0.26	0.29	68.53
Lythrum hyssopifolia	0.02	0.08	0.48	70.91
Nitella spp.	0.07	0.00	0.70	73.19
Limosella australis	0.08	0.00	0.46	75.07
Damasonium minus	0.08	0.00	0.33	76.83
Chara spp.	0.04	0.00	0.48	78.30
Gratiola pumilo	0.01	0.01	0.71	79.67
Ranunculus spp.	0.00	0.05	0.31	81.03

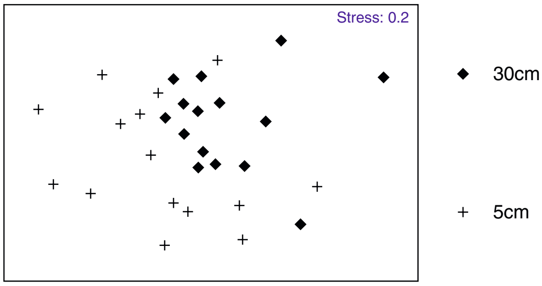


Fig. 6 NMDS ordination showing the relative similarity of plant community composition between the 5 cm (high elevation) and 30 cm (low elevation) flooded samples in the seed bank experiment. Based on Bray–Curtis similarity of the dry weight (square root transformed) of taxa recorded in samples flooded to 5 cm and 30 cm

$P = 0.49$). Plant taxa that explain most of the dissimilarity in plant community composition between the areas of low elevation and high elevation were dominated by those with a greater biomass in the shallow water depth, including *Azolla filiculoides*, *Alisma lanceloata*, *Callitriche hamulata*, *Eleocharis acuta*, *Limosella australis* and *Juncus holoschoenus* (Table 4). Apart from *A. filiculoides* and *C. hamulata*, these wetland plants are all perennial emergent macrophytes for which germination appeared to be limited when flooded to a depth of 30 cm. *Damasonium minus* and the charophytes *Nitella* spp. and *Chara* spp. were more common in the samples from a low elevation flooded to 30 cm. However, the average dissimilarity/standard deviation ratio was relatively low for many of the taxa listed (Table 4), indicating the variability in the response of taxa within and between water depths.

Spatial patterns and the influence of environmental variables on seed bank composition

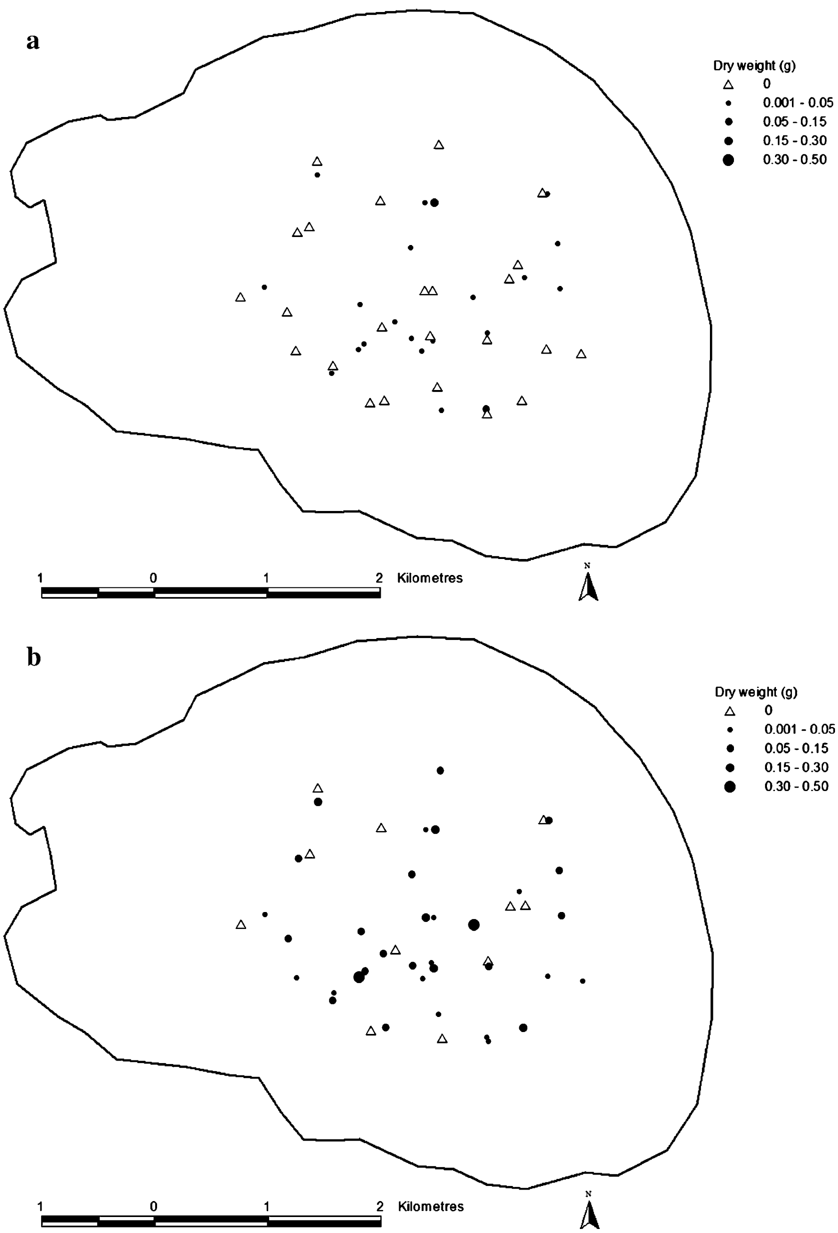
Spatial patterns in the establishment of plants from the seed bank were analysed by comparing the distribution and abundance of plants across the 45 sites sampled in Kanyapella Basin (Fig. 2). Mapping of selected plant species and vegetation indices within a GIS provided a visual indication of potential impact of the two water management scenarios on plant composition in different regions of the wetland. For example, Fig. 7 illustrates the distribution and biomass of *Myriophyllum* spp. that established at the 45 sites that were sampled. *Myriophyllum* spp. established more frequently and was more abundant when flooded, but was not aggregated in particular regions.

