THE INFLUENCE OF WATER REGIME ON THE FLORISTIC COMPOSITION OF LOWER RIVER MURRAY WETLANDS

Mark Anthony Siebentritt

Cooperative Research Centre for Freshwater Ecology &

Department of Environmental Biology,

University of Adelaide

October 2003

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24 / 10 / 2003

Can papyrus grow where there is no marsh?

Book of Job

Eastern floodplain, Banrock Station wetland, South Australia (Photo: Ben Taylor)

Ndiwelimilambo enamagama - I have crossed famous rivers

Xhosa saying (Mandela 1994)

ACKNOWLEDGEMENTS

I would first like to acknowledge the substantive contribution my supervisors George Ganf and Keith Walker have made to my PhD studies. Over a number of years George and Keith have helped hone my analytical skills, challenged me to clarify the questions I ask and encouraged me to communicate my research concisely. George and Keith allowed me time to develop my own ideas and shared with me their passion for learning. Together they have shown a great deal of persistence and patience and for this I thank them.

To my wife Kathryn Calaby I am forever indebted. You have given unwavering love from the beginning to end of my thesis, tolerated my frequent absence of body and mind and felt every bump and grind of the journey – thankyou for hanging in there! To my mother Julie and father Otto, sister Carly and broader Siebentritt and Calaby families and my many dear friends, thankyou for your encouragement and support throughout my studies, for not forgetting me when it may have seemed that I had done so to you and for reminding me of the virtues of the world beyond a PhD.

To the staff and students of the Department of Environmental Biology and prior to that Botany at the University of Adelaide: thankyou for our wide ranging discussions over coffee and caramel slices, for sharing your enthusiasm for the natural world and for helping me to develop my thoughts and ideas.

I would like to acknowledge the efforts of those who waded through wetlands on cold winter days and trekked across floodplains in the heat of summer including Christian Hodgson, Damien Victorsen, Melissa Stone, Prue Tucker, Ben Taylor, Tim Kinchington, Jim George and Sonja Olsen. Thanks also go to my colleagues at the Murray-Darling Basin Commission, especially Tony McLeod, for their support in the final stages of this thesis.

I would like to thank the Faculty of Science, University of Adelaide and the Cooperative Research Centre for Freshwater Ecology for PhD scholarship support and recognise the financial contributions of the Australian Landscape Trust, the River Murray Catchment Water Management Board and the Cooperative Research Centre for Freshwater Ecology to my research.

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EXECUTIVE SUMMARY

This thesis examines the influence of 'water regime', or spatial and temporal patterns in the presence of water, on the floristic composition of wetlands on the River Murray in South Australia (henceforth Lower Murray). It explores the hypothesis that the composition of wetland vegetation is determined by components of the water regime, namely depth, duration and the rate and timing of flood and drawdown. This was tested by examining the influence of water regime variations on:

1) floristic composition in individual wetlands;
2) regeneration (establishment, growth, reproduction) and extirpation of species; and
3) morphological and physiological responses of species.

Two field studies and one controlled pond experiment were undertaken. In the first field study, four wetlands characterised by managed flood and drawdown and two unmanaged, permanently inundated wetlands were monitored between October 1999 and March 2001. Periodic flood and drawdown significantly changed the vegetation in the managed wetlands, whereas plants in the permanently inundated wetlands did not respond. Floristic differences between these wetlands increased as the managed wetlands were drawn down, but converged after re-filling. As a result, water regime management over this 18-month period did not consistently promote more diverse or unique floras.

The establishment and extirpation of species indicated responses to flood and drawdown governed by a) the depth, duration, timing and rate of flood and drawdown, b) the prior vegetation, as influenced by c) previous flood and drawdown events. Changes were greatest in the initial 1-3 months of flooding because of extirpation of mudflat annuals such as *Centipda cunninghamii* (common sneeze-weed, Asteraceae), *Persicaria lapathifolia* (pale knotweed, Polygonaceae) and *Rorippa palustris* (marsh watercress, Brassicaceae) and establishment of the submerged macrophyte *Vallisneria americana* (ribbonweed, Hydrocharitaceae) and emergent macrophyte *Typha domingensis* (cumbungi, Typhaceae).

A model was developed to predict the presence/absence of species and functional groups. It incorporates water regimes of 3, 4, 5 and 6 months duration and estimated preferences for species and functional groups in a permanently inundated Lower

Murray wetland. Predictions for species were more accurate (76-86%) than for functional groups (64-74%). Predictions were more successful as the duration of hydrograph increased because fewer predictions were made of annuals, which tolerated < 100 days of flood or drawdown. Water regime preferences proved useful for predicting the presence and absence of Lower Murray wetland plants in permanently inundated wetlands where perennials are dominant.

The second field study examined the influence of manipulated water regimes on floristic composition at sites inundated during an enhanced flood in October 2000. Vegetation at three sites was surveyed before and after the flood. Among 32 recorded species, *Atriplex vesicaria* (bladder saltbush, Chenopodiaceae), *Sporobolus mitchellii* (rats tail couch, Graminae) and *Sarcocornia quinqueflora* (samphire, Chenopodiaceae) accounted for 82% of the total cover/abundance. Vegetation changes across the floodplain were due to the growth and germination of flood-tolerant and flood-dependent species (e.g. *S. mitchellii*) and the senescence of flood-intolerant species (e.g. *A. vesicaria*). No aquatic plants germinated or established, despite favourable conditions, suggesting an impoverished seed bank or heavy grazing by native herbivores.

Examination of *S. mitchellii* and the perennial shrub *Muehlenbeckia florulenta* (tangled lignum, Polygonaceae) revealed that vegetative growth was the most significant response to floodplain inundation. However, these responses were not strictly aligned with elevation suggesting a non-uniform response to flooding.

Morphological and physiological responses underlying vegetation change were examined through a pond experiment. Four common emergent macrophytes - *Bolboschoenus caldwellii* (three-cornered rush, Cyperaceae), *Cyperus gymnocaulos* (spiny sedge, Cyperaceae), *Juncus aridicola* (tussock rush, Juncaceae) and *Schoenoplectus validus* (river club-rush, Cyperaceae) - were subject to regimes of slow (1 cm d^{-1}) and rapid (5 cm d^{-1}), shallow (20 cm) and deep (60 cm) flood and drawdown. Relative growth rate was correlated with emergent photosynthetic area and root mass for all species. Culm extension enabled *B. caldwellii* and *S. validus* to maintain emergent photosynthetic area when flooded and thus growth. Similarly, root extension was a feature of those plants that maintained growth when exposed to drawdown. These responses were most pronounced when plants were subject to rapid, deep flood and drawdown. Combined with the ability to extend roots, the timing and magnitude of stomatal conductance changes suggest that *C. gymnocaulos* and *J. aridicola* may be better suited to periodic drawdown.

Optimal growth rates led to optimal investment in asexual reproduction for all bar *S. validus*, which decreased culm production despite maintenance of growth when flooded. *B. caldwellii* maintained numerical increase when slow deep flooded by reducing the proportional allocation of biomass to tubers, whereas *S. validus* sacrificed numerical increase to retain investment in rhizomes. The latter response was observed for both species when exposed to deep drawdown. No trade-off was evident between asexual and sexual reproduction for any of the study species.

The pond experiment suggests that tolerance of drawdown requires specific morphological and physiological strategies in the same way that flooding does. A further conclusion is that strategies for responding to drawdown are equally as important as strategies for responding to flooding in determining the distribution of emergent macrophytes across the littoral zone of wetlands.

CHAPTER 1

INTRODUCTION

1.1 The influence of flood and drawdown on access to plant resources

Carbon dioxide, light, nutrients, oxygen and water support fundamental plant processes such as respiration and photosynthesis. The ability to acquire these resources determines the capacity of plants to support, for example, maintenance, vegetative growth and reproduction. Access to plant resources is influenced by a range of abiotic (e.g. physical and chemical) and biotic (e.g. grazing and competition) factors that vary in magnitude and importance between ecosystems (Begon *et al.* 1990). In temporary wetlands, access to plant resources is influenced by the rise and fall of water levels (Sculthorpe 1967; Kirk 1983).

Flooding affects the quantity and quality of light available for plant growth (Spence 1982; Kirk 1983) and reduces concentrations of oxygen and carbon dioxide by impeding gas exchange (most gases diffuse about 10 000 times slower in water than air: Armstrong *et al.* 1994). Low oxygen concentrations coupled with increased microbial activity and root respiration subject the majority of the root zone to anoxia (Armstrong *et al.* 1994). Anoxic sediment, through denitrification, can inturn reduce the amount of nitrate available to plants. However, anoxia can also increase phosphate availability by stimulating iron-reducing bacteria to liberate phosphate from ferric minerals (Baldwin and Mitchell 2000).

Drawdown aerates sediment promoting nitrification and microbial activity leading to organic matter decomposition and nitrogen release. This may be enhanced if sediment drying causes bacterial mortality (Qiu and McComb 1995). In contrast, phosphate availability may be reduced as aerated soil oxidizes reduced ferric-based compounds (Baldwin and Mitchell 2000). The major impact of drawdown for plants is sediment drying. In the absence of groundwater, soil moisture reserves are depleted through a combination of evapotranspiration, evaporation and seepage.

Flood and drawdown are not the only factors that influence access to plant resources in periodically filled wetlands. Others include sediment characteristics (e.g. fertility, pH, salinity: Anderson and Kalff 1988; Carr and Chambers 1998; Lenssen *et al.* 1999) and biotic factors such as competition (Wilson and Keddy 1986; Wilson and Keddy 1991; Budelsky and Galatowitsch 2000; Siebentritt and Ganf 2000). The effect of abiotic and biotic factors may also be modified by flood and drawdown. For example, competition may be less intense lower on the elevation gradient, where the stress of water depth is greater, and more intense at higher elevations where flooding stress is reduced (Grace and Wetzel 1981; Siebentritt and Ganf 2000). Flooding can also modify the response of emergent macrophytes to highly reductive organic sediments (van den Brink *et al.* 1995) and influence recovery following temporary increases in soil water salinity (Howard and Mendelssohn 2000).

1.2 Water regime: importance and characterisation

The ability of flood and drawdown to regulate access to plant resources and modify the effect of abiotic and biotic factors means that hydrology has a significant impact on the growth, reproduction and survival of wetlands plants and hence their distribution and abundance (e.g. Sculthorpe 1967; Armstrong 1994). This supports the conclusion of a number of authors that hydrology is a key factor shaping wetland floristic composition (Spence 1982; Blom *et al.* 1990; Keddy 1999).

Rather than describe general hydrological patterns, many researchers refer to water regime. Water regime is a complex variable and describes the rate, duration, frequency, timing and depth of flood and drawdown (Brownlow *et al.* 1994). These features are scale dependent and related to one another in space and time (Boulton and Brock 1999). Water regime may be defined at the scale of the wetland with reference to, for example, how often filling and drying occur (frequency) and the period of inundation (duration: Bunn *et al.* 1997). Water regime may also be defined for specific positions across the elevation gradient. Quantification of water regime at this scale has been done by calculating the number of days elevations are exposed or flooded within particular depth ranges (Brownlow *et al.* 1994; Blanch *et al.* 1999b). Water regime will be considered and described at both scales throughout this thesis.

1.3 Plant strategies for tolerating and responding to flood and drawdown

Strategies describe a suite of adaptations used by plants to tolerate, respond or avoid different combinations of environmental conditions. Plants that tolerate or respond to permanent inundation of at least their below ground tissues are termed 'macrophytes' or 'vascular hydrophytes' (Spence 1982; Blom *et al.* 1990).

Emergent macrophytes are rooted in the sediment with at least part of their photosynthetic canopy above the water surface and have a limited capacity to use aqueous forms of carbon dioxide. They avoid carbon starvation of photosynthesis by maintaining shoot and leaf contact with the atmosphere (Cizkova-Koncalova *et al.* 1992). Therefore, a common response when flooded is to increase shoot and leaf height (Squires and van der Valk 1992; Coops *et al.* 1996; Siebentritt and Ganf 2000; Cooling *et al.* 2001). Increased height may be achieved via reallocation of biomass from storage organs such as tubers, corms and rhizomes and/or the preferential allocation of newly captured resources (Rea and Ganf 1994b; Blanch *et al.* 1999a). Soil anoxia poses another challenge for emergent macrophytes. This may be overcome through the development of aerenchyma to allow for the transport of air from the leaves and stems to the rhizomes and roots (Armstrong *et al.* 1994).

