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WATER REGIMES AND LITTORAL PLANTS IN FOUR WEIR POOLS OF THE RIVER MURRAY, AUSTRALIA

STUART J. BLANCH[a,b,*], KEITH F. WALKER[a,b] AND GEORGE G. GANF[a]

[a] *Department of Environmental Biology, University of Adelaide, Adelaide, South Australia 5005, Australia*
[b] *Cooperative Research Centre for Freshwater Ecology, Albury, NSW, Australia*

ABSTRACT

The composition and distribution of littoral vegetation in four weir pools of the lower Murray were surveyed in summer 1994. Between-weir gradients in the amplitude of water level fluctuations were reflected in the typical distributions of plants, with a 4–6 m elevational range in upper-pool sites, where levels fluctuate most, and a 1–1.5 m band in the lower-pool sites, where levels are more stable. Forty-one of 48 species occurred across much of the longitudinal × elevational site matrix within this cone-shaped distribution, indicating considerable tolerance to flooding and exposure; this was especially apparent for *Phragmites australis*, *Cyperus* spp. and *Centipeda* spp. The 41 species were represented in seven of nine water-regime groups identified by cluster analysis. The remainder, found within ± 1 m of the water surface in lower-pool reaches, were aquatic macrophytes such as *Vallisneria americana* and *Typha* spp. and amphibious 'mudmats' such as *Glossostigma elatinoides*. Water regimes at given sites were measured by the number of days in 2 years flooded to any depth (>0 cm), or to 0–30 cm, and by days exposed by >100 cm. Inter-pool differences in the median number of days flooded to >0 cm and 0–30 cm were 3–30% and <8%, respectively, for all species except *Typha* spp. but an order of magnitude for the number of days exposed by >100 cm. However, eight of 14 common or representative species analysed showed significant inter-pool differences in the number of days flooded to >0 cm, indicating that sufficient variation exists to necessitate considerable intra-pool replication to allow for the detection of statistical differences in a multi-pool experiment. The practice of maintaining stable weir pool levels limits vegetation processes, e.g. germination, recruitment, decomposition. An increase in the amplitude of river level fluctuations during low flows, from the current 10–20 cm range to 20–50 cm, would reinstate water regimes suitable to the majority of species surveyed. Copyright © 2000 John Wiley & Sons, Ltd.

KEY WORDS: floodplain; littoral; macrophyte; Murray; regulation; vegetation; water regime; weir

INTRODUCTION

'Water regime', referring to patterns in the spatial and temporal distribution of water, is a key variable for the littoral vegetation of regulated, lowland rivers (e.g. Rørslett, 1989; Bornette and Amoros, 1991, 1996; Wilcox and Meeker, 1991; Shaltout and El-Sheikh, 1993; Fischer and Claflin, 1995; Nilsson *et al*., 1997), especially in arid and semi-arid regions (e.g. Breen *et al*., 1988; Rea and Ganf, 1994; Brock, 1999; Casanova, 1999). In Australia, the lower River Murray (the 830 km stretch below the Murray–Darling confluence) is a focus for studies of this kind. The Murray–Darling system is regulated by upstream dams, and the lower Murray is further controlled by ten weirs and barrages, each 3 m high (e.g. Walker and Thoms, 1993). Two surveys (1989, 1994) have shown that the composition and distribution of vegetation along the weir pool margins are associated with gradients of water regime related to weir operations (Walker *et al*., 1994; Blanch and Walker, 1997; Blanch *et al*., 1999).

This paper complements analyses of the 1994 survey, in which the aims were to determine the distributions of littoral plants along longitudinal and vertical gradients in a single pool, and to describe the water regime requirements of representative plants. Inter-pool variation in optimum water regimes is examined for common species in the present study. If variation is minimal, pools may be cautiously considered as replicates for the purposes of research and management.

* Correspondence to: Inland Rivers Network, 33 George Street, Sydney, NSW 2000, Australia. E-mail sblanch@irnnsw.org.au

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METHODS

The distribution and cover or abundance of 48 plants were surveyed over 14 days in four weir pools (3, 5, 6, 9), all relatively little affected by grazing, vegetation clearance and urban or agricultural development. Species distributions were compared by plotting them relative to pool length (hence proportional rather than absolute distances). This assumes that the water-regime gradients between weirs are independent of pool length (cf. Maheshwari *et al*., 1995). Surveys were made in January and February 1994, 1–2 months after flooding. Two floods occurred during this period, both rising about 4 m above pool level. The 1992 flood commenced in August, peaked in November and receded to pool level by February. In 1993, the river rose to 1–1.5 m above pool level from April–June, peaked in November and returned to pool level by January 1994. All quadrats surveyed, except those at the highest floodplain elevations in the upper pools, were inundated by both floods.