Geospatial investigations for other taxa showed similar results, in that while there were often obvious differences in the abundance and number of sites where taxa were observed between treatments, for most taxa, the seeds and vegetative propagules were widely dispersed. The distribution and abundance of introduced taxa were mapped to compare the potential impact of the two hypothetical water management scenarios on eliminating weed species. A GIS grid model of the cover-abundance of introduced plants from prior field surveys of the vegetation between 2000 and 2002 (Robertson 2006) were also plotted. The number of sites impacted, and the biomass of introduced species of terrestrial plants was much

Table 4 Species that contributed to 80% of the differences in plant community composition between samples flooded to 5 cm (high elevation) and 30 cm (low elevation) (SIMPER analysis). Species are listed in order of their contribution to the dissimilarity between the two elevation zones. Based on Bray–Curtis similarity of the dry weight (square root transformed) of taxa recorded in samples flooded to 5 cm and 30 cm

Taxa	Avg. biomass (g) (5 cm)	Avg. biomass (g) (30 cm)	Avg. dissimilarity/ SD ratio	Cumulative % contribution to dissimilarity
Azolla filiculoides	2.55	0.10	0.88	17.86
Alisma lanceloata	1.01	0.16	1.02	30.80
Callitriche hamulata	0.49	0.27	1.06	41.54
Eleocharis acuta	0.21	0.07	1.07	47.95
Limosella australis	0.21	0.00	0.68	53.57
Juncus holoschoenus	0.10	0.05	0.77	58.19
Myriophyllum spp.	0.05	0.09	1.16	62.70
Damasonium minus	0.06	0.14	0.45	67.12
Elatine gratioloides	0.06	0.05	1.04	71.12
Nitella spp.	0.02	0.07	0.96	74.82
Amphibromus spp.	0.18	0.00	0.60	78.26
Chara spp.	0.00	0.06	0.67	80.96

Fig. 7 Abundance (dry weight) of *Myriophyllum* spp. from the seed bank for the 45 sites sampled in Kanyapella Basin. (a) Dry treatment, (b) Flooded treatment



greater under dry conditions (Fig. 8). Although pest plants were not particularly common in the extant vegetation at the sites where the soil cores were collected, this seed bank experiment shows the potential for future weed establishment under dry conditions. The abundance of introduced emergent *Alisma lanceolata* in the flooded treatment of the seed bank experiment suggested that a range expansion in *A. lanceolata* might occur in Kanyapella Basin under favourable conditions. Figure 9 compares the distribution and abundance of *A. lanceolata* from the seed bank study with its cover-abundance modelled from the extant vegetation, which indicates that *A. lanceolata* has the potential to establish at many sites where it does currently occur in the wetland.