Despite the prevalence of drying in wetlands, few studies have examined the mechanisms that allow drought and/or drawdown tolerance by emergent macrophytes. Intuitively, their persistence during drawdown will be influenced by their ability to maintain root contact with groundwater. Where groundwater is absent or too deep, mechanisms that regulate the survival of water stressed terrestrial plants such as stomatal conductance are likely to be important (Kirkman and Sharitz 1993).

Submerged macrophytes utilise dissolved inorganic carbon and do not need to maintain access with the atmosphere (Bowes and Salvucci 1989; Madsen and Sand-Jensen 1991). The major limitation to their depth distribution is the underwater light climate (Middleboe and Markager 1997). Species may survive at depths of > 30 m in clear water (characean algae: Schwarz and Hawes 1997) compared to < 1 m in turbid waters (*Vallisneria americana*: Blanch *et al.* 1998).

Most submerged species have desiccation intolerant tissues and populations are susceptible to extensive dieback following drawdown (Cooke 1980). However, plants may persist if soils remain moist, preserving below ground tissues (e.g. van Wijck and de Groot 1993).

When environmental conditions exceed tolerance limits, emergent and submerged macrophytes can persist via the storage of seed and clonal propagules in the sediment (Britton and Brock 1994; Brock and Rogers 1998). Seed storage is a strategy also exploited by annual wetland species that possess few adaptations for tolerating the stresses of flooding or soil drought (van der Sman *et al.* 1993). Annual wetland species are known by various names - pioneer species, colonizer species, herbaceous annuals - but for consistency will henceforth be referred to as 'mudflat annuals'. Mudflat annuals germinate and establish on moist, exposed mudflats, grow rapidly and set seed preferably before re-flooding or soil drought occurs (Salisbury 1970; van der Sman *et al.* 1993; Houle and Belleau 2000).

The germination traits of many emergent macrophytes are similar to those of mudflat annuals with germination occurring on moist, bare, exposed mudflats (Shipley *et al.* 1989). Some species are also able to germinate and establish in shallow water (e.g. *Typha domingensis*: Nicol and Ganf 2000). Germination is generally increased under high soil moisture and alternating high to moderate temperatures (Galinato and van der Valk 1986; Welling *et al.* 1988b). Germination for submerged species only occurs when the sediment is inundated (Sculthorpe 1967) and may be regulated by the underwater light climate (Farmer and Spence 1987).

1.4 The influence of water regime on floristic composition

When water levels remain static, zonation patterns may develop reflecting the depth tolerance of the species present (Spence 1982). However, in systems where water levels fluctuate, vegetation change is common and wetland plant communities are rarely fixed entities. Instead, communities are assemblages of species co-existing under a given set of environmental conditions with an assemblage persisting only as long as suitable conditions remain (van der Valk 1987).

When water levels fluctuate beyond the tolerance of some species (thus acting as a stress) or meet the establishment requirements of others, extirpation (loss) and establishment (addition), respectively, promote vegetation change. Throughout this thesis 'stress' will be used to describe a reduction in access to resources that leads to decreased plant growth (*sensu* Grime 1979). This differs from a 'disturbance' that causes the partial or total destruction of a plant.

Periods of stress prevent the dominance of one or a few species (Barrat-Segretain 1996). This inturn provides other plants with access to resources such as space, light and nutrients and facilitates the maintenance of diverse plant assemblages. This idea is implicit in theories such as the Intermediate Disturbance Hypothesis (Connell 1978) and the Patch Dynamics Concept (Townsend 1989).

It has been demonstrated experimentally (Weiher and Keddy 1995; Casanova and Brock 1996; Nielsen and Chick 1997) and through field studies (Cooke 1980; Sjoberg and Danell 1983; Thibodeau and Nickerson 1985; van der Valk *et al.* 1989; ter Heerdt and Drost 1994; David 1996; Tyser *et al.* 2001) that changing water regime will change the floristic composition of a wetland. General patterns of vegetation change can be described for different hydrological phases (van der Valk and Davis 1980).

1.5 Changes in floristic composition under fluctuating water levels

During drawdown falling water levels expose the wetland bed starting a dry phase. Provided propagules are present, the sediment is bare (reducing inter-specific competition) and germination cues are met, an array of emergent macrophytes (commonly from the families Cyperaceae, Typhaceae, Juncaceae) and mudflat annuals will establish (Kadlec 1962; Smith and Kadlec 1983; ter Heerdt and Drost 1994). The rapid growth of mudflat annuals allows them to dominate recently drawndown wetlands (Kadlec 1962; Galinato and van der Valk 1986).

The balance between areas colonised by emergent macrophytes versus mud flat annuals may be influenced by season. Emergents dominate after early drawdown (spring) while annuals are more prevalent after a late drawdown (summer) where hot periods accelerate mudflat drying (Harris and Marshall 1963; Salisbury 1970; ter Heerdt and Drost 1994). The effect of the rate of drawdown has received comparatively little investigation.

The duration of drawdown governs the survival of established vegetation. As soil drought continues, changes in species dominance are a function of relative drought tolerances (Kirkman and Sharitz 1993). In general, emergent macrophytes and mudflat annuals exhibit reduced growth rates and survivorship under continued soil drought (Haslam 1978; van der Valk and Davis 1980).

Continued drawdown causes the loss of all wetland plants and the establishment of more drought tolerant, terrestrial species. For example, Harris and Marshall (1963) observed that after two years of drawdown in marshes within the Agassiz National Wildlife Refuge in north-western Minnesota, there was a loss of emergent macrophytes and mud flat annuals and an increase in the abundance of plants from areas above the floodplain. This trend continued in areas drawndown for a third and fourth year. If wetlands are drawndown for extended periods (e.g. > 10 years), as is the case when they have been drained for agricultural use, the store of dormant propagules can be reduced in richness and density, potentially inhibiting any future attempts at restoration (Wienhold and van der Valk 1989).

A period of drawdown also causes the dieback of submerged macrophytes (Cooke 1980; Briggs *et al.* 1985; van Wijck and de Groot 1993). The extent of dieback is controlled by the ability of below ground organs to persist; this may be enhanced if soil moisture levels remain high (van Wijck and de Groot 1993). The susceptibility of submerged species to drawdown has been exploited in the control of nuisance growths of aquatic plants by dewatering sediments under extremes of heat and cold (Nichols 1975; Cooke 1980).

The procession from less to more drought tolerant plants is based on the premise that as water levels are drawndown, soil moisture is depleted. Intuitively, where groundwater remains accessible to plants, this transition may be slowed or even halted. This interaction has received little attention in the literature and will be examined in more detail in this thesis.

Upon re-filling, most mudflat annuals die back and emergent macrophytes spread vegetatively (Harris and Marshall 1963; van der Valk and Davis 1980). If flooding is shallow it will provide suitable conditions for the growth and clonal spread of emergent macrophytes (Grace 1989; Coops *et al.* 1996; Blanch *et al.* 1999a; Siebentritt and Ganf 2000). The timing of flooding is significant, with spring rather than summer flooding often favouring the development of more productive and species-rich assemblages (Robertson *et al.* 2001).

Re-filling also provides an opportunity for germination and clonal propagule emergence of submerged species (Leck and Brock 2000). Underwater light quantity and quality affects both processes (Baskin and Baskin 2001) and thus establishment may be influenced by the rate of filling and the turbidity and colour of the surrounding water (Payne 1998).

If flooding continues emergent macrophytes in deeper water (> 80-100 cm) are extirpated, creating large areas of open water and leaving a narrow band of emergent vegetation around the perimeter of the wetland (Sjoberg and Danell 1983; Bukata *et al.* 1988; Wallsten and Forsgren 1989; van der Valk 1994; van der Valk *et al.* 1994). Although inundation for more than one year may cause plant death, some species can survive longer because of below ground carbohydrate reserves (van der Valk 1994; van der Valk *et al.* 1994) and there may be little dieback for up to 3 years (Thibodeau and Nickerson 1985).

Submerged macrophytes are favoured while wetlands remain flooded and may colonise large areas via clonal growth (Spence 1982; Farmer and Spence 1987). The duration of flood can be used by wetland managers to influence the ratio of emergent macrophytes to open water, which determines the suitability of habitat for waterfowl (Kadlec 1962; Murkin *et al.* 1982).

Changes in floristic composition will differ with wetland elevation. Wetlands located in depressions in the floodplain will likely spend more time flooded and thus develop assemblages characterised by more flood responsive plants. Elevations higher on the floodplain will receive comparatively less flooding and develop vegetation more characteristic of a dry phase.

1.6 Floristic composition of wetlands in regulated river systems

The alteration of water regime has been identified by Bunn *et al.* (1997) as the highest priority issue in the management of Australian wetlands. Where flow regulation results in reduced water level variability, wetlands at low elevations may experience water level stabilisation and permanent inundation, while sites at higher elevations may become isolated from floodwaters.

The first casualty of water level stability is regeneration because of the loss of alternating wet and dry periods to promote establishment. A further consequence is that without periodic stress competitively superior plants may come to dominate a wetland. This is common in shallow water of permanently inundated wetlands where monodominant communities may develop (van der Valk and Davis 1980). Common invading species include *Typha* spp. (Wilcox *et al.* 1985) and *P. australis* (Gusewell and Klotzli 1998).

Once established, competitively dominant species may be difficult to remove, particularly if they can withstand several years of continuous flooding (e.g. *Typha* spp.: Payne 1998). A combination of limited establishment opportunities and pressure from competitively dominant species may lead to an overall decline in species richness in permanently inundated wetlands (Wilcox and Meeker 1991; van der Valk 1994; Nielsen and Chick 1997).

Wetlands that become isolated from floodwaters also experience reduced plant diversity, abundance and productivity (Scholte *et al.* 2000; Madera 2001b). Reduced flooding may favour the establishment of perennial shrubs and trees at the expense of emergent macrophytes and mudflat annuals (Duever 1982; Thibodeau and Nickerson 1985) and promote the colonisation of terrestrial over flood tolerant vegetation (Zunzunegui *et al.* 1998; Madera 2001b).

1.7 The Murray-Darling Basin and the Lower River Murray

1.7.1 Description

The Murray-Darling Basin covers 1.1 million km^2, approximately one-seventh the area of continental Australia, and has two main river systems, the Murray and the Darling. With the exception of their headwater reaches, both are typical lowland rivers with significant floodplains watered by the main channel and, in places, numerous anabranches.

The River Murray rises in the Snowy Mountains that drain the western side of the Great Dividing Range in south eastern New South Wales and north eastern Victoria and flows 2530 km to the river mouth at Goolwa, South Australia (Figure 1.1). The Darling flows from south-eastern Queensland and travels about 1700 km to meet the Murray at Wentworth. The lower River Murray, referred to throughout this thesis as the Lower Murray, relates to the section of river below the junction of the two rivers.

The Lower Murray flows through four sections distinguished by geomorphological and hydrological differences (Pressey 1986). The first is the *Valley* section that extends from the confluence, downstream 906 km to Overland Corner (Figure 1.2). This section has a broad floodplain (5-10 km wide) with numerous wetland types including anabranches, billabongs and deflation basins. From Overland Corner the river enters a 30 m deep limestone gorge called the *Gorge* section that has a constrained floodplain of 2-3 km, which then emerges into the *Swamplands* section upstream of Murray Bridge. The river empties into the *Lakes* section at Wellington, consisting of the shallow Lake Alexandrina and Lake Albert (average depth 2-3 m).

Climate differs greatly across the Basin. Precipitation in the headwaters of the Murray exceeds 2000 mm per annum and falls mostly in winter and spring. The headwaters comprise less than 2% of the Murray-Darling Basin, but contribute nearly 40% of the inflow to the Murray (Maheshwari *et al.* 1995). The remainder of the catchment lies primarily in the arid and semi-arid zone and is subject to unpredictable summer rainfall events (see Walker *et al.* 1992 for a summary). The Darling itself contributes only 12% of long-term average discharge (Walker and Thoms 1993). Despite the large catchment area, the discharge of the Basin as a whole is low in comparison to other rivers of similar length across the world (Walker *et al.* 1995).