Survey methods are described by Blanch *et al*. (1999). Plants were scored on a scale that incorporated estimates of abundance and cover (Table I). At each site, three 5 m wide transects were selected randomly over a 100 m section of bank perpendicular to the river. Plant distributions were scored in quadrats equivalent to a vertical height-change of 20–100 cm above and below the water level, measured by dumpy level and staff. Quadrats below the surface and over the first 150 cm above the surface were 20 cm high; thereafter 50 and 100 cm high. This reflected more rapid changes in plant zonation near pool level. Transects extended from 1 m below the surface to the top of the bank, and where possible included up to 20 m of adjacent floodplain. At each site, species scores were averaged across transects within quadrats at the same elevation.

Cluster analysis (flexible UPGMA) identified water regime groups across pools, and these were overlaid with a minimum spanning tree of species similarities (Belbin, 1993; see Blanch *et al*., 1999). Water regimes were defined by the number of days, during the 2 years (730 days) before the survey, for which a quadrat was flooded to any depth (>0 cm) or to 0–30 cm, or exposed by >100 cm. Although they detect only a portion of the ecologically important aspects of water regime, these three indices were chosen because they identify the most relevant aspects for the species studied. A 2-year period was considered an adequate compromise between the temporal scales relevant for recruitment, growth and reproduction in annuals (weeks to months) and perennials (years for species such as lignum, *Muehlenbeckia florulenta*). Daily stage data for each quadrat were derived by linear interpolation of gauged data for the nearest weirs (courtesy South Australia Water), and indices were calculated for all quadrats in all transects using a program written in QBASIC. Indices refer to the midpoint rather than the base of a vertical quadrat (cf. Blanch *et al*., 1999), to better represent flooding and drying patterns across the whole quadrat.

Plant distributions are shown as a proportion of weir pool length, rather than in absolute distances, to facilitate comparisons. In the lower River Murray the river consists entirely of weir pools, extending from the downstream side of one weir to the upstream side of the next. Actual pool lengths between weirs (river kilometres) were 83 km (Pool 3), 58 km (Pool 5), 77 km (Pool 6) and 61 km (Pool 9). Forty-eight species were identified in 543 quadrats. Only species found in at least three quadrats are included here, and trees also were excluded. In the field it was necessary to group *Typha domingensis* with *T. orientalis*, *Centipeda cunninghamii* with *C. minima* and *Xanthium californicum* with *X. occidentale*. Nomenclature follows Black (1980), allowing for revisions by Jessop (1993), Munir (1993; *Phyla canescens*) and Jacobs and Frank (1998; *Vallisneria americana*).

RESULTS

Vegetation patterns

Most species showed a 'cone-shaped' longitudinal distribution (that is, they occurred at an elevation of 4–6 m in the uppermost 10% of weir pools, narrowing to 1–1.5 m in the lower 10%) (Figure 1). This corresponds to water regime gradients established between weirs (Maheshwari *et al*., 1995; Blanch *et al*., 1999). Fluctuations in the tailwaters (upper pools) promote germination and growth across a wider range of elevations than in the comparatively stable reaches above each weir (lower pools).

Table I. Hybrid cover/abundance scale used for surveying plants

Cover/abundance score		Plant size (growth forms and examples)		
		Small (herbs, mudmats) *Centipeda*, *Phyla*, *Pratia*	Medium (tussock and creeping grasses, low sedges and shrubs) *Paspalidium*,*Cyperus gymnocaulos*, *Cynodon*, *Senecio*	Large (reeds, tall rushes, tall sedges and shrubs) *Typha*, *Muehlenbeckia*, *Phragmites*, *Cyperus exaltatus*, *Bolboschoenus*
1	Rare	1 or 2 m^{-2}	1 ramet/runner m^{-2}	—
2	Individuals: very few or few. Infrequent	3, 4, 5 or 6 individuals or ramets m^{-2}	2 ramets/runners m^{-2}	1 small individual or ramet m^{-2}
3	Individuals: few-large or many-small. Frequent.	7, 8, . . . , 20 individuals or ramets m^{-2}	3, 4, 5 or 6 m^{-2}	2 small individuals or ramets m^{-2}
4	Individuals: very abundant. One large individual or band of emergents along water's edge	> 20 m^{-2}	7, 8, 9, . . . m^{-2}	
5	Nearly continuous. Common.	Many overlapping 'clumps' but still some gaps	Most ramets touching adjacent conspecifics, but still some gaps	Dominant overstorey with groundcover
6	Continuous (sparse to monospecific)	All individuals touching adjacent conspecifics	All individuals touching adjacent conspecifics	Dense, no other species common