The degree to which the abundance of introduced taxa and other vegetation indices recorded from the extant vegetation correlated with the seed bank was investigated. None of the correlations

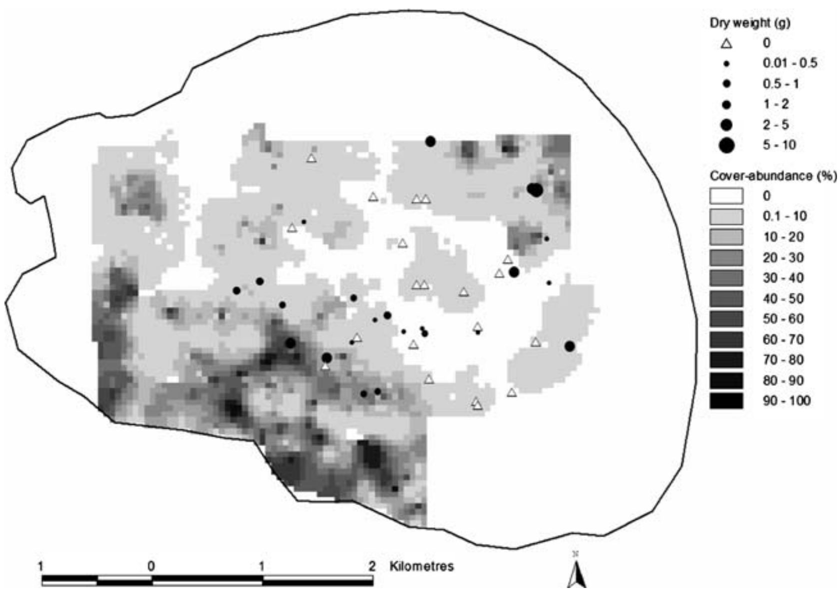


Fig. 8 Abundance (total dry weight) of introduced terrestrial plants that established from the dry treatment of the seed bank experiment for the 45 sites sampled in Kanyapella Basin (points), relative to the total cover-abundance of introduced terrestrial plants modelled from extant vegetation surveys (grid) (Robertson 2006). *Note*: No introduced terrestrial plants established from seed bank in the flooded treatment

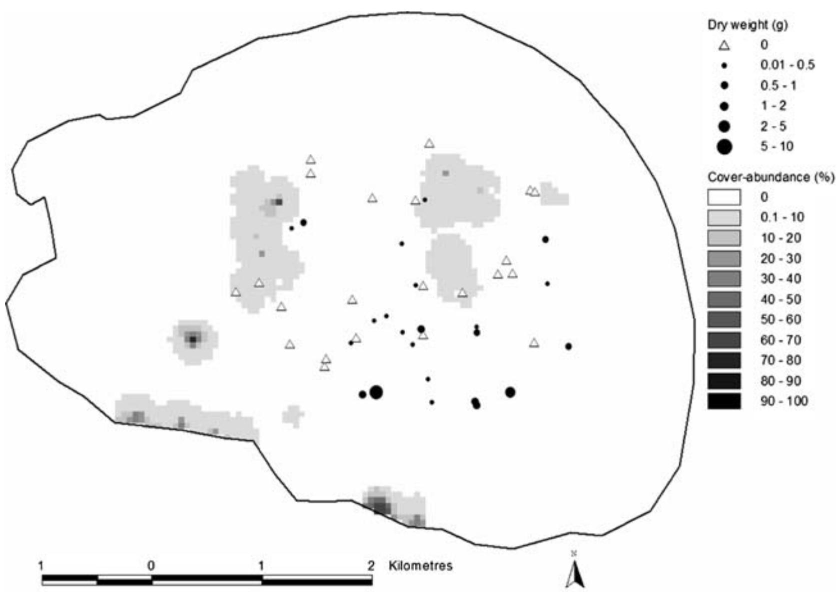


Fig. 9 Abundance (total dry weight) of *Alisma lanceolata* that established from the flooded treatment of the seed bank experiment for the 45 sites sampled in Kanyapella Basin (points), relative to the total cover-abundance of *A. lanceolata* modelled from extant vegetation surveys (grid) (Robertson 2006). *Note*: *A. lanceolata* established from the seed bank in only one sample in the dry treatment

between vegetation indices from the flooded seed bank treatment and indices from the extant vegetation indicated a relationship (Table 5). However, this was not surprising given the wetland has been predominantly dry for the past decade which has influenced the extant vegetation. However, comparing the dry seed bank treatment and the modelled extant vegetation produced two significant relationships. The biomass of introduced and terrestrial plants that established under dry conditions in the seed bank trials was related to the abundance of introduced taxa in the extant vegetation and the abundance of terrestrial plants (Table 5).