As a result of the Basin's climatic variability, the natural flow regime of the River Murray is inherently variable. Annual flow variation prior to river regulation was high, driven mainly by higher precipitation in winter and spring in the Murray's headwaters (Walker 1992). For instance, height fluctuations of over 6 m were recorded downstream of Kingston-on-Murray prior to the construction of Lock 3 in 1926 (Figure 1.3). Inter-seasonal flow variability is also high in the Lower Murray and influenced by the atmospheric circulation phenomenon the El Nino Southern Oscillation, which results in drought and flood dominated regimes that may last for up to five years (Simpson *et al.* 1993).

1.7.2 Flow regulation and its hydrological impacts

Flow regulation in the Murray-Darling Basin began in earnest during the period 1922-1940 with the construction of a series of low-level weirs across the Murray, the construction of Hume Dam in the headwaters of the Murray and the installation of barrages near the river mouth. At the same time annual diversions rose and by the late

1930s had reached 3,000 gigalitres (GL)/year (Close 1990). Regulation continued and by 1990, diversions had exceeded 10,000 GL/year (Crabb 1997).

Regulation has caused a significant reduction in average annual and monthly flows, with the median annual discharge of the Murray now reduced to 27% of the natural median (A. Close, Murray-Darling Basin Commission, MDBC, pers. comm.). Regulation has impacted most on mid range flows, leaving the river dominated by low flows (< 5000 GL for 66% of the time) and infrequent high flows (Walker 2001).

In the Lower Murray, river levels now remain at or near bank full capacity through a combination of reduced flows and weir operations that aim to keep levels within ± 0.05 m of an operational pool level (Walker and Thoms 1993). Water level stabilisation is most pronounced just above the weirs. For example, levels above Lock 3 for the period 1 January 1997 to 1 March 2001 remained within ± 0.05 m of the target weir pool level (9.80 m Australian Height Datum = m AHD, equivalent to metres above mean sea level) for 81% of the time (Figure 1.4).

Prior to regulation most floodplain wetlands across the Lower Murray were temporary, filling only during periods of overbank flow. However, as a result of flow regulation over 70% are now permanently flooded with reduced water level variability under minimum regulated flows (Pressey 1986). Although permanently inundated sites may provide drought refuge, anecdotal evidence suggests they typically have lower diversity and productivity than areas with periodic water level fluctuations (Thompson 1986).

A range of management options have recently been proposed to introduce greater water level variability, including:

- the temporary separation of wetlands from the river via the use of regulators to allow drawdown (Sharley and Huggan 1994; Jensen 1998).
- weir level manipulations to influence water level height across river reaches (Thoms *et al.* 2000); and
- environmental flow releases to enhance flooding (Thoms *et al.* 2000)

1.8 Wetland plants in the Lower Murray

Detailed studies on the distribution of plants across the littoral zone of the Lower

Murray have only been undertaken in the past 15 years. These have shown that distribution is influenced by aspects of bank slope, current and wave exposure (Roberts and Ludwig 1991) and that the composition and relative abundance of littoral plant assemblages is correlated with water level fluctuations in weir pools (Walker *et al.* 1994).

To date, the most substantive study on plants in the Lower Murray was by Blanch in the late 1990s. The objective of this work was to examine the role of water regime in structuring littoral plant assemblages in the Lower Murray channel. Field studies revealed five species clusters correlated with the duration of flooding to 0-20 cm and 20-60 cm and exposure to ≥ 100 cm (Blanch *et al.* 1999). Clusters identified species from the permanently flooded littoral to the infrequently flooded littoral. The distribution of plants was also found to vary across weir pools with plants occupying a greater range of elevations in upper pool sites where levels fluctuate most and a 1-1.5 m band in lower pool sites where levels fluctuate least (Blanch *et al.* 2000).

The studies of Walker *et al.* (1994) and Blanch *et al.* (2000) both support the hypothesis that species present in permanent backwaters and floodplain wetlands prior to regulation have now colonised the main river channel. Despite enabling the colonisation of the main channel, Blanch *et al.* (2000) concluded that the practice of maintaining stable weir pool levels limits vegetation processes such as germination, recruitment and decomposition.

The reduced frequency and magnitude of flooding has led to a general decline in the condition (Margules and Partners *et al.* 1990) and cover (Bren 1988) of vegetation. Specifically this has affected populations of the floodplain tree *Eucalyptus camuldulensis* and the shrub *Muehlenbeckia florulenta* (Craig *et al.* 1991; Thorburn *et al.* 1994; Jolly 1996). The impact of regulation on perennial shrubs and floodplain tree species has received some attention, but little is known of the response of understorey species.

As yet, no studies have examined the floristic response of Lower Murray floodplain wetlands to periodic flood and drawdown. The work presented in this thesis complements that of Blanch's and extends understanding of vegetation processes, their outcomes and drivers, from the main channel of the Lower Murray into the numerous wetlands that are a feature of this part of the river system.

1.9 Thesis outline

This thesis examines the influence of water regime on the floristic composition of Lower Murray wetlands. It explores the hypothesis that the effect of water regime on floristic composition is determined by more than just whether an elevation or wetland is wet or dry, but by the characteristics of flood and drawdown. The term wetland is used here in its broader sense and includes depressions in the floodplain and the floodplain itself. The response of plant assemblages is assessed in three ways:

1) the response of morphological and physiological variables for individual plants;
2) the influence of water regime on regeneration (establish, growth and reproduction) and extirpation; and
3) changes in floristic composition at the scale of the wetland.

These topics are addressed through two field studies and one pond experiment. In the first field study, six floodplain wetlands were monitored between October 1999 and March 2001; four were characterised by managed flood and drawdown regimes and two were unmanaged and permanently inundated. This is referred to as the 'floodplain wetland' study.

This study examined the influence of water regime on the floristic similarity of wetlands (Chapter 2). It was predicted that periodic flood and drawdown would promote greater establishment opportunities and result in a more diverse and unique array of species than in the permanently inundated wetlands. It was also anticipated that as water regime variability increased, floristic composition would become less similar to that in permanently inundated wetlands.

The influence of flood and drawdown on vegetation change was examined through consideration of establishment and extirpation (Chapter 3). The data from all wetlands were then combined to construct a model that predicts the presence, absence and establishment of species and/or functional groups derived from a pool of common species described in Chapters 2 and 3 (Chapter 4). The species pool was filtered using hydrographs of 3-6 months duration.

In the second field study the influence of water regime on floristic composition was examined for floodplain areas inundated during an enhanced flood in October 2000. This is referred to as the 'enhanced flood' study. It was anticipated that flooding would result in an increase in the distribution and abundance of flood tolerant and responsive plants and that this would be greatest at elevations flooded more deeply and for a longer period. In contrast, species characteristic of more terrestrial environs were expected to experience reductions in distribution and abundance at flooded elevations (Chapter 5).

Another survey was undertaken to monitor the response of two common floodplain species, the perennial creeping grass *Sporobolus mitchellii* and the perennial shrub *Muehlenbeckia florulenta* to periodic floodplain inundation (Chapter 6). The aim was to determine the growth and reproductive response of plants and to assess which variables were most responsive to flooding.

The cause of changes in floristic composition in response to water level fluctuations was further explored by examining the morphological and physiological response of four common emergent macrophytes from Lower Murray wetlands – *Bolboschoenus caldwellii*, *Cyperus gymnocaulos*, *Juncus aridicola* and *Schoenoplectus validus* - to contrasting water regimes in a controlled pond experiment. Water level fluctuations were set to mimic those that may be experienced across the littoral zone of either backwaters or the main channel.

The experiment tested the hypothesis that plants characteristic of more frequently inundated habitats would be better able to respond and tolerate rapid flooding to greater depths than those from less frequently inundated sites because of a greater ability to extend culms to maintain an emergent canopy. In contrast, plants from less frequently inundated habitats were expected to be better able to survive rapid drawdown because of a greater ability to extend roots (Chapter 7). Data were also analysed to assess how contrasting water regimes influence investment in growth and asexual and sexual reproduction (Chapter 8).

Chapters have been prepared to aid in the development of papers for scientific journals and hence there is some repetition of information, predominantly in chapter introductions.

Figure 1.1. The Murray-Darling Basin. Source data: AUSLIG (topographic 250k) Murray-Darling Basin Commission.


Tambo
Augathella
Charleville
Morven
Roma
Chinchilla
Dalby
Tara
Toowoomba
BRISBANE
Warwick
QUEENSLAND
Cunnamulla
Bollon
St George
Goondiwindi
Stanthorpe
Hungerford
Tenterfield
Moree
Wanaaring
Bourke
Walgett
Narrabri
White Cliffs
Darling River
Armidale
Coonamble
Gunnedah
Coonabarabran
Tamworth
Wilcannia
Cobar
SOUTH AUSTRALIA
Broken Hill
Menindee Lakes
NEW SOUTH WALES
Dubbo
Wellington
Ivanhoe
Forbes
Orange
Lachlan River
Bathurst
Lake Victoria
Morgan
Renmark
Wentworth
Mildura
Cowra
SYDNEY
RIVER MURRAY
Hay
Griffith
Leeton
Young
ADELAIDE
Mannum
Balranald
Murrumbidgee River
Narrandera
Murray Bridge
Gundagai
Yass
Goolwa
Wagga Wagga
CANBERRA
Meningie
Lake Alexandrina
Swan Hill
Deniliquin
Kerang
Albury
Hume Dam
Wodonga
Echuca
Dartmouth Dam
Cooma
Horsham
Bendigo
Shepparton
Omeo
Seymour
0
100
200 km
VICTORIA
MELBOURNE

Figure 1.2. The lower River Murray showing seven of 10 weirs. Numbering of locks and weirs commences at the lock furthest downstream (between Murray Bridge and Manuum). NSW = New South Wales, SA = South Australia, VIC = Victoria. Source data: AUSLIG (topographic 250k) Murray-Darling Basin Commission.