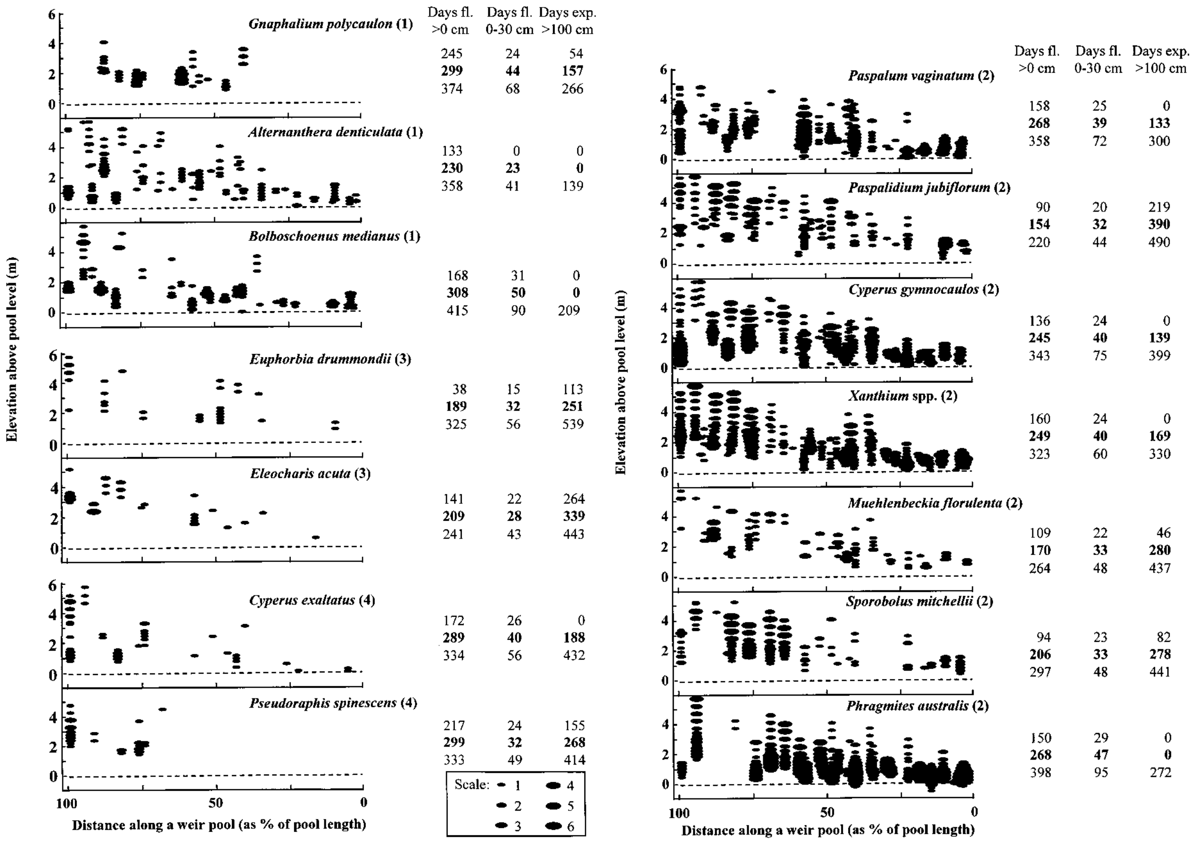

Figure 1. Similarities in species distribution and cover/abundance in 21 littoral plants across four weir pools in the lower River Murray. Data for the four pools are overlain. Position along a weir pool is standardized across the four pools: 0% at the downstream end of the pool, and 100% at the upstream end of the pool. The direction of flow is left to right. Cover/abundance scores are represented by ovals (see Table I). Flooding and drying preferences are indicated by 25th, 50th (median) and 75th percentiles (proceeding down the page for each species, with medians in bold) for three water regime indices: numbers of days in the two preceding years flooded to >0 cm (any depth) and 0–30 cm, and exposed by >100 cm (max. days: 730). UPGMA groups are in parentheses for each species (see Figure 2). Dashed lines indicate the design weir pool level

Many species occurred across sites with diverse water regimes, indicating wide tolerances to flooding and exposure. The ten most common species were *Xanthium* spp. (52% of 543 quadrats), *Phragmites australis* (46%), *Centipeda* spp. (42%), *Cyperus gymnocaulos* (40%), *Paspalum vaginatum* (31%), *Paspalidium jubiflorum* (27%), *Alternanthera denticulata* (21%), *Bolboschoenus medianus* (16%) and *M. florulenta* (14%). The rarest included species were *Elatine gratioloides* (1%), *Persicaria prostrata* (2%), *Cyperus rigidellus* (2%), *V. americana* (3%) and *Pseudoraphis spinescens* (4%).

Cover/abundance scores generally concur with observed flooding and drying requirements. Thus, species in the often-flooded littoral had higher scores at lower elevations (e.g. *B. medianus*, *P. australis*), but floodplain species had higher scores at higher elevations (e.g. *P. canescens*, *Sporobolus mitchellii*). Aquatic species were restricted to the lower third of weir pools, generally within ± 1 m of pool level (*Schoenoplectus validus*, *Typha* spp., *V. americana*). Mudmat species (*E. gratioloides*, *Glossostigma elatinoides*), found in often-flooded shallow silted areas, and the rooted emergent *Myriophyllum papillosum* occurred rarely in the first 30% of pools, from the wave wash-zone (± 0.30 m) to about 0.40 m below pool level.