The BIOENV statistical routine was applied to investigate whether the variation in overall plant community composition across different samples within the flooded and dry treatments could be explained by a single environmental variable, or set of environmental variables, related to the location of the sample site. Flooded and dry

Table 5 Spearman's rank correlation (Þ$_s$) and significance (*P*-value) comparing selected vegetation indices from the flooded and dry seed bank experimental treatments against indices modelled from the extant vegetation in Kanyapella Basin

Indice—Seed bank (based on dry weight, g)	Indice—Extant vegetation (based on % cover abundance)	Flooded treatment		Dry treatment	
		p_s	*P*-value	p_s	*P*-value
Introduced taxa	Introduced taxa	0.082	0.596	0.450	0.002*
Introduced Aquatic taxa	Introduced Aquatic taxa	0.101	0.514	0.191	0.215
Introduced Amphibious taxa	Introduced Amphibious taxa	–0.126	0.417	0.046	0.769
Introduced Terrestrial taxa	Introduced Terrestrial taxa	–	–	0.208	0.176
Aquatic taxa	Aquatic taxa	–0.033	0.831	0.107	0.488
Amphibious taxa	Amphibious taxa	0.035	0.821	0.017	0.914
Terrestrial taxa	Terrestrial taxa	0.078	0.614	0.452	0.002*
Aquatic taxa	Aquatic + Amphibious taxa	–0.037	0.809	0.145	0.347
Annual taxa	Annual taxa	–0.274	0.071	0.180	0.243

samples were analysed independently as the presence or absence of water was assumed to be the dominant factor between these treatments and not other environmental variables. Water quality variables (dissolved oxygen, pH, salinity, turbidity and water temperature) were included as environmental variables for the flooded samples, but were not available for the dry samples. Other environmental variables included the density of River Red Gum (*E. camaldulensis*) and Black Box (*E. largiflorens*), the cover-abundance of introduced taxa and native taxa, and cover-abundance of aquatic, amphibious and terrestrial taxa recorded from the extant vegetation surveys.

For the flooded treatment, no single environmental factor was significantly correlated with the response of the seed bank. The cover abundance of introduced plants produced the closest match (Þ = 0.386). Best results from the BIOENV selected between four and six variables for the flooded treatment, but on no occasion produced a Þ greater than 0.5, which indicates that the differences in the seed bank composition were not significantly explained by these parameters. BIOENV produced similar, non-significant results for the dry treatment (i.e. no single or set of environmental parameters explained much of the similarity or dissimilarity in species composition between the 45 samples). Again the cover abundance of introduced plants in the extant vegetation produced the closest match (Þ = 0.355). Prior correlation of plant indices (Table 5) indicated that the extant vegetation was more similar to the community that established under dry conditions. However, investigation using the entire species assemblage did not produce a high correlation between the resultant seed bank community and the site-based environmental parameters.

Discussion

Seed bank potential of Kanyapella Basin

This investigation of the establishment of plants from the soil seed bank showed that the return of a flood regime to the wetland is likely to have a significant impact on the composition of the wetland vegetation. Kanyapella Basin had been predominantly dry since 1993 (Robertson and McGee 2003), therefore the significant growth of amphibious and aquatic plants from the seed bank indicates the presence of a persistent seed bank (c.f. transient seed bank), tolerant of desiccation. Similarly, Leck and Brock (2000) observed that temporary wetlands in Australia typically contain a persistent and species-rich seed bank, due in part to the unpredictability of the hydrological regime. As well as high species richness (59 taxa), a diverse range of aquatic, amphibious and terrestrial plants were represented in this study (Table 1). Such diversity of wetland plants is common for Australian wetlands, especially temporary systems were there is a high degree of spatial and temporal variability at the wet/dry ecotone (Leck and Brock 2000). However, anthropogenic disturbances may also have had an effect on the diversity of the seed bank. The clearing of *Eucalyptus* trees, the construction of levee banks, and past agricultural practices have fragmented the vegetation at Kanyapella Basin, potentially opening up niches for plants that did not previously occur.

Plant species not previously observed in the extant vegetation (Robertson 2006) were also recorded during the seed bank study (Table 1) including *Callitriche umbonata*, *Gratiola pumilo*, *Juncus holoschoenus*, *Nitella* spp., all of which are native and are tolerant of complete or partial inundation for a period of time (Walsh and Entwisle 1994, 1996, 1999; Romanowski 1998; Sainty and Jacobs 2003). Notably, *Gratiola pumilo* and *Callitriche umbonata* are listed as 'rare' in the state of Victoria (Department of Sustainability and Environment 2005). These results suggest, initially at least, that reestablishing a wetting and drying regime to Kanyapella Basin will provide conditions suitable for the return of native wetland plants. However, the prevalence of a few vigorous introduced aquatic plant species in the seed bank indicated increased flooding might also provide conditions for some unwanted aquatic plants. The impact of these introduced aquatic plants on the ecology of Kanyapella Basin also has to be considered during future wetland rehabilitation.