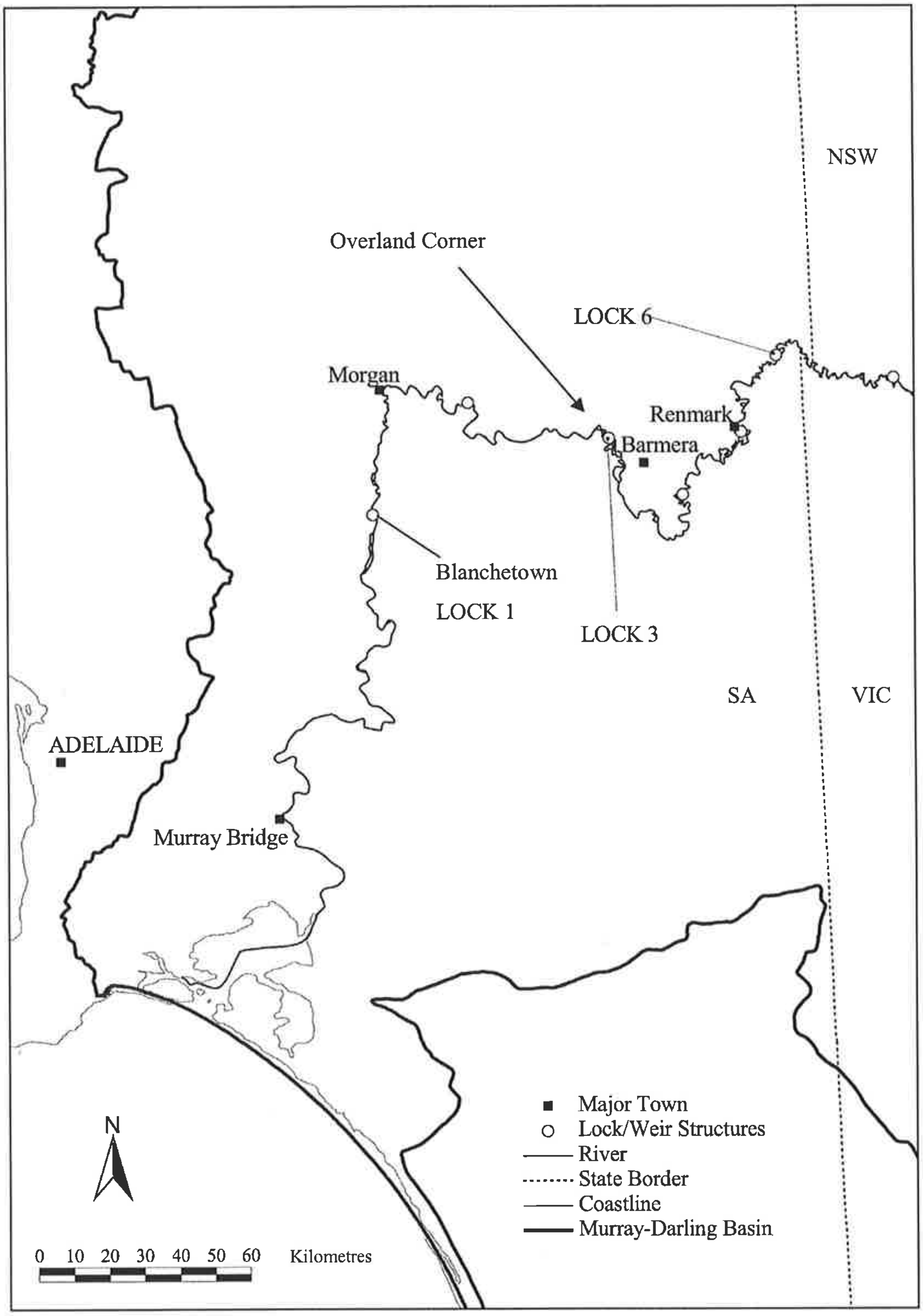
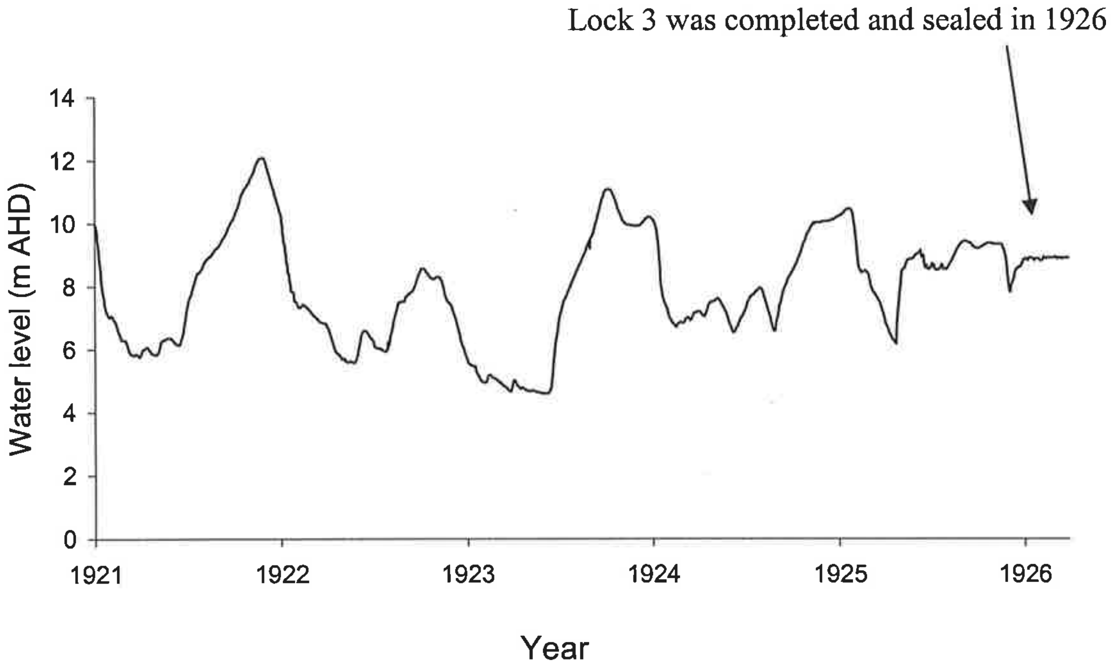
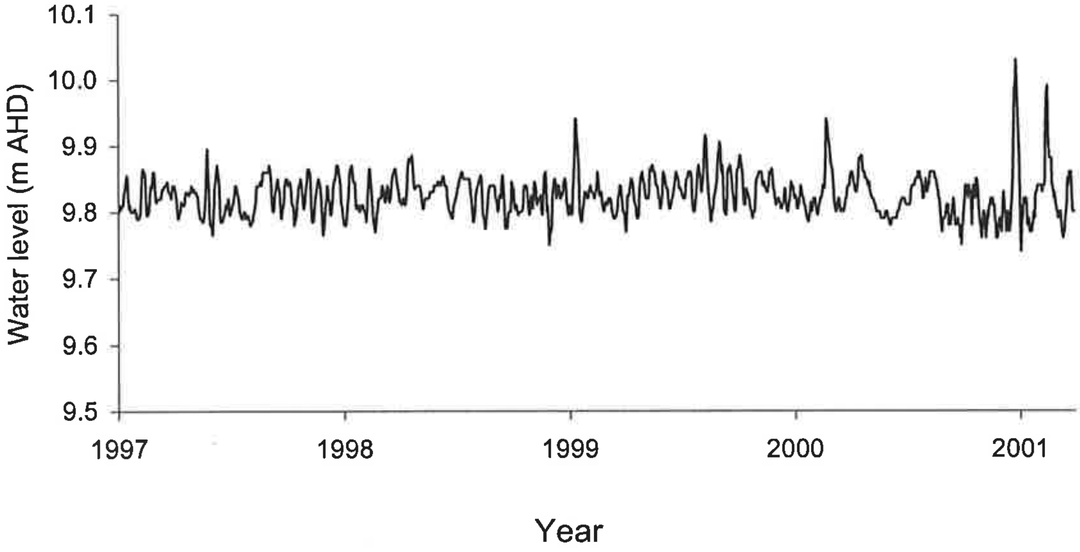

NSW
Overland Corner
LOCK 6
Morgan
Renmark
Barmera
Blanchetown
LOCK 1
LOCK 3
SA
VIC
ADELAIDE
Murray Bridge
N
■ Major Town
○ Lock/Weir Structures
River
State Border
Coastline
Murray-Darling Basin
0 10 20 30 40 50 60 Kilometres

Figure 1.3. The hydrograph downstream of Kingston-on-Murray on the lower River Murray during the early to mid 1920s at the site where Lock and Weir 3 were eventually constructed. Source: K.F. Walker pers. comm..

Figure 1.4. The hydrograph at Lock 3 between 1 January 1997 and 1 March 2001. Water levels remained within ± 0.05 m of the target pool level (9.80 m AHD) for 81% of the time.


Lock 3 was completed and sealed in 1926
Water level (m AHD)
14
12
10
8
6
4
2
0
1921
1922
1923
1924
1925
1926
Year


Water level (m AHD)
10.1
10.0
9.9
9.8
9.7
9.6
9.5
1997
1998
1999
2000
2001
Year

CHAPTER 2

FLORA OF WETLANDS WITH CONTRASTING WATER REGIMES

2.1 Abstract

This study compared the influence of periodic flood and drawdown versus permanent flooding and stable water levels on floristic composition in six Lower Murray wetlands. Vegetation was monitored during six surveys between November 1999 and March 2001. Flood and drawdown created unique vegetation cycles in three of the managed wetlands, whereas the water regime of permanently inundated wetlands failed to stimulate change. The floristic similarity of wetlands departed as the three managed wetlands entered drawdown phases and then became more similar following their re-filling. Across the six wetlands, the trend was for increasing water regime variability to promote greater differences in floristic composition. Although floristic differences were observed during the study, periodic flood and drawdown did not necessarily promote more diverse or unique floras than recorded in permanently flooded wetlands.

2.2 Introduction

Flood and drawdown provide both regeneration opportunities for wetland plants and impose periods of stress (*sensu* Grime 1979). Exposure of a wetland bed after a period of flooding may lead to the dieback of desiccation intolerant submerged macrophytes (van Wijck and De Groot 1993) but provide an opportunity for emergent macrophytes and mudflat annuals to establish (van der Valk and Davis 1980). Combinations of flood and drawdown are generally seen as necessary to maintain diverse plant assemblages (Wilcox and Meeker 1991).

In regulated river systems weirs stabilise water levels and may permanently inundate wetlands. When this occurs, flood stress in deep water leads to the loss of emergent macrophytes (Sjoberg and Danell 1983; Bukata *et al.* 1988; van der Valk *et al.* 1994) and competitive interactions intensify in shallow water favouring competitively dominant species (e.g. *Typha* spp.: Finlayson *et al.* 1983). Germination and establishment opportunities for emergent macrophytes and herbaceous annuals are also reduced (Nielsen and Chick 1997). A combination of these factors may lead to a decline in species richness in permanently inundated wetlands (Wilcox and Meeker 1991; van der Valk 1994; Nielsen and Chick 1997).

Prior to regulation, floodplain wetlands across the Lower Murray experienced periodic flood and drawdown (Pressey 1986; Walker and Thoms 1993). Since regulation, the water regime in many wetlands has been controlled by a series of low-level weirs (Walker and Thoms 1993) and as a consequence at least 70% of Lower Murray wetlands are permanently inundated under normal operational conditions (Pressey 1986). The effect of water level stabilisation has been to limit vegetation processes such as germination and recruitment (Blanch *et al.* 2000).

Pressey (1986) suggested that restoration of permanently inundated River Murray wetlands required re-instatement of more natural flood and drawdown regimes. He proposed the periodic separation of wetlands from the river to allow drying of some or all of their beds. This has been addressed through the construction of regulators on the inlets and outlets of selected Lower Murray wetlands. An objective of most managers has been to manipulate water levels to 'maintain' and 'enhance' biodiversity.

This study compared the floristic composition of six Lower Murray wetlands between November 1999 and March 2001; two were permanently inundated and four were managed with periodic drawdown.

It was anticipated that:

1) water regimes characterised by periodic flood and drawdown would provide greater establishment opportunities and result in more diverse and unique arrays of species than found in permanently inundated wetlands;
2) the floristic similarity of managed wetlands would change between surveys as flood and drawdown promoted vegetation change; and
3) increasing deviation from stable water levels would create increasingly different floristic compositions when compared to permanently flooded wetlands.

For the purpose of this chapter, water regime between wetlands is differentiated at the level of the wetland by comparing a) patterns in the depth, duration, timing and rate of flood and drawdown and b) the mean deviation from the target pool level.

2.3 Study Sites

The study sites were: Banrock Station (BA: 439000 E, 6216000 N), Big Mussel (BM: 443000 E, 6207000 N), Chambers Creek (CC: 443000 E, 6213000 N), Little Duck (LD: 462500 E, 6203500 N), Old Petes (OP: 443500 E, 6208250 N) and Pilby Creek (PI: 489750 E, 6239000 N). They are located on the floodplain of the Lower Murray between Locks 3 and 6 in South Australia (Figure 2.1). BA is the largest (86 ha) and LD and OP the smallest (5 ha: Table 2.1).

BA, BM, LD and PI have managed water regimes with periodic exposure of their wetland beds. Prior to recent management all were permanently inundated. Water regime has been manipulated for the longest period in PI (1992) and more recently in LD (1997: Table 2.1). The water regimes of CC and OP are not managed and under normal operational conditions their water regime is governed by the river level at Lock 3.

With the exception of BA, which is privately owned and operated, government agencies and community groups manage all wetlands and surrounding floodplain areas (Table 2.1). In managed wetlands, drop-board weirs across inlet(s) and outlet(s) are used to separate the wetland from the river (Plate 2.1). Water levels then fall primarily via evaporation. Seepage may also contribute to drawdown.

In all wetlands except BA, the water level when inlets and outlets to the wetland are open is controlled by the nearest downstream lock and weir. For this chapter and Chapter 3 this level will be referred to as the 'operational pool level'. When BA is not in a management phase, water levels are maintained between 8.45 and 8.7 m AHD (m Australian Height Datum). This is the operational pool level range of BA.