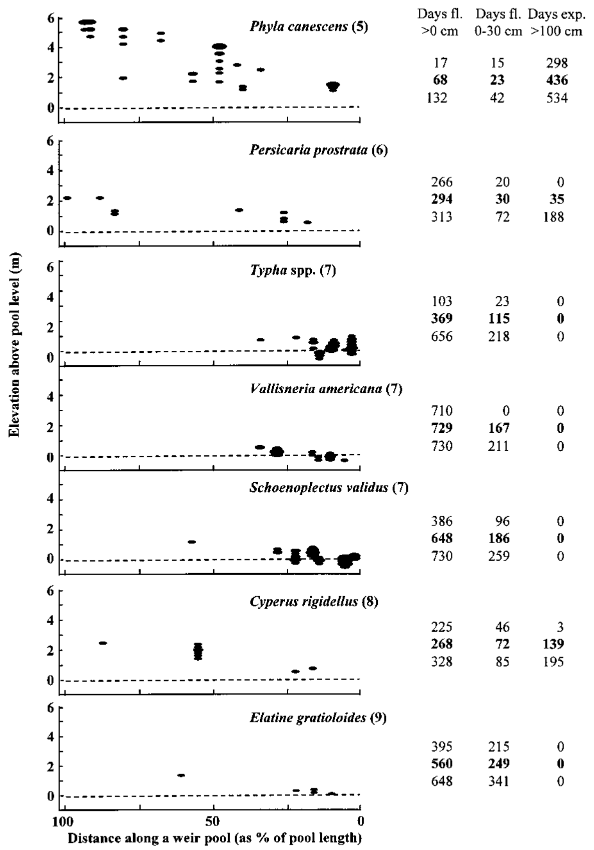

Figure 1 (*Continued*)

Water regime indices

Species distributions, shown on the left hand side of Figure 1, correspond with measured indices of water regime, shown on the right. For example, the herb *Gnaphalium polycaulon* occurred in areas flooded to >0 cm for a median 299 in 730 days, and in areas exposed by >100 cm for a median 157 in 730 days. This accords with its observed range of 40–85% along a pool, at 1–4 m elevation. Similarly, the submersed ribbonweed *V. americana* occurred where flooding was virtually continuous (median 729 in 730 days flooded to >0 cm), and never where exposure was >100 cm (but see Blanch *et al.*, 1999). The floodplain grass *P. spinescens* was most common in the upper 25% of each pool at elevations of 1.5–5 m, where exposure to >100 cm is nearly as frequent as flooding (medians 268 and 299 in 730 days, respectively), and shallow flooding is uncommon (median 32 in 730 days).

Inter-pool variation in optimum water regime

Eight of the 14 species in Table II showed significant differences ($p = 0.01$) between pools in the number of days flooded to >0 cm. The 14 species were considered to be of particular ecological significance, being either common or representative of other species with similar habit, or possessing a narrow range of apparent water regime tolerances. However, inter-pool variation in median indices generally were low for the number of days flooded to >0 cm and 0–30 cm. Variation in the median number of days flooded to >0 cm was low for *Centipeda* spp. (34–44% of 730 days), *M. florulenta* (21–28%), and *Xanthium* spp. (34–41%), but higher in *A. denticulata* (22–51%) and *C. gymnocaulos* (17–44%).

Table II. Water-regime preferences of 14 common or representative plant species in four weir pools