There are many factors that determine the seed bank potential of floodplain wetlands. This includes the longevity (persistence) and viability of seed banks in the absence of inundation, the rate of depletion and renewal of the seed bank, the germination strategies and traits of the constituent species, and the impacts of habitat disturbance on vegetation growth, reproduction and seed dispersal (Leck 1989; Keddy 2000). One of the main threats to the seed bank potential of Kanyapella Basin is the lack of flood events. While wetland plants have evolved a number of strategies to tolerate dry and unpredictable conditions, such as the dormancy, rapid growth, and large number of oospores produced by charophytes (Casanova and Brock 1999), the impacts of river regulation and agricultural development on isolating floodplain wetlands in southeastern Australia due has significantly altered wetland hydrology. While the response of the seed bank at Kanyapella Basin showed native wetland vegetation is likely to regenerate if an environmental water allocation is implemented, lack of flooding in the longer-term may affect the renewal of the seed banks, due to the reduced abundance of sexually-reproducing plants in the community.

Loss of the dispersal mechanism of flooding (hydrochory) may also limit efforts to rehabilitate floodplain wetland vegetation communities (Abernethy and Willby 1999). One advantage of the reduced spatial influence of hydrochory is that it removes a vector for the invasion of aquatic pest plants that occur at upstream aquatic sites.

Effect of water regime and elevation on plant community composition

Significant differences in the response of the seed bank to the flooded and dry treatments were observed in the experiment (Figs. 4, 5). Although the differential response of vegetation to the presence of water is what defines a wetland plant community (Mitsch and Gosselink 2000), there are few studies for degraded floodplain wetlands in southeastern Australia that describe how plant communities respond under different conditions. Understanding the response of wetland species to different regimes will allow managers to drive plant community structure in a desired direction. The plant species that explain the differences between the flooded and dry treatments may be suitable indicators for future management (e.g. Table 3).

It is well established that water depth is a driver of wetland plant community composition (e.g. van der Valk et al. 1994), which is related to the bathymetry of a particular system. Nicol et al. (2003) observed that the distribution of species across an elevation gradient is due principally to differential germination responses to water depth as opposed to differences in the seed bank composition. The flat nature of Kanyapella Basin meant the water depths applied in this study ranged from only 5 cm to 30 cm inundation along the elevation gradient (based on the hypothetical flood to 93.5 mAHD). Nonetheless, there were significant differences in the response of the seed bank between the samples inundated to 5 cm and 30 cm (Fig. 6). This indicates the likely outcome of an environmental water allocation of 3000 ML is a mosaic of floodplain wetland vegetation across Kanyapella Basin. The taxa that explained differences in species composition between the 5 cm and 30 cm water depths were dominated by those with high abundance in shallow water (Table 4). For example, a number of emergent macrophytes (e.g. *Alisma lanceolata*, *Eleocharis acuta*, *Limosella australis*) and wetland grasses (e.g. *Amphibromus* spp., *Polypogon monspelinesis*) did not establish in samples that were inundated to 30 cm. However, many of these species do grow in wetlands in water that is deeper than 30 cm, which may be the result of vegetative growth and propagation rather than germination by seed. Most of these plants were emergent species that are probably advantaged once some of their body parts are out of the water (Cronk and Fennessy 2001). From a management perspective, if a greater coverage of the plant community that established from the samples flooded to 30 cm is desired, a greater volume of environmental water may be needed. However, overall vegetation zonation was not evident in the dispersal of seed bank propagules, with plants typically widely dispersed across the wetland (e.g. Fig. 7), in contrast to the localised distribution of many of the plant species represented in the extant vegetation (Robertson 2006). Abernethy and Willby (1999) also found that vertical zonation was weakly developed with regard to propagule banks in floodplain aquatic habitats. Therefore, while previous water levels and period of inundation would differ depending on the position in the landscape from which the suite of cores were collected, results from this study also suggest that propagules for a diverse range of taxa were dispersed along the elevation gradient.

Differences in the abundance of introduced plants between the flooded and dry treatment, and along the elevation gradient also provided valuable information on the likely threat of introduced plants, including pest plants, under alternative management regimes. Large numbers of introduced terrestrial species are likely to establish if Kanyapella Basin remains dry (Figs. 3, 4). Flood events resulting from delivery of an environmental water allocation provide a tool for terrestrial but not aquatic weed control in wetlands such as Kanyapella Basin. Introduced plants were not excluded from the flooded samples, and a few aquatic pest plants, such as *Alisma lanceolata* often produced a large biomass and were widely distributed. Howell and Benson (2000) noted that while environmental flows are advocated to benefit native vegetation, in some situations environmental water can favour the spread and establishment of weeds, and identified the season and water level of floods as factors that determine the overall effect on management of native vegetation. Interestingly, the native fern *Azolla filiculoides* completely covered the water surface in some of the tubs in the experiment. Morris et al. (2003) observed a similar situation, where *Azolla* covered experimental mesocosms and reduced light conditions and dissolved oxygen in the water column. Although possibly an artifact of the experiment, due to ability of *Azolla* to cover the surface water in a confined area, the rapid growth of *Azolla* highlighted a vegetation response that may need to be monitored during flood events.