At BA and PI the inlet(s) and outlet(s) 'straddle' a weir creating a hydraulic gradient between them. This enables drawdown to occur rapidly and greatly exceed evaporative rates that range from 0.5-1.5 cm d^{-1} (data source: Department for Water, Land and Biodiversity Conservation, South Australia, (DWLBC). Pumping has also been used to accelerate drawdown in LD.

2.4 Methods

2.4.1 Vegetation sampling

The floristic composition of wetlands was determined by scoring the cover/abundance of plants in five 1 × 1m cells contained within 5 × 1m quadrats located at five elevations on permanent transects across each wetland's littoral zone. Quadrats were placed at the highest point on the littoral zone (where the bank of the wetland met the floodplain), the lowest point and at elevation changes of 25%, 50% and 75%.

At some sites, there was a step on the bank at the water's edge (a result of erosion from long periods of near stable water levels). If an elevation was located on the vertical face of the step, vegetation was sampled at the top of the step instead. If two elevations occurred across the step, the vegetation at the top and bottom was sampled.

Elevation was determined using a theodolite. Cover/abundance scores were recorded using a scale from 0-6, with 0 representing a plant that was absent, 1 rare and up to 6 for species with continuous cover (adapted from Blanch *et al.* 1999b: Table 2.2). Henceforth, measurements of 'cover/abundance' will be referred to interchangeably as 'cover' or 'abundance'.

A pilot study was undertaken in October 1999 to determine the number of transects needed to represent each wetland. Transects were distributed in wetlands at a frequency of one per 200-400m of littoral zone. This gave 11 transects for BA, 16 for BM, 13 for CC, 11 for LD, 7 for OP and 10 for PI.

For logistical reasons the number of transects needed to be reduced. Cluster analysis was used to identify groups of transects with similar vegetation and the number of transects in each group was reduced to three. This gave nine transects for BA, 12 for BM, nine for CC, six for LD, three for OP and six for PI. The cluster analysis determined similarity between transects using the Sorensen distance metric (equivalent to the Bray-Curtis metric) and assigned clusters using the Group Average Linkage method (equivalent to Unweighted Paired Groups Means Analysis, UPGMA, PC-ORD version 4.21: McCune and Mefford 1999).

Table 2.1. A description of each wetland: surface area at operational pool level (area); the year management commenced (date); drawdown frequency (frequency); drawdown timing (timing); the method used to drawdown water levels (method); the closest lock and weir (lock and weir); the organisation that manages the wetland (manager). NB. 'hydraulic' refers to wetlands where there is a large hydraulic gradient between inlet and outlet structures enabling rapid drawdown.

	Banrock Station	Big Mussel	Chambers Creek	Little Duck	Old Petes	Pilby Creek
Area	86 ha	70 ha	68 ha	5 ha	5 ha	18 ha
Date	1995	1995	NA	1994	NA	1992
Frequency	1 in 1 y	1 in 1-2 y	NA	1 in 1-2 y	NA	unpredictable
Timing	winter	late-summer	NA	late-summer	NA	unpredictable
Method	hydraulic+ evaporation	evaporation	NA	pumping+ evaporation	NA	hydraulic+ evaporation
Lock and weir	Lock 3†	Lock 3	Lock 3	Lock 4	Lock 3	Lock 6
Wetland Manager	Banrock Station Wine & Wetland Centre (BRL Hardy)	South Australian Field and Game Association, Barmera-Moorook Branch	South Australian National Parks & Wildlife Service	Wetland Care Australia	South Australian Field and Game Association, Barmera-Moorook Branch	Pilby Creek Management Committee

† Water levels at BA are set by wetland managers and are independent of levels at Lock 3.

Sampling times coincided with different stages in the hydrological cycle of the wetlands: prior to re-flooding, post re-flooding, during the flooded phase, prior to drawdown and during drawdown. The resultant survey dates were 15-20 November 1999 (November 1999), 10-15 February 2000 (February 2000), 15-20 May 2000 (May 2000), 2-7 August 2000 (August 2000), 15-20 December 2000 (December 2000) and 26-30 March 2001 (March 2001).

2.4.2 Analysis

The % total cover/abundance (TCA) for each species was calculated by summing the cover of all species within a wetland for a *single* survey and then determining the proportion of total cover accounted for by each. Where % total cover/abundance has been calculated for *all* surveys combined, TCA^a is used.

The floristic composition of each wetland was described using species with $TCA^a >$ 0.1%. While 0.1% is low in comparison to other suggested cut off percentages (Clarke and Warwick 1994), it was selected because species common in one survey may be uncommon in others and thus have a low % TCA^a overall. This reduced the species pool from 72 to 44 species.

Unbalanced NPMANOVA (Non-parametric multivariate analysis of variance) was used to test for differences in the floristic composition between wetlands (Anderson 2000). An unbalanced design was used because each wetland had a different number of transects (n = 3-12). The analysis was a one-way test (factor = wetland) with six levels (one for each wetland) and used Bray-Curtis dissimilarities to compare floristic similarity between wetlands. Data were standardised by row (sample) sums. P values were calculated using 5000 permutations and hence the lowest possible P-value was 0.0002. Pair-wise *a posteriori* tests were used to determine differences between levels of the factor wetland (Anderson 2000).

To visualise the multivariate patterns between wetlands, Non-metric Multidimensional Scaling (NMS) was performed on Relative Sorensen distances for each survey (PC-ORD version 4.21). The Relative Sorensen metric is equivalent to a standardised Bray-Curtis metric. It is most useful for ecological community data and when compared to Euclidean distance, retains sensitivity in more heterogeneous data sets and gives less weight to outliers (McCune and Mefford 1999). To aid in interpretation and presentation, ordination plots were kept to 2-dimensional

Table 2.2. The scale used to score the cover/abundance of plants in the study wetlands (modified from Blanch *et al.* 1999b).

Cover/abundance score	Description	Plant size (growth form examples)		
		Small (herbs, mud-mats)	Medium (tussock and creeping grasses, low sedges)	Large (reeds, tall rushes and sedges)
0	Absent	-	-	-
1	Rare	1-2 m^{-2}	1 ramet/runner m^{-2}	1 ramet m^{-2}
2	Individuals: very few or few	3-6 individuals or ramets m^{-2}	2-5 ramets/runners m^{-2}	2-3 ramets m^{-2}
3	Individuals: few-large or many small	7-20 individuals or ramets m^{-2}	5-10 ramets/runners m^{-2}	3-5 ramets m^{-2}
4	Individuals: very abundant	> 20 m^{-2}	10-15 ramets/runners m^{-2}	5-10 ramets m^{-2}
5	Nearly continuous, some gaps remain	Many overlapping individuals, some gaps remain	Many overlapping individuals, patchy ground cover	Dominant overstorey with ground cover
6	Continuous	All individuals touching adjacent conspecifics	All individuals touching adjacent conspecifics	Dominant species, no ground cover

(2D) solutions despite stress values of 20-30%.

Species contributing to differences in floristic composition were determined by overlaying ordination plots with joint plots and by performing Indicator Species Analysis (ISA: Dufrêne and Legendre 1997) in PC-ORD. The maximum number of permutations for ISA was 1000 and hence the lowest possible *P*-value was 0.001. Joint plots are represented on ordination plots by lines that radiate from the centroid of ordination scores. The angle and length of the line indicate the direction and strength of the relationship. Joint plot cutoff values were set at $r^2 = 0.25\text{-}0.30$. A joint plot is similar to a bi-plot but does not follow the strict set of rules required for a true bi-plot (Jongman *et al.* 1987).

Blocked Multi-Response Permutation Procedures (MRPP) in PC-ORD was used to determine if floristic composition within wetlands changed between surveys. Repeated measures non-parametric Friedman ANOVA together with nonparametric post-hoc multiple comparisons (Statistica for Windows, StatSoft 1997) assessed whether any of the species that influenced the difference in floristic composition between wetlands (identified from joint plot analysis and ISA) had significant changes in cover/abundance during the study.

'Common' species were those that occurred in all wetlands for at least one survey. 'Unique' species were those recorded in only one wetland during a survey. Hence, unique is a relative rather than absolute term, with a species possibly unique in one survey, but common in others. Diversity for wetlands was determined by calculating species richness.

To obtain an estimate of water regime variability in each wetland, the mean of the daily deviation (mean deviation) from the target pool level of the nearest downstream lock and weir was calculated for 1 November 1999 to 31 March 2001. This measure is non-directional and has units of m d^{-1}.

2.4.3 Hydrograph determination

Water level data are collected daily in m AHD at all locks in the study region and were obtained from DWLBC.

Water levels in CC and OP were assumed to be the same as at Lock 3 (target pool level = 9.80 m AHD). Of the managed wetlands, water level data were most detailed in BA where levels were recorded daily during the irrigation season but less frequently during non-irrigation months.

Water level measurement at BM coincided with the opening or closing of regulation structures. When no direct measurements were available and regulation structures closed, regional net evaporation and precipitation rates were used to determine drawdown rates (data source: DWLBC). When structures were open, water levels were assumed to be the same as at Lock 3 (target pool level = 9.80 m AHD). As for all wetlands, seepage may have contributed to drawdown, but an estimate was not available.

Other than during the first five days of drawdown in August 1999, groundwater levels were only recorded on three occasions in LD. After this, regional evaporation and precipitation rates were used to determine falls in water level. When the structures were open, levels were assumed to be the same as at Lock 4 (target pool level = 13.20 m AHD).

The least information was available for PI, where other than during a partial fill in May 2000, managers collected no water level data. Water levels were estimated by considering the date that structures opened and closed, with the knowledge that filling occurs in less than a week. In the case of drawdown, net evaporation and precipitation rates from Lock 5 were used. When structures were open, water levels from Lock 6 were used (target pool level = 19.25 m AHD).

2.5 Results

2.5.1 Wetland hydrology

Chambers Creek and Old Petes

CC and OP were flooded for the entire study. The total water level variation from 1 January 1999 to 31 March 2001 was 26 cm (Figure 2.2) and the mean deviation from pool level (Lock 3) was 0.03 m d^{-1}. Water levels remained between 9.8 and 9.9 m AHD for 75% of the time, reaching a peak of 10.02 m AHD on 24 December 2000, and a low of 9.76 m AHD on 24 November 2000 (Figure 2.2).

Table 2.3. Species with a % total cover/abundance (TCA^a) > 1% for all surveys. Combined, they account for 90.1% TCA^a.

Species	% TCA^a	Species	% TCA^a
P. australis	17.8	*B. caldwellii*	2.9
P. distichum	14.4	*L. minor*	2.7
T. domingensis	13.1	*C. dactylon*	2.5
A. filiculoides	13 0	*P. lapathifolia*	2.0
C. gymnocaulos	5.1	*A. subulatus*	1.8
V. americana	4.2	*S. quinqueflora*	1.7
S. mitchellii	3.8	*J. aridicola*	1.6
S. validus	2.9	*R. palustris*	1.0

Banrock Station

Drawdown commenced in May 1999 and there was no surface water during June and July 1999. After re-filling, a managed flood was initiated that peaked on 5 October at 1.23 m above the bottom of the wetland and lasted until November 1999 (Figure 2.3). Managed floods are created in BA by raising the height of boards in regulating structures to elevate water levels above the normal, operational pool level range. Another drawdown was initiated in June 2000, during which, the sediment in the base of the wetland remained moist because cool ambient temperatures (mean daily maximum temperature for June/July 2000 = 18°C) and evaporation rates (1.2 mm d^{-1}) were insufficient to evaporate residual pools (< 5 cm deep).

Refilling commenced in August 2000. This was followed by a managed flood in November 2000 and augmented by a natural flood in December (Figure 2.3). In early January water levels returned to pool level and remained there until the end of the study. The mean deviation from the managed pool level was 0.16 m d^{-1}.

Big Mussel

Water levels fell via evaporation from 9.86 to 9.37 m AHD between 14 January and 7 December 1999 (Figure 2.4). The bottom of BM is at 8.80 m AHD. Re-filling occurred in late December 1999 and water levels rose by 44 cm in 15 days. The wetland remained at pool level until another slow evaporative drawdown commenced in May 2000. Water levels fell via evaporation until re-filling in October 2000 during high river flows. Levels remained at pool until the completion of the study. The mean deviation from pool level (Lock 3) was 0.17 m d^{-1}.