Species	Pool 3			Pool 5			Pool 6			Pool 9			F	p
	>0	0–30	>100	>0	0–30	>100	>0	<30	>100	>0	<30	>100		
Alternanthera denticulata	25	5	0	40	5	0	14	3	10	12	2	17		
(29, 24, 51, 14)	**39**[ab]	**9**	**0**	**51**[a]	**8**	**0**	**33**[bc]	**5**	**40**	**22**[c]	**3**	**61**	12.97	<0.001
	54	13	27	62	10	27	42	8	60	24	5	75		
Bolboschoenus medianus	34	4	0	28	6	0	5	4	0	41	6	0		
(33, 26, 24, 9)	**49**[ab]	**7**	**0**	**45**[a]	**8**	**0**	**27**[b]	**6**	**15**	**45**[ab]	**13**	**0**	4.20	0.008
	60	13	20	63	13	45	49	9	45	60	22	0		
Centipeda spp.	29	4	6	27	5	0	14	3	6	23	3	23		
(77, 27, 67, 60)	**39**	**6**	**27**	**44**	**6**	**0**	**34**	**6**	**30**	**36**	**4**	**39**	3.14	0.026
	46	10	44	55	9	32	51	10	55	42	6	59		
Cynodon dactylon	20	3	8	27	5	0	12	3	28	26	3	1		
(78, 34, 37, 56)	**29**[ab]	**5**	**38**	**39**[a]	**7**	**21**	**21**[b]	**5**	**43**	**34**[a]	**4**	**38**	7.97	<0.001
	41	8	56	44	11	39	35	7	67	40	6	58		
Cyperus gymnocaulos	18	3	0	27	5	0	6	3	0	5	3	0	8.80	<0.001
(93, 53, 30, 44)	**29**[b]	**5**	**36**	**44**[a]	**8**	**0**	**17**[c]	**5**	**6**	**37**[ab]	**5**	**4**		
	41	8	60	62	12	37	51	6	41	44	11	56		
Muehlenbeckia florulenta	18	3	15	18	3	42	10	3	10	17	3	0		
(44, 6, 14, 11)	**28**	**5**	**40**	**23**	**5**	**56**	**22**	**5**	**38**	**21**	**5**	**40**	1.21	0.31
	41	7	62	30	6	60	38	9	60	28	6	64		
Paspalidium jubiflorum	12	3	50	21	5	37	3	2	40	19	2	0		
(39, 25, 46, 29)	**18**[bc]	**4**	**60**	**31**[a]	**6**	**41**	**16**[c]	**3**	**57**	**23**[ab]	**4**	**49**	6.98	<0.001
	24	5	71	39	8	59	32	6	78	28	6	66		
Paspalum vaginatum	22	4	0	41	5	0	13	3	2	21	4	0		
(74, 29, 54, 12)	**33**[b]	**5**	**19**	**52**[a]	**6**	**0**	**34**[b]	**5**	**28**	**36**[ab]	**8**	**2**	11.19	<0.001
	46	2	48	63	12	27	48	8	44	51	14	55		
Phragmites australis	20	3	0	27	6	0	12	3	0	27	5	0		
(89, 61, 57, 55)	**32**[bc]	**5**	**13**	**42**[a]	**8**	**0**	**23**[c]	**6**	**26**	**43**[ab]	**7**	**0**	9.41	<0.001
	46	12	54	63	16	22	50	10	60	60	15	1		
Pseudoraphis spinescens	27	4	22	28	3	55	24	5	25	—	—	—		
(20, 2, 3, 0)	**41**	**4**	**37**	**29**	**4**	**56**	**46**	**7**	**28**	—	—	—	NA	
	46	7	56	30	4	58	49	9	54	—	—	—		
Sporobolus mitchellii	16	3	9	17	5	0	5	2	21	—	—	—		
(63, 13, 21, 0)	**28**	**5**	**42**	**31**	**5**	**37**	**19**	**4**	**45**	—	—	—	2.12	0.125
	41	6	64	42	7	40	40	7	67	—	—	—		

Table II. (Continued)

Species	Pool 3			Pool 5			Pool 6			Pool 9			F	p
	>0	0–30	>100	>0	0–30	>100	>0	<30	>100	>0	<30	>100		
Typha spp.	51	18	0	100	0	0	12	4	0	68	41	0		
(2, 3, 20, 2)	**52**	**22**	**0**	**100**	**0**	**0**	**26**	**7**	**0**	**79**	**49**	**0**	NA	
	54	25	0	100	13	0	81	30	12	89	56	0		
Vallisneria americana	89	23	0	100	0	0	—	—	—	—	—	—		
(9, 6, 0, 0)	**100**	**27**	**0**	**100**	**0**	**0**	—	—	—	—	—	—	NA	
	100	32	0	100	0	0	—	—	—	—	—	—		
Xanthium spp.	22	3	5	27	6	0	16	3	8	24	3	0		
(84, 51, 92, 61)	**36**[a]	**5**	**31**	**41**[a]	**8**	**0**	**34**[b]	**5**	**37**	**34**[ab]	**5**	**1**	7.43	<0.001
	44	8	54	55	12	37	45	8	52	42	6	40		

Numbers in the body of the table are percentages of 2 years (730 days) when plants were flooded to depths indicated by each column (flooded to >0 cm or 0–30 cm, and exposed by >100 cm). Tolerance ranges are indicated by 25th, 50th (median, in bold) and 75th percentiles, proceeding down the page for each species. One-way ANOVA was conducted on the number of days flooded to >0 cm followed by Tukey's Honestly Significant Difference test for unequal n ($p < 0.01$). Normality was tested using the Shapiro–Wilk statistic, and homoscedasticity was tested with Bartlett's chi-squared test: data were $\log_e$-transformed if found to be not normally distributed. Different letters indicate a significant difference at $p = 0.05$ between pools (Zar, 1996). For each species, pools with <5 records were not analysed. NA, no analyses. Numbers in parentheses show the number of quadrats in which each species was recorded in the four respective pools.

The median numbers of days flooded to >0 cm were highest in Pool 5 for all species (or not significantly lower than in other pools), and lowest for Pool 6 (or not significantly higher than for other pools). The reason for such consistency is unclear.

Variation in the median number of days flooded to 0–30 cm was $<8\%$ for all species (except *Typha* spp., for which there are insufficient data). No difference in median values was observed across the four pools for *M. florulenta*, with differences of 3% amongst 75th percentile values.

Inter-pool variation for the median number of days exposed by >100 cm was higher by an order of magnitude or more for eight species, including *C. gymnocaulos* (4–36%) and *P. australis* (0–26%).