Effect of extant vegetation and environmental variables on the seed bank response

Many studies of wetland vegetation report there is little correlation between the plant communities that established from the seed bank and the extant vegetation (e.g. van der Valk and Davis 1976; Leck 1989; Nicol et al. 2003). This implies there are other factors driving the development of the vegetation that are not reflected in the seed bank trials. This questions the usefulness of seed bank studies in evaluating the impact of different management options on wetland vegetation. Using a geospatial framework, we investigated whether the seed bank communities were similar to the extant vegetation across the 45 sites examined at Kanyapella Basin. Not surprisingly, no patterns were observed between the extant vegetation and the plant community that established under flooded conditions. Kanyapella Basin had been predominantly dry for a number of years, which is reflected in the terrestrial nature of the extant vegetation. Extant vegetation was a predictor of the soil seed bank response under dry conditions to some degree (Table 5). While much of the study area of Kanyapella Basin was not severely impacted by introduced taxa compared to other regions of the wetland, the emergence of terrestrial introduced plants in many samples shows the potential for the plant community to change. Geospatial analysis also highlighted how some areas, which are currently 'weed-free', have the potential to become colonized, and potentially dominated by introduced plants if the wetland is not managed appropriately (Fig. 8). That much of the study area currently contains an intact River Red Gum (*E. camaldulensis*) forest with a substantial cover of leaf litter may be one factor limiting the establishment of terrestrial weeds.

The influence of other environmental variables on the variation in the seed bank was also investigated. The variables included GIS grid models of plant indices from the extant vegetation and other variables measured at sample sites and during the course of the experiment. The water quality of the flooded samples did not appear to influence the final floristic composition, although this is not surprising given the limited variation in water quality between treatments. There were no significant relationships observed between a single environmental variable, or set of environmental variables, related to the location of the soil core sample sites in the wetland and the seed bank plant community. While the search for other factors explaining the variation in plant composition was unsuccessful based on BIOENV results, the application of GIS to collate large datasets that describe the spatial variation of environmental variables was a valuable exploratory technique, which may be applied to similar studies elsewhere.

Use of soil seed bank investigations in floodplain wetland rehabilitation

The germination of buried viable propagules from degraded wetland systems is frequently the target of rehabilitation but is rarely explicitly stated in wetland management projects. Resilience of floodplain wetlands to prolonged periods of drought, or mismanagement, may be assessed through seed bank studies. While understorey vegetation at Kanyapella Basin is currently depleted due to the dry conditions (Robertson 2006), wetland vegetation responded rapidly from the seed bank in response to inundation. This is valuable information for natural resource managers and can be used provide a basis for wetland conservation through the use of environmental water allocations. Nias et al. (2003) described a number if instances in New South Wales, Australia where environmental water allocations were distributed to wetlands on private properties, many of which were dry and degraded prior to inundation. Native wetland vegetation returned significantly to most of these private wetlands demonstrating the presence of a resilient seed bank.

For seed bank studies to be useful to wetland management, the experimental design of the studies is important. Failure to consider the extent of inundation and the spatial variation in water depth and other environmental factors may reduce the applicability of results to floodplain wetland rehabilitation. The recent availability of high-resolution DEM for river-floodplain ecosystems in southeastern Australia provides many opportunities for the application of geospatial technologies to floodplain wetland rehabilitation, including seed bank studies. Van der Valk (2000) also identified there is much potential application of geospatial technologies in wetland rehabilitation. This study used GIS to relate seed bank results to the extant vegetation, and for assessing the spatial pattern of plant communities that established from the seed bank. In future, results from the seed bank study can be integrated into models that predict the change in vegetation under alternative water management scenarios.

Conclusion

Seed bank studies of floodplain wetlands can direct conservation actions by identifying the diversity and composition of wetland plant communities that may establish under alternative water management scenarios. However, to be applicable to management, the spatial variation of wetland inundation must be taken into consideration in the design of seed bank investigations.

Information gained from the seed bank study at Kanyapella Basin supported the aim of management to implement an environmental water allocation, highlighting that native wetland plants are likely to reestablish. This knowledge is highly valuable to conservation management and decision-making.

Acknowledgments Constructive reviews of earlier drafts of the manuscript were received from Keely Ough, Dr James Fitzsimons and Brooke Turner. Thanks also to Keely Ough for assistance with plant identification and advice on seed bank experiment methodology, Tricia Paradise for help harvesting plants, and Dr Sabine Schreiber for advice on experimental design. Deakin University, Field and Game Australia, Australian Research Council, Goulburn–Murray Water, Parks Victoria, Victorian Department of Sustainability and Environment, Goulburn-Broken Catchment Management Authority and the River Basin Management Society provided financial and/or in-kind support for this project.