Little Duck

Drawdown in July 1999 was initially assisted by pumping whereupon water levels dropped from 13.29 to 12.96 m AHD in seven days (Figure 2.5). Water levels were sub-surface from October 1999 until October 2000 when the wetland was filled by floodwaters. Three measurements of groundwater depth during this period indicated that levels varied from 20-80 cm beneath the wetland bed. After re-filling, the wetland remained full for the remainder of the study (Figure 2.5). The mean deviation from pool level (Lock 4) was 0.57 m d^{-1}.

Pilby Creek

No surface water was present when the study began in November 1999 as a result of rapid drawdown in May 1999. The wetland was partially re-filled in March 2001 to approximately 35 cm for just over one month after which water levels were drawndown again (Figure 2.6). No surface water was present until overbank flooding in October 2000 filled it from approximately 17.57 to 19.44 m AHD in < 10 days (Figure 2.6). The wetland remained full until March 2001. The mean deviation from the pool level (Lock 6) was 1.06 m d^{-1}, the highest of all wetlands.

2.5.2 General characteristics of the floristic composition

Cover/abundance

Seventy two species were recorded between November 1999 and March 2001 of which 44 had a $TCA^a > 0.1\%$. A species list is presented in Appendix 1. The 16 most abundant species in the study ($TCA^a > 1\%$) accounted for 90.1% of TCA^a (Table 2.3).

Species richness

The number of species recorded during each survey varied from 34 in March 2001 to 40 in February 2000. With the exception of February, BA had the greatest species richness (22-27: Table 2.4). Next was BM, which although having consistently more species than CC, LD and PI, did have similar richness to OP in all but February. OP

Table 2.4. The species richness and number of unique species (in brackets) for each wetland in each survey (for explanation of wetland codes see Section 2.3). The values below the survey date represent the total species richness and total number of unique species for all wetlands combined.

	Wetland					
Survey	BA	BM	CC	LD	OP	PI
November 1999 (39/12)	22 (3)	23 (1)	14 (1)	14 (1)	19 (1)	17 (5)
February 2000 (40/7)	27 (3)	29 (1)	14 (1)	16 (1)	22 (1)	14 (0)
May 2000 (39/11)	27 (4)	21 (3)	10 (0)	15 (0)	20 (1)	17 (3)
August 2000 (35/10)	24 (5)	21 (1)	10 (0)	13 (1)	18 (0)	14 (0)
December 2000 (36/10)	27 (6)	19 (0)	14 (1)	13 (2)	23 (0)	11 (1)
March 2001 (34/9)	23 (3)	20 (2)	13 (0)	13 (2)	19 (0)	12 (2)

had an intermediate level of richness compared to other wetlands (18-23). The least number of species were always recorded in CC, LD and PI, with the lowest, 10, recorded in CC during May and August 2000 (Table 2.4).

Common species

Phragmites australis was found in all wetlands in all surveys and was the most common plant, accounting for 17.8% TCA[a] (Table 2.3). *Typha domingensis* (13.1% TCA[a]) and *Cyperus gymnocaulos* (5.1% TCA[a]) were recorded in all wetlands in five surveys and *Paspalum distichum* in three (14.4% TCA[a]: Table 2.3).

Unique species

Twenty five of the species with TCA[a] > 0.1% were unique, i.e. recorded in only one wetland during a survey. The number of unique species ranged from seven in February 2000 to 12 in November 1999. BA had at least one unique species during each survey and, apart from November, also had the most during each (Table 2.4). PI had the next highest (Table 2.4). The remaining wetlands had zero to three unique

Table 2.5. A comparison of the floristic composition of wetlands for each survey (for explanation of wetland codes see Section 2.3). The analysis was undertaken using an Unbalanced NPMANOVA. Results of the pair-wise *a posteriori* tests apply to rows (survey times). Superscripts indicate wetlands with similar floristic compositions (α=0.05).

Survey	*F* (df), *P*	Wetland					
November 1999	7.67 (5,39), 0.0002	BA^{a}	BM^{b}	CC^{c}	LD^{d}	OP^{bc}	PI^{e}
February 2000	7.17 (5,39), 0.0002	BA^{a}	BM^{b}	CC^{c}	LD^{d}	OP^{e}	PI^{f}
May 2000	5.96 (5,39), 0.0002	BA^{a}	BM^{b}	CC^{b}	LD^{c}	OP^{d}	PI^{e}
August 2000	6.35 (5,39), 0.0002	BA^{a}	BM^{bc}	CC^{b}	LD^{d}	OP^{cd}	PI^{e}
December 2000	5.26 (5,39), 0.0002	BA^{a}	BM^{b}	CC^{c}	LD^{d}	OP^{e}	PI^{f}
March 2001	3.64 (5,39), 0.0002	BA^{a}	BM^{b}	CC^{c}	LD^{c}	OP^{bcd}	PI^{d}

species for each survey. Although unique, some plants were found in more than one wetland in other surveys. For example, *Persicaria lapathifolia* was only found in PI during December 2000 but in BM, LD and PI in November 1999.

2.5.3 Comparison of the floristic composition of wetlands for each survey

November 1999

BA, LD and PI all had different floristic compositions whereas BM and CC were the same as OP (Table 2.5). BA transects were located to the bottom left of the ordination plot suggesting a correlation with *A. filiculoides* and *T. domingensis* (ordination plot, r^2=0.70, stress = 23.7%: Figure 2.7). Both species, along with *Sarcocornia quinqueflora* and *Persicaria decipiens,* were indicators of BA (Table 2.6). The positive correlation of *Centipeda cunninghamii*, *Centipeda minima*, *Persicaria lapathifolia* and *Rorippa palustris* with Axis 2 reflected the absence of these plants in BA. The position of PI transects indicated that its vegetation was the most dissimilar of all wetlands to BA (Figure 2.7).

PI transects had a similar distribution in ordination space and were influenced by *C. cunninghamii*, *C. minima*, *P. lapathifolia* and *R. palustris* (Figure 2.7). These species made up four of the seven that were indicators of PI in November 1999 (Table 2.6).

Although LD had a unique composition some of its transects (e.g. LD5) had a similar position in ordination space to some BM transects (Figure 2.7). The distribution of LD transects indicated a relationship with *P. distichum*, which although was not a significant indicator, was the second most abundant plant in LD (26.2% TCA). The distribution of LD transects also reflected the presence of *R. palustris* (5.7% TCA).

BM, CC and OP transects were highly dispersed, with a number from each displaying greater similarity to transects from other wetlands than from their own e.g. BM with LD, CC and OP (Figure 2.7). The high dispersion of BM transects related mostly to variable *P. distichum* cover. BM differentiated from CC because of its correlation with *C. cunninghamii*, *P. lapathifolia* and *R. palustris*, all of which were absent from CC *and* OP. OP and CC transects were similar in position on the ordination plot, but their compositions were differentiated by *Myriophyllum papillosum*, an indicator unique to OP (Table 2.6).

February 2000

Each wetland had a different floristic composition (Table 2.5). BA transects grouped to the bottom left of the ordination plot suggesting a relationship with *S. quinqueflora*, *T. domingensis* and *V. americana* (ordination plot, $r^2 = 0.74$, stress = 21.6%: Figure 2.8). The former and latter species were indicators of BA (Table 2.6). *Eragrostis australis* and *Wilsonia rotundifolia* were also indicators unique to BA (Table 2.6), although they occurred in low abundance (1.6% and 0.7% TCA).

PI transects had contrasting distributions to BA transects and most were correlated with *P. lapathifolia*, the second most abundant plant in PI (29.7% TCA). Along with the less abundant *C. minima* (5.1% TCA) and *R. palustris* (2.7% TCA), *P. lapathifolia* was also an indicator of PI (Table 2.6).

A. denticulata and to a lesser extent *P. lapathifolia* contributed most to LD's dissimilarity to other wetlands (Figure 2.8), with the former also an indicator species (Table 2.6). While not strongly correlated with the ordination axes, *P. distichum* was an indicator and the most abundant plant in LD (29.4% TCA). Although the overall

Table 2.6. Indicator species for each survey. Wetland codes indicate in which wetland a species was an indicator (for explanation of wetland codes see Section 2.3). Codes in bold and italics indicate a species that was only found in that wetland for that survey. Numbers represent the % TCA in respective wetlands. Indicator Species Analysis used 1000 permutations and hence the lowest possible *P*-value was 0.001. * $P < 0.05$, ** $P < 0.01$, ***P=0.001.

	November	February	May	August	December	March
A. denticulata		LD* 1.6	LD* 0.5	___LD___* 0.6		
A. filiculoides	BA** 12.0	CC** 9.4	CC* 15.6			
A. subulatus	BM* 3.2	BM* 2.9.0	OP* 1.0			
B. basaltica	___PI___** 0.3		PI** 0.3			___PI___* 0.1
B. caldwellii		BA* 4.0	BA* 2.7	BA* 2.5	BA*** 3.2	BA** 2.4
B. medianus					___LD___* 0.6	___LD___* 0.3
C. cunninghamii	PI*** 1.5	BM* 0.7		___PI___** 0.4		
C. minima	___PI___*** 0.4	PI*** 0.5	PI* 0.3			
C. pumilio	___PI___** 0.5	PI* 0.2				
E. australis		___BA___* 0.4	BA* 0.7			
E. dielsii				___BA___* 0.4		
H. curassavicum	BM* 0.8		OP** 0.6	OP* 0.4	OP** 0.5	
L. minor			PI*** 4.0	___PI___* 0.5		LD* 2.3
M. papillosum	___OP___** 1.0	OP** 1.0	OP** 0.4	OP** 0.4	OP*** 0.6	OP*** 0.5
M. repens	BM* 1.6	BM* 1.6				
M. verrucosum		___BM___*** 0.9		___BA___* 0.2		
P. decipiens	___BA___* 0.2	BM* 0.7	___BA___* 0.5	___BA___* 0.2	___BA___* 0.5	___BA___* 0.3
P. distichum		LD* 12.4	LD* 16.9	LD* 17.3		
P. crispus					___CC___* 0.3	
P. lapathifolia	PI*** 3.6	PI* 2.8	PI* 2.7	PI*** 2.8	___PI___* 0.2	
P. luteo-album	___PI___* 0.1					
R. palustris	PI*** 3.4	PI* 0.2		PI*** 1.8		
S. mitchellii				OP* 3.9	OP* 3.8	OP* 4.0
Sonchus sp.		OP* 0.5				
S. quinqueflora	BA** 1.4	BA*** 1.9	BA** 2.0	BA** 2.0	BA** 1.7	BA** 1.3
T. domingensis	BA* 12.0					BM* 16.8
V. americana	BA** 2.9.0	BA* 2.9	BA** 4.6	BA** 3.7		
W. rotundifolia		___BA___* 0.2	___BA___* 0.3			___BA___* 0.2

composition of LD differed from other wetlands, some transects, especially LD 5, were more similar to some BM transects.

BM transects were dispersed across the ordination plot suggesting contrasting abundances of *T. domingensis* and *V. americana* versus *P. australis* (Figure 2.8). However, BM was still different to other wetlands because of the indicators *A. subulatus*, *C. cunninghamii*, *M. repens* and *M. verrucosum*, with the latter also unique to BM (Table 2.6).

CC transects were clustered, with their distribution reflecting the absence of *A. denticulata*, and contrasting contributions of *T. domingensis* and *P. australis* (Figure 2.8). OP transects were dispersed with no strong relationship to any species.

May 2000

With the exception of BM and CC, all wetlands had a different floristic composition (Table 2.5). Only four species had strong correlations with the ordination plot (ordination plot, $r^2 = 0.73$, stress = 23.2%: Figure 2.9).

The distribution of BA transects suggests a positive relationship with *T. domingensis* - the second most abundant plant in BA in May 2000 (15.7% TCA) - and a negative relationship with *P. australis*. The dissimilarity of BA to other wetlands was also influenced by the indicators *P. decipiens*, *S. quinqueflora*, *V. americana* and *W. rotundifolia* that combined contributed 19.2% TCA (Table 2.6). The similarity of BA and PI was greater in May compared to previous surveys.