The data suggest that, whilst there are strong similarities in the water regime indices for most species across the four pools, sufficient variation exists to necessitate considerable intra-pool replication to allow for the detection of statistical differences in a multi-pool experiment. Sources of inter-pool variation include heterogeneous sediments (coarse sands to heavy clays and organic loams), nutrient availability, shading, current velocity and impacts of currents upon propagule dispersal. Also, species such as *P. prostrata* and *E. gratioloides* were in few surveyed quadrats, or in only one to two pools, making balanced comparisons difficult.

Pattern analyses and water regime requirements

Nine water regime groups identified by UPGMA clustering (Figure 2) were overlaid on a 'minimum spanning tree' of species similarities (Figure 3). Groups 1–2 included nearly half of the 48 species recorded (11 and 12 species, respectively), and included the most common species. Together, these exhibit diverse morphological and reproductive adaptations that equip them for a range of water regimes, allowing occupation of essentially any sites except those underwater at 25–100% along a pool. Conspicuous adaptations include clonal growth (e.g. *P. vaginatum*), rapid seed production (*Xanthium* spp.), underground carbohydrate storage (*B. medianus*) and a rapidly elevating canopy (*P. australis*) (Blanch *et al*., 1999).

Group 1 is primarily herbs and shrubs in frequently flooded and exposed areas (e.g. *A. denticulata*), but all, except for *G. polycaulon* and perhaps *B. medianus*, are vulnerable to prolonged inundation. Group 1 species occur at 0–6 m elevation along the length of the pools (Figure 1). Cover/abundance is highest at lower elevations. *G. polycaulon* occurred only on sandy beaches on protected inner bends in the upper halves of pools.

Group 2 species are widespread and common, with broad tolerances to flooding and drying. They are predominantly clonal, rhizomatous monocotyledons (*Cynodon dactylon*, *P. vaginatum*, *P. australis*, *C. gymnocaulos*), fecund herbs (*Centipeda* spp., *Xanthium* spp.), and drought-tolerant shrubs (*M. florulenta*, *Glycyrrhiza acanthocarpa*). Six of seven grasses recorded are in this group. Both Groups 1 and 2 have similar water regime indices, but Group 2 species had higher cover/abundance scores (means 1.00, 1.75 for Groups 1 and 2, respectively).

Groups 3–6 were at sites similar to those in Groups 1–2, but were less common (mean scores 0.51–1.16) and had narrower flooding and drying tolerances. There is a progression from species in Groups 3 and 5, which prefer drier conditions in the upper littoral (medians of 168 days and 169 days (in 730 days) flooded to >0 cm, and 402 days and 362 days exposed to >100 cm, respectively), to species in Groups 4 and 6, at lower elevations (median 254 days and 288 days flooded to >0 cm, and 280 days and 188 days exposed to >100 cm, respectively).

Group 3 species inhabit mainly the drier upper littoral and floodplain, and did not generally occur at elevations <1.5–2 m in the lower 50% of each pool (e.g. *E. acuta*, Figure 1). Group 5 species such as *P. canescens* had higher cover/abundance scores at the upper ranges of their distributions. Group 4 species are mainly monocotyledons with protected below-ground anchorage and desiccation-resistant foliage (e.g. *C. exaltatus*, *P. spinescens*). Group 6 species such as *P. prostrata* are uncommon in the lower littoral.