References

Abernethy VJ, Willby NJ (1999) Changes along a disturbance gradient in the density and composition of propagule banks in floodplain aquatic habitats. Plant Ecol 140:177–190

Aston HI (1993) New Australian species of *Triglochin* L. (JUNCAGINACEAE) formerly included in *T. procerum* R. Br. Muelleria 8:85–97

Aston HI (1995) A review of the tuberous-rooted species of *Triglochin* L. (JUNCAGINACEAE) in Australia. Muelleria 8:331–364

Britton DL, Brock MA (1994) Seasonal germination from wetland seed banks. Australian J Mar Fresh Res 45:1445–1457

Brock MA, Casanova MT (1997) Plant life at the edge of wetlands: ecological responses to wetting and drying patterns. In: Klomp N, Lunt I (eds) Frontiers in ecology: building the links. Elsevier Science, Oxford, pp 181–194

Brock MA, Theodore K, O'Donnell L (1994) Seed-bank methods for Australian wetlands. Australian J Mar Fresh Res 45:483–493

Brown SC (1998) Remnant seed banks and vegetation as predictors of restored marsh vegetation. Can J Bot 76:620–629

Brown SC, Bedford BL (1997) Restoration of wetland vegetation with transplanted wetland soil: an experimental study. Wetlands 17:424–437

Bunn SE, Arthington AH (2002) Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. Environ Manage 30:492–507

Casanova MT, Brock MA (1999) Life histories of Charophytes from permanent and temporary wetlands in eastern Australia. Australian J Bot 47:383–397

Casanova MT, Brock MA (2000) How do depth, duration and frequency of inundation influence the establishment of wetland plant communities? Plant Ecol 147:237–250

Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. Australian J Ecol 18:117–143

Clarke KR, Gorley RN (2000) PRIMER 5 for Windows. PRIMER-E, Plymouth

Clarke KR, Warwick RM (2001) Change in marine communities: an approach to statistical analysis and interpretation. 2nd edn. PRIMER-E, Plymouth

Coops H, van der Velde G (1995) Seed dispersal, germination and seedling growth of six helophyte species in relation to water-level zonation. Fresh Biol 34:13–20

Commonwealth Bureau of Meteorology (2001) Climate records from Echuca aerodrome weather station, Victoria. Commonwealth Bureau of Meteorology, Australia. Source: http://www.bom.gov.au. Accessed September 2001

Cronk JK, Fennessy MS (2001) Wetland plants: biology and ecology. Lewis Publishers, Boca Raton, Fl

Cunningham GM, Mulham WE, Milthorpe PL, Leigh JH (1992) Plants of Western New South Wales, 2nd edn. NSW Soil Conservation Service, NSW Government Printing Office, Sydney

Department of Natural Resources and Environment (2002). Kanyapella Basin 1m Ground DEM and 1 m First DEM LiDAR Geographic Information System Data. Land Information Group, Department of Natural Resources and Environment, Melbourne

Department of Sustainability and Environment (2005). Advisory list of rare or threatened plants in Victoria – 2005. Department of Sustainability and Environment, East Melbourne

Galatowitsch SM, van der Valk AG (1996) The vegetation of restored and natural prairie wetlands. Ecol Appl 6:102–112

Howell J, Benson D (2000) Predicting potential impacts of environmental flows on weedy riparian vegetation of the Hawkesbury-Nepean River, south-eastern Australia. Austral Ecol 25:463–475

Jensen JR, Narumalani S, Weatherbee O (1992) Predictive modelling of cattail and waterlily distribution in a South Carolina reservoir using GIS. Photo Eng Rem Sens 58:1561–1568

Keddy P (2000) Wetland ecology: principles and conservation. Cambridge University Press, Cambridge

Leck MA (1989) Wetland seed banks. In: Leck MA, Parker VT, Simpson RL (eds) Ecology of soil seed banks. Academic Press Inc., San Diego, CA

Leck MA, Brock MA (2000) Ecological and evolutionary trends in wetlands: Evidence from seeds and seed banks in New South Wales, Australia and New Jersey, USA. Plant Species Biol 15:97–112

Legendre P, Legendre L (1998) Numerical ecology (2nd English edn). Elsevier Science, Amsterdam, The Netherlands

Lehmann A, Lachavanne JB (1997) Geographic information systems and remote sensing in aquatic botany. Aqu Bot 58:195–207