The difference between LD and other wetlands was due primarily to *P. distichum*, which was an indicator species and the most abundant plant in LD (32.7% TCA), and *P. australis*, the second most abundant plant (26.4% TCA; Figure 2.9). The dispersion of some LD transects suggests contrasting contributions of *P. distichum* and *P. australis*.

The dispersion of OP transects suggests contrasting cover of *P. australis* and *T. domingensis* (Figure 2.9). OP's difference to other wetlands was presumably because of the indicators *M. papillosum*, *A. subulatus* and *H. curassavicum* (Table 2.6). CC transects were more tightly grouped than OP's but still imply contrasting abundance of *P. australis* and *T. domingensis*. The distribution of BM transects suggest compositions that differ mainly in the cover of *P. distichum* (Figure 2.9).

August 2000

Only BA and PI had distinct floristic compositions (Table 2.5). The floristic composition of BM did not differ from CC or OP, and LD was the same as OP (Table 2.5). The location of BA transects suggests that the difference between BA and other wetlands was due to *T. domingensis* and *S. quinqueflora*, with the latter also an indicator (ordination plot, $r^2 = 0.74$, stress = 21.7%: Figure 2.10; Table 2.6). In contrast, the distribution of PI transects suggests a relationship with the indicators *P. lapathifolia*, the most abundant plant in PI in August (30.1% TCA), and *R. palustris* (Figure 2.10; Table 2.6).

As for previous surveys, *P. distichum* was an indicator of LD and along with *P. australis*, had a strong influence on the distribution of LD transects (Figure 2.10). Transects LD5 and LD6 were separated the most in ordination space, suggesting contrasting abundances of *P. distichum* and *P. australis*. The similarity of OP's and LD's floristic compositions was attributable to *P. australis* and *P. distichum*.

The similarity in the compositions of BM, CC and OP was attributable to a combination of *P. australis*, *C. gymnocaulos* and *T. domingensis* (Figure 2.10). BM transects in particular were highly dispersed, with BM7-9 more similar to BA transects than others within BM.

December 2000

All wetlands had different floristic compositions (Table 2.5). BA transects suggest a relationship with *T. domingensis* and *V. americana* (ordination plot, $r^2 = 0.68$, stress = 29.9%: Figure 2.11). *P. decipiens* was also unique and an indicator of BA (Table 2.6). BA transects were more dispersed in December than in previous surveys.

PI and LD transects occupied the opposite side of Axis 1 to BA (Figure 2.11). For both wetlands this reflected the absence of *V. americana*. There was also variability in the distribution of LD and PI transects suggesting contrasting abundances of *T. domingensis* and *P. australis* among transects (Figure 2.11). Notably, *P. distichum* and *P. lapathifolia* and other mudflat annuals did not influence the distribution of LD and PI.

The distribution of BM, CC and OP transects suggests they were the most similar wetlands in December (Figure 2.11). Transect distribution was influenced most by *P. australis* and *T. domingensis*. The dispersion of OP was contributed to by

V. americana, which was present at OP1 and OP2 but absent from OP3. The difference in their floristic compositions was attributable to the indicators *Potamogeton crispus* in CC, and *Sporobolus mitchellii* and *M. papillosum* in OP, with the latter unique to OP (Table 2.6).

March 2001

The floristic similarity of wetlands was greatest in March 2001, with only BA having a distinct flora (Table 2.5). There was no difference between CC, LD and OP, and BM was the same as OP. Similarly, PI was the same as OP; this was the first time during the study that PI did not have a unique floristic composition. Unlike previous surveys there were no distinct clusters of transects for any wetland (ordination plot $r^2 = 0.75$, stress = 25.8%: Figure 2.12).

The distribution of BA's transects suggests that it was more similar to other wetlands than for previous surveys (Figure 2.12). The difference in composition, however, was attributable to *T. domingensis* as well as the indicators *B. caldwellii, S. quinqueflora, P. decipiens* and *W. rotundifolia* with the latter two unique to BA (Table 2.6).

PI transects were highly dispersed across the ordination plot and did not correlate with any one species (Figure 2.12). BM transects were also dispersed indicating contrasting compositions of *T. domingensis* versus *P. australis* and *P. distichum*. The distribution of CC, LD and OP transects suggest similar contributions of *C. gymnocaulos, P. australis* and *P. distichum* (Figure 2.12).

2.5.4 Changes in floristic composition in wetlands through time

The floristic composition in BA, BM, LD and PI changed from November 1999 to March 2001 (Table 2.7). In contrast, the cover of species in CC and OP remained the same and there was no overall change in floristic composition (Tables 2.7 and 2.8).

Banrock Station

The composition changed from one survey to the next, but during March 2001 was the same as February, May and August 2000 (Table 2.7). Of the 47 species recorded between November 1999 and March 2001, only six had a significant change in cover. Of these, only two differentiated BA from other wetlands (see Section 2.5.3). The first, A. filiculoides, was the second most abundant plant in BA in the study (16.3%

Table 2.7. Changes in the floristic composition of wetlands between each of the six surveys. Analysis was performed using blocked Multi-Response Permutation Procedures (*A* denotes the test-statistic).

WETLAND	*A*, *P*	SURVEY					
Banrock Station	0.13 (5,48), <0.0001	Nov^{1}	Feb^{2}	May^{3}	Aug^{4}	Dec^{5}	Mar^{2,3,4}
Big Mussel	0.13 (5,66), <0.0001	Nov^{1}	Feb^{2}	May^{3}	Aug^{3}	Dec^{3,4}	Mar^{4}
Chambers Creek	0.02 (5,48), 0.11	Nov^{1}	Feb^{1}	May^{1}	Aug^{1}	Dec^{1}	Mar^{1}
Little Duck	0.16 (5,30), <0.0001	Nov^{1}	Feb^{1,2}	May^{2,3}	Aug^{3}	Dec^{4}	Mar^{5}
Old Petes	0.02 (5,12), 0.23	Nov^{1}	Feb^{1}	May^{1}	Aug^{1}	Dec^{1}	Mar^{1}
Pilby Creek	0.25 (5,30), <0.0001	Nov^{1}	Feb^{2}	May^{3}	Aug^{1}	Dec^{3}	Mar^{4}

TCA^{a}) and had a peak median cover in November 1999 (41: Table 2.8). The second, *M. verrucosum* fluctuated in cover and was found in only three surveys, all at low abundances (Table 2.8).

Big Mussel

The majority of change in floristic composition occurred between November 1999 and May 2000 (Table 2.7). In comparison, the composition only changed between December 2000 and March 2001 after there had been no change from May to December 2000 (Table 2.7).

Forty eight species were recorded between November 1999 and March 2001, of which 15 had changes in cover (Table 2.8). Of these, eight contributed to differences in the floristic composition between BM and other wetlands (see Section 2.5.3).

A. denticulata, *A. subulatus*, *C. cunninghamii*, *H. curassavicum*, *M. repens* and *M. verrucosum* declined in cover after February 2000 and with the exception of *A. subulatus* and *H. curassavicum*, none were recorded after May 2000. In contrast, *T. domingensis* increased in median cover from 9 in November 1999 to 30.5 in March 2001 (Table 2.8). Similarly, *V. americana* increased to a median cover of 10 in March 2001, after being absent in November 1999 (Table 2.8).

Little Duck

Change was greatest across the first four surveys followed by significant changes from August to December 2000 and December 2000 to March 2001 (Table 2.7). Twenty four species were recorded during the study. Six had a change in cover with four important in differentiating LD from other wetlands: *B. medianus, L. minor, P. distichum* and *P. lapathifolia.*

P. lapathifolia was present in only the first four surveys. *B. medianus* and *L. minor* were absent or in low abundance in the first four surveys, but increased in the final two with the former peaking in March 2001 (0.5) and the latter in December 2000 (13: Table 2.8). *P. distichum* was the most influential plant distinguishing LD from other wetlands and increased from a median cover of 37 in November 1999 to a peak of 51 in August 2000, but then declined to 17 and 18 in November 1999 and March 2001 respectively (Table 2.8).

Pilby Creek

Significant changes in floristic composition occurred between each survey (Table 2.7). Changes were cyclical with the composition during November 1999 and August 2000 the same and likewise for May 2000 and December 2000 (Table 2.7). Thirty eight species were recorded overall.

C. cunninghamii, *C. minima*, *C. pumilio*, *P. lapathifolia* and *R. palustris*, all indicators of PI for at least one survey, had peak median covers in November 1999 and then declined in February and May 2000 (Table 2.8). *C. cunninghamii*, *P. lapathifolia* and *R. palustris* increased again in August 2000 following the partial fill and subsequent drawdown (Table 2.8). After August, *C. cunninghamii*, *C. minima* and *R. palustris* were not found and *C. pumilio* and *P. lapathifolia* were recorded at reduced abundances. *L. minor* was only observed in May and December 2000 (Table 2.8).

2.6 Discussion

2.6.1 Similarity of floristic compositions

Water regime was assumed to be the driver of vegetation change in the study wetlands. Climate (e.g. seasonal weather patterns) was an unlikely agent in managed wetlands given that CC and OP had no change in vegetation and were located in the

Table 2.8. Changes in the median cover/abundance of species within wetlands (italics represent minimum and maximum values). *P* values < 0.0001 are written as 0.0001. Superscripts indicate surveys where median cover was similar (α=0.05).

Wetland	Species	November 1999	February 2000	May 2000	August 2000	December 2000	March 2001	χ_r^2 (df), *P*
Banrock Station	*A. filiculoides*	41^{a} *17-63*	15^{ab} *0-50*	27^{ab} *5-50*	20^{b} *0-44*	0 *0-35*	25^{ab} *0-50*	21.1 (5), 0.0008
	M. verrucosum	0 *0-23*	0	0	0 *0-5*	0	0	17.1 (5), 0.004
Big Mussel	*A. denticulata*	0 *0-23*	0 *0-23*	0	0	0	0	20.2 (5), 0.001
	A. subulatus	11.5^{a} *0-26*	6.5^{a} *0-30*	0^{b} *0-1*	0^{ab} *0-9*	0^{ab} *0-10*	0^{ab} *0-9*	29.3 (5), 0.0001
	C. cunninghamii	0 *0-15*	1 *0-11*	0	0	0	0	29.7 (5), 0.0001
	H. curassavicum	1 *0-16*	0 *0-4*	0 *0-1*	0 *0-2*	0 *0-2*	0 *0-2*	15.3 (5), 0.009
	M. repens	2.5 0-27	3.5 *0-42*	0	0	0	0	29.8 (5), 0.0001
	M. verrucosum	0^{a} *0-1*	3.5^{b} *0-16*	0^{ab} *0-20*	0	0	0	41.3 (5), 0.0001
	T. domingensis	9^{c} *0-32*	22.5^{abc} *0-40*	23^{bc} *0-29*	12.5^{c} *0-37*	28^{ab} *10-50*	30.5^{a} *6-95*	25.5 (5), 0.0001
	V. americana	0^{c}	0^{bc} *0-3*	0^{abc} *0-30*	1.5^{abc} *0-25*	12.5^{ab} *0-40*	10^{a} *0-30*	31.9 (5), 0.0001
Little Duck	*B. medianus*	0 *0-6*	0	0	0	0 *0-17*	0.5 *0-12*	10.3 (5), 0.06
	L. minor	0^{b}	0^{b}	0^{b}	0^{b}	13^{a} *5-32*	5^{ab} *2-10*	29.8 (5), 0.0001
	P. distichum	37^{abc} *7-58*	43^{abc} *10-55*	45^{a} *2-78*	51^{a} *8-75*	17^{bc} *0-32*	18^{cd} *1-46*	21.1 (5), 0.0008
	P. lapathifolia	0.5 *0-7*	8 *0-20*	7.5 *0-31*	0 *0-2*	0	0	11.5 (5), 0.04
Pilby Creek	*C. cunninghamii*	8^{a} *2-12*	0^{ab} *0-8*	0^{ab} *0-1*	2.5^{ab} *0-9*	0^{b}	0^{b}	22.8 (5), 0.0004
	C. minima	3.5 *0-8*	2.5 *0-9*	0.5 *0-8*	0 *0-2*	0	0	16.8 (5), 0.004
	C. pumilio	2.5 *0-14*	0 *0-3*	0 *0-1*	0	0	0 *0-1*	11.4 (5), 0.04
	L. minor	0^{b}	0^{b}	15^{ab} *10-20*	0^{b}	12^{a} *2-31*	0^{b}	28.9 (5), 0.0001
	P. lapathifolia	26.5^{a} *18-45*	18.5^{ab} *0-43*	13^{ab} *0-37*	21^{ab} *0-43*	0^{b} *0-5*	0^{b} *0-1*	20.9 (5), 0.0008
	R. palustris	17.5^{a} *2-29*	1^{ab} *0-5*	0^{ab} *0-13*	14.5^{a} *7-30*	0^{b}	0^{b}	25.3 (5), 0.0001

same climatic region. Furthermore, no significant sediment erosion or deposition was observed in any wetland, suggesting that altered edaphic factors were not the stimulus.