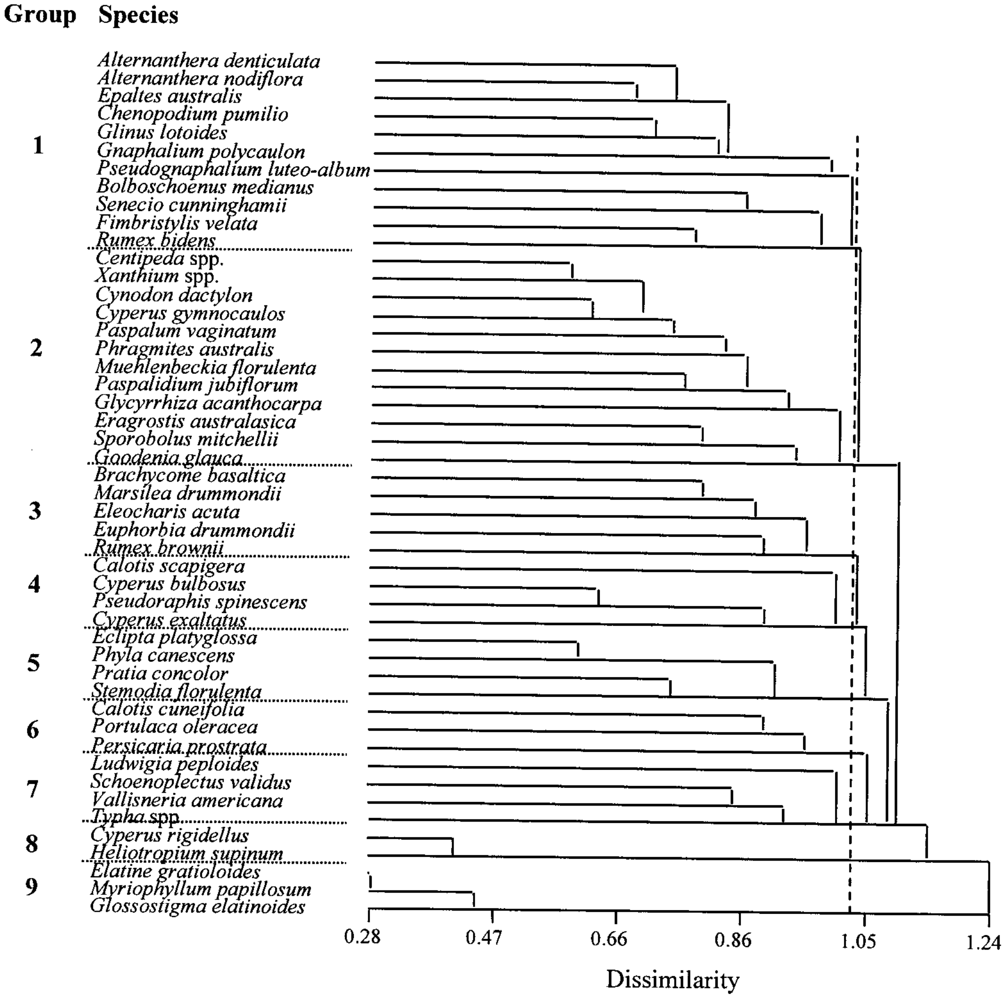

Figure 2. Dendrogram for 48 species across four weir pools, using flexible UPGMA clustering

Group 7 includes aquatic macrophytes recorded in quadrats with a median 419 days (of 730 days) flooded to >0 cm and no exposure to >100 cm. Mudmats (*E. gratioloides*, *Glossostigma elatinoides*) and one rooted emergent macrophyte (*M. papillosum*) species in Group 8 had even narrower tolerances to flooding and drying (median 395 days (of 730 days) flooded to >0 cm, and lower and upper quartiles of 271 days and 604 days, respectively). Group 9 contains two species with narrow water regime requirements, but few were recorded (seven and nine for *Heliotropium supinum* and *C. rigidellus*, respectively).

Potamogeton tricarinatus and *M. verrucosum* occurred in only two quadrats and were excluded from analyses, but their water regime requirements appear to be most similar to those in Group 7 and, to a lesser extent, Group 9.

E. gratioloides and *M. papillosum* are the most 'similar' species according to cluster analysis (the line joining them in the minimum spanning tree (Figure 3) is the shortest of all species–species links). This is perhaps because they were in very few (but shared) quadrats. *Xanthium* spp. and *Centipeda* spp. also were similar, although among the three commonest species (pairwise association 0.58).