Mantel N (1967) The detection of disease clustering and a generalized regression approach. Cancer Res 27:209–220
Mitsch WJ, Gosselink JG (2000) Wetlands. John Wiley and Sons, Inc., New York
Morris K, Bailey PC, Boon PI, Hughes L (2003) Alternative stable states in the aquatic vegetation of shallow urban lakes. II. Catastrophic loss of aquatic plants consequent to nutrient enrichment. Mar Fresh Res 54:201–215
Narumalani S, Jensen JR, Althausen JD, Burkhalter S, Mackey HE Jr (1997) Aquatic macrophyte modeling using GIS and logistic multiple regression. Photo Rem Sens 63:41–49
Nias DJ, Alexander P, Herring M (2003) Watering private property wetlands in the Murray Valley, New South Wales. Ecol Manage Rest 4:5–12
Nicol JM, Ganf GG, Pelton GA (2003) Seed banks of a southern Australian wetland: the influence of water regime on the final floristic composition. Plant Ecol 168:191–205
Poiani KA, Johnson WC (1993) A spatial simulation model of hydrology and vegetation dynamics in semi-permanent prairie wetlands. Ecol Appl 3:279–293
Quinn GP, Keough MJ (2002) Experimental design and data analysis for biologists. Cambridge University Press, Cambridge
Roberts J, Ludwig JA (1991) Riparian vegetation along current-exposure gradients in floodplain wetlands of the River Murray. Australian J Ecol 79:117–127
Roberts J, Marston F (2000) Water regime of wetland and floodplain plants in the Murray-Darling Basin: a source book of ecological knowledge. CSIRO Land and Water, Canberra
Roberts J, Young B, Marston F (2000) Estimating the water requirements of plants of floodplain wetlands: a guide. Occasional Paper 04/00, Land and Water Resources Research and Development Cooperation, Canberra
Robertson HA, James KJ (2002) Determining the water requirements for the rehabilitation of wetland habitat at Kanyapella Basin. Victoria Ecol Manage Rest 3:220–221
Robertson HA, James KJ (2005) Environmental Management Plan for Kanyapella Basin. Prepared for Department of Primary Industries and Department of Sustainability and Environment, Victoria. School of Ecology and Environment Deakin University, Burwood
Robertson HA, McGee TK (2003) Applying local knowledge: the contribution of oral history to wetland rehabilitation at Kanyapella Basin. Australian J Environ Manage 69:275–287
Robertson HA (2006) Environmental water requirements of isolated floodplain wetlands: Kanyapella Basin, Australia. Unpublished PhD Thesis submitted for examination February 2006, Deakin University, Burwood
Romanowski N (1998) Aquatic and wetland plants: a field guide for non-tropical Australia. UNSW Press, Sydney
Ross JH, Walsh NG (eds) (2003) Census of the vascular plants in Victoria. Royal Botanical Gardens, Melbourne
Sainty GR, Jacobs SWL (2003) Waterplants in Australia, 4 edn. Sainty and Associates Pty Ltd, Potts Point, NSW
Schofield N, Burt A, Connell D (2003) Environmental water allocation: principles, practices, policies, progress and prospects. Land and Water Australia, Canberra
Smith SM, McCormick PV, Leeds JA, Garrett PB (2002) Constraints of seed bank species composition and water depth for restoring vegetation in the Florida Everglades. U.S.A. Rest Ecol 10:138–145
van der Valk AG (2000) Vegetation dynamics and models. In: Murkin HR, van der Valk AG, Clark WR (eds) Prairie wetland ecology: the contribution of the Marsh Ecology Research Program. Iowa State University Press, Ames, Iowa, pp 125–161
van der Valk AG, Davis CB (1976) The seed bank of prairie glacial marshes. Can J Bot 54:1832–1838
van der Valk AG, Davis CB (1978) The role of seed banks in the vegetation dynamics of prairie glacial marshes. Ecology 59:322–335
van der Valk AG, Squires L, Welling CH (1994) Assessing the impacts of an increase in water level on wetland vegetation. Ecol Appl 4:525–534
Walsh NG, Entwisle TJ (eds) (1994) Flora of Victoria Volume 2: ferns and allied plants, conifers and monocotyledons. Inkata Press, Melbourne
Walsh NG, Entwisle TJ (eds) (1996) Flora of Victoria Volume 3: dicotyledons - Winteraceae to Myrtaceae. Inkata Press, Melbourne
Walsh NG, Entwisle TJ (eds) (1999) Flora of Victoria Volume 4: dicotyledons – Cornaceae to Asteraceae. Inkata Press, Melbourne
Wilson SD, Moore DRJ, Keddy PA (1993) Relationships of marsh seed banks to vegetation patterns along environmental gradients. Fresh Biol 29:361–370
Williams DC, Lyon JG (1997) Historical aerial photographs and a geographic information system (GIS) to determine effects of long-term water level fluctuations on wetlands along the St. Marys River USA. Aqu Bot 58:363–378
Young WJ (eds) (2001) Rivers as ecological systems: the Murray-Darling Basin. Murray-Darling Basin Commission, Canberra