The absence of change in permanently flooded wetlands was consistent with the predicted impact of permanent inundation on plant regeneration and extirpation processes. This supports Blanch *et al.*'s (2000) hypothesis that the practice of maintaining stable weir pool levels in the Lower Murray limits vegetation processes e.g. germination and recruitment. Using the terminology of van der Valk and Davis (1980), permanently flooded wetlands remained continuously in the lake phase.

Floristic comparisons revealed that water regimes characterised by periodic flood and drawdown did not necessarily create more diverse or unique plant assemblages than those in permanently flooded wetlands. For example, in November 1999, May 2000, August 2000 and March 2001 at least two managed and unmanaged wetlands had the same composition. This finding rejects the first hypothesis of this study.

The similarity of wetlands to one another changed between surveys, a function of vegetation changes within managed wetlands. Managed wetlands generally differed in composition from permanently flooded wetlands during drawdown when the exposed bed was colonised by predominantly mudflat annuals. The compositions of managed and permanently flooded wetlands then became more similar as flooding extirpated most vegetation. Hence rather than flood and drawdown creating assemblages that are different from those in permanently flooded wetlands in perpetuity, they promote unique patterns of vegetation cycling. BA was the only exception among managed wetlands because mudflat annual colonisation failed to occur upon drawdown; this was most likely a result of the winter drawdown not triggering germination.

Differences in floristic composition were contributed to by species that responded both positively and negatively to flood and drawdown. The greatest response was from mudflat annuals and emergent macrophytes. Mudflat annuals germinate, grow and flower rapidly on recently exposed mudflats (Salisbury 1970; van der Sman *et al.* 1993; Houle and Belleau 2000) but posses few adaptations for tolerating the stresses of extended flood and drought (van der Sman *et al.* 1993). During November 1999 and February 2000 wetlands with mudflat annuals including *A. denticulata*, *C. cunninghamii*, *P. lapathifolia* and *R. palustris* (i.e. BM, LD and PI), were distinguished from those without (i.e. CC, OP). Notably, BM, LD and PI were subject to drawdown during these surveys. Subsequent flooding resulted in the dieback of these species and as a result differences in floristic composition during December 2000 and March 2001 were attributable only to a small number of perennial species.

Of the perennial species, *P. distichum* and *T. domingensis*, the second and third most abundant plants for all surveys and wetlands, influenced changes in floristic composition the most. *P. distichum*, because of its high abundance, differentiated LD from other wetlands between November 1999 and August 2000. However, after peaking in August 2000, it died back upon re-filling and had less of an influence in December.

T. domingensis had the greatest impact on changes in floristic similarity for BM. In addition to mature fringing stands, it established at lower elevations during the re-fill between November 1999 and February 2000 and colonised the littoral zone, becoming an indicator of BM in March 2001.

Some of the differences in floristic composition between wetlands were also attributable to species largely unaffected by flood and drawdown. These contributed to inherent differences in floristic composition (i.e. differences that exist apparently independent of the effects of recent flood and drawdown). For example, *P. decipiens*, *S. quinqueflora*, *T. domingensis* and *V. americana* consistently differentiated BA from other wetlands and yet none had a change in cover in BA. Their abundance in BA compared to other wetlands may have been a function of water regime history prior to November 1999 or edaphic factors. The latter applies to *S. quinqueflora*, a halophytic plant characteristic of moderately flooded saline areas (Jessop and Toelken 1986), given that salt scalds were common across the littoral of BA.

P. australis had the greatest influence on inherent differences in floristic composition. It had no changes in cover in any wetland and was the most abundant and common species for all surveys combined. This concurs with Blanch *et al.* (2000), who found that along with *C. gymnocaulos*, *P. australis* was the most abundant and widespread species in the littoral zone of the Lower Murray river channel.

The importance of *P. australis* for differentiating the floristic similarity of wetlands changed between surveys. This was due to a change in the cover of plants other than *P. australis*. For example, in PI the death of most of the vegetation, especially

P. lapathifolia, after filling in October 2000 resulted in *P. australis* becoming the most abundant species, accounting for 70% TCA in March 2001 compared to 26% TCA in August 2000.

A feature of BA was the low abundance of *P. australis*. This was a primary reason for the difference between BA and other wetlands. *P. australis* is intolerant of high salinity (Chapman 1960) and its low abundance was most likely a result of the anticipated high soil salinities at BA.

The difference in floristic composition between wetlands was due primarily to varying abundances of common rather than unique species. For example, of the 25 unique species, only five contributed to differences in floristic composition and none were the principle cause. In contrast, 12 of the 16 most abundant plants were important in determining the difference in floristic composition during at least one survey.

The managed wetlands varied in the extent to which their floristic compositions differed from permanently flooded wetlands. Assuming that increasing water regime variability increases the difference in establishment opportunities and flood and drought stress between wetlands, it was predicted that increasing water regime variability would increase the difference in floristic composition compared to permanently inundated wetlands. This prediction held for all wetlands except BA. For instance, PI had the greatest water regime variability and aside from BA was the most dissimilar wetland to OP and CC. In contrast, BM had the least variable water regime and was the most similar to CC and OP. The difference between BA and other wetlands suggests that when other factors become important, such as salinity in BA, the influence of water regime on floristic differences may decline.

Along with inter-wetland differences in floristic composition, there was also variability between transects within wetlands. For example, the distribution of BM transects in ordination space suggested there was always some difference in their composition that was attributable to *T. domingensis* and *P. australis*. Similarly, OP transects were highly dispersed on account of the absence of *V. americana* from one transect and its high abundance in the other two. Differences between PI transects were also heightened when re-flooding caused the dieback of *P. lapathifolia*, resulting in floristic compositions based primarily upon *P. australis*, a species absent from three transects. This suggests that heterogeneity is also a feature of the floristic composition within these wetlands.

2.6.2 Influence of water regime on floristic diversity

A common aim of wetland management is to maintain and enhance biodiversity. This has various interpretations including maximising species richness within individual wetlands or maximising the diversity of vegetation types in wetlands across a region or river reach. The former has been an aim in some Lower Murray wetlands. Indeed, two of the managed wetlands, BA and BM, continually had the highest species richness. However, water regime characterised by drawdown did not necessarily lead to high species richness. For example, richness in LD was lower than in OP for every survey and richness in PI was less than in OP for all but one survey.

Not only did flood and drawdown not necessarily lead to high species richness but the two aforementioned management aims conflicted. BM consistently had the highest or second highest species richness of all wetlands and yet in May and August 2000 had the same floristic composition as CC (based upon relative cover) that had about half the number of species as BM. Furthermore, aims of high species richness may ignore wetlands that already have different floristic compositions. For example, PI, LD and CC had similar species richness throughout the study, but had different floristic compositions for all but LD and CC in March 2001. These results suggest that species richness alone is not a good measure of restoration success.

It is not uncommon for wetland restoration aims to conflict (Zedler 2000). For example, aims of maximising biodiversity and functional attributes such as productivity cannot always be achieved in the same wetland given that species richness is often lowest where productivity is highest due to the dominance of single species. Conflicting biodiversity aims appear to have been reported less often.

Plate 2.1. A water regulation structure straddling the inlet channel to Big Mussel lagoon in the Loveday Wetland Complex. The structure is made from concrete and possesses four drop-board weirs, each containing multiple boards. Two weirs are located each side of the central buttress.

Figure 2.1. The lower River Murray showing the location of study wetlands (BA = Banrock Station, BM = Big Mussel, CC = Chambers Creek, LD = Little Duck, OP = Old Petes, PI = Pilby Creek). The lower River Murray forms at the junction of the Darling River and River Murray at Wentworth in New South Wales.

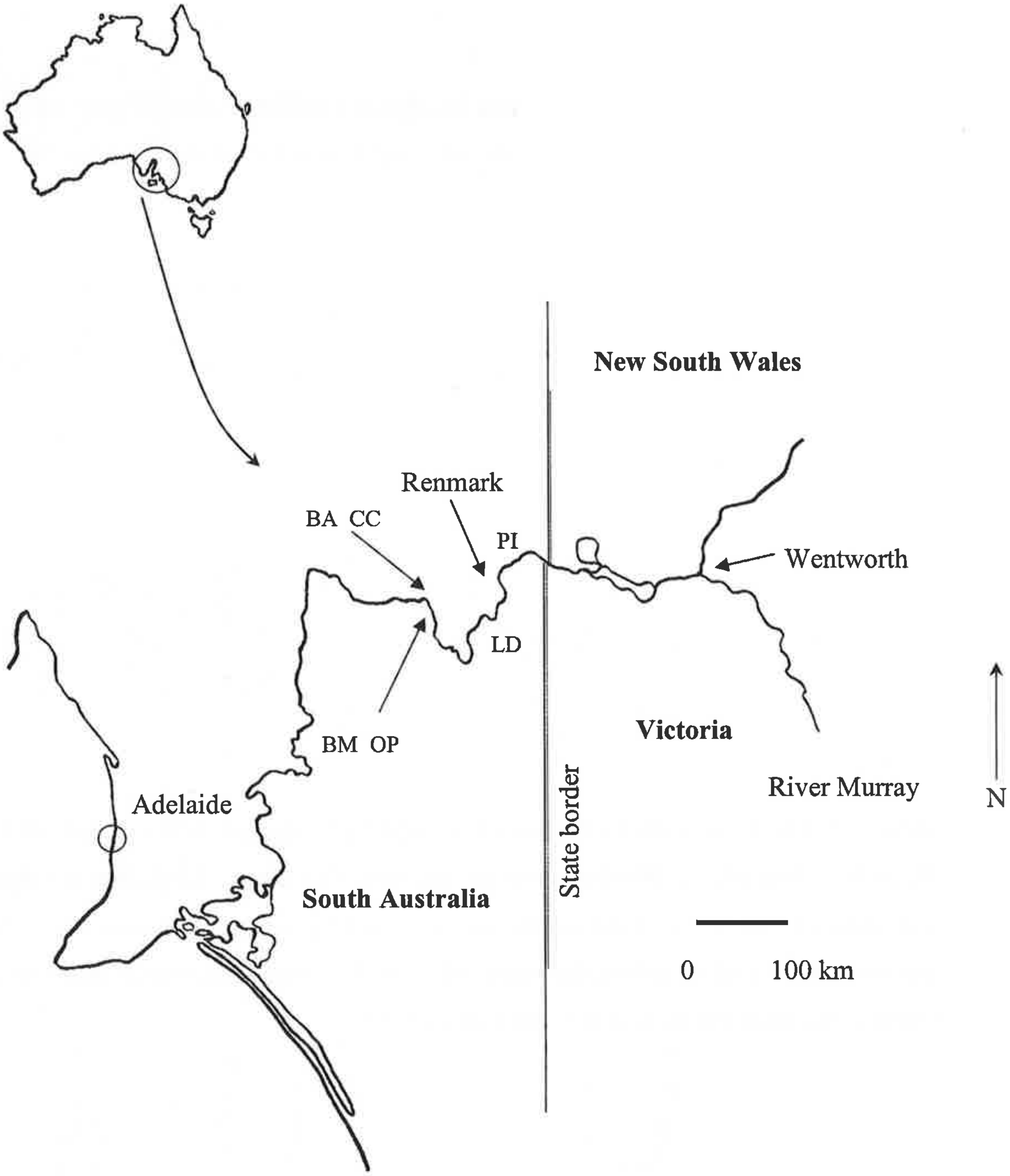