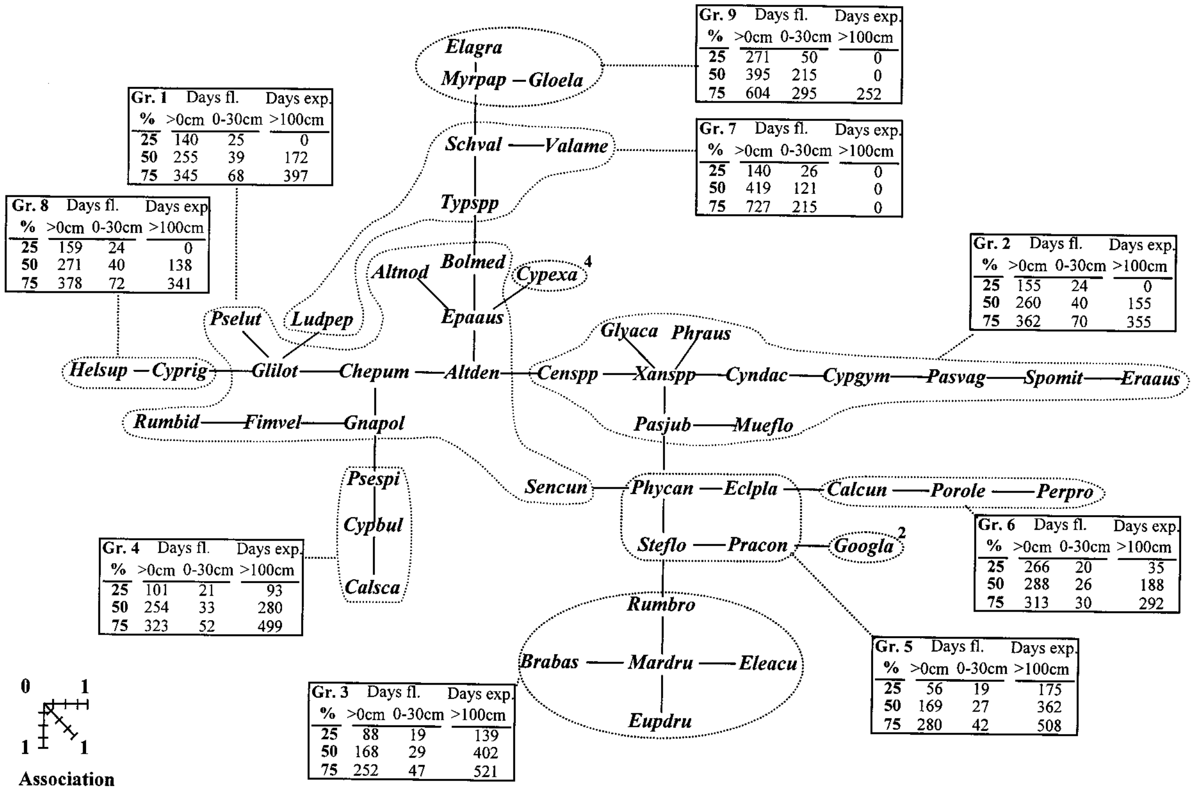

Figure 3. Minimum spanning tree analysis of species relationships with UPGMA groups superimposed. Six-letter codes are the first three letters in the genus and species names (see Figure 2). Line length is proportional to species similarity (short lines reflect greater similarity), based on pairwise association values. Water regime indices are shown for each group (Groups 1–9). Flooding and drying tolerance ranges are indicated by 25th, 50th (median) and 75th percentiles. *Cyperus exaltatus* (Group 4) and *Goodenia glauca* (Group 2) could not be included in the superimposed groups in two dimensions, hence their group numbers are indicated separately

DISCUSSION

Species distributions, water regime preferences and inter-pool similarities

The distribution and cover/abundance of littoral plants in Pools 3, 5, 6 and 9 of the lower Murray clearly reflect the between-weir gradients in water regime (Figure 1). Indeed, there are broadly similar vegetation patterns across all 10 weir pools (Blanch, personal observation).

Eighty-five percent of the 48 species surveyed are broadly tolerant of flooding and drying (all except Groups 7 and 9; Figure 3). These tolerant species occur at potentially all positions along a pool, and at all elevations prone to inundation. Many possess traits that permit survival under a variable hydrologic regime, and are capable of rapid regrowth after flooding. Similarly, Blanch *et al.* (1999) reported that in Pool 5 half of the 26 plant species occur in four or more of the seven water regimes described here.

Only seven of the 48 recorded species are restricted to permanently or very frequently flooded sites, in water sufficiently shallow to allow photosynthesis (turbidity 30–80 nephelometric turbidity units (NTU)). Their ranges may vary with river flows: *Potamogeton* spp., *V. americana* and *Myriophyllum* spp. colonized relatively large areas of Pools 2–3 in February 1988, following three years of sustained low discharge (Walker *et al.*, 1994).

In effect, each weir resets the pool water level gradients. Inter-pool differences in the median days flooded to >0 cm for eight of 14 species (Table II) indicate that pools cannot be treated as exact replicates. Given the high spatial and temporal variation in biotic and abiotic factors within the littoral zone of floodplain rivers, such a result is surprising and should be interpreted by experimenters as a strong caution to replicate adequately both within and between pools (Gore and Shields, 1995; Sparks, 1995; Blanch *et al*., 1996). Experiments might be devised to test hypotheses concerning the responses of vegetation to altered water regimes. For example, the hypothesis that increasing flooding frequency increases diversity could be tested, given sufficient intra- and inter-pool replication.

Changes to weir operations

It is notable that the littoral vegetation in some reaches of the lower Murray is an artefact of weir construction: historical information suggests the banks of the unregulated river were largely devoid of plants for long periods (Walker *et al*., 1994). The weir pools and seasonally more stable flow regime have allowed numerous wetland species to invade the river channel, where they provide a vital habitat for aquatic and terrestrial animals, compensating for the reduction in floodplain area and inundation frequency. The littoral plant community therefore warrants special consideration in conservation and management. If some elements of the natural flow regime were to be restored, including greater seasonal variability and more frequent floodplain inundation, the distributions of some littoral plants would change correspondingly. In particular, the in-channel distribution of submersed species and mudmats (Groups 7 and 9; Figure 3) probably would be constricted, spatially and temporally.

The practice, by water resource agencies, of maintaining river levels within 10–20 cm of a weir's design level has had a profound impact on littoral vegetation processes in the lower Murray, and should be relaxed. Restoration of a more nearly natural flow regime, including more frequent shallow flooding and longer periods of inundation, would benefit many species. Figures 1 and 3 suggest that the distribution and abundance of all species, except those in Groups 7 and 9, are likely to increase with greater hydrologic variability. Weir manipulations that restore some of the lost natural variability in water level should be incorporated into routine weir operations. Regular fluctuations of 20–50 cm over several weeks are technically feasible and are unlikely to greatly affect infrastructure and irrigation, at least in Pools 7–9 (Ohlmeyer, 1991).

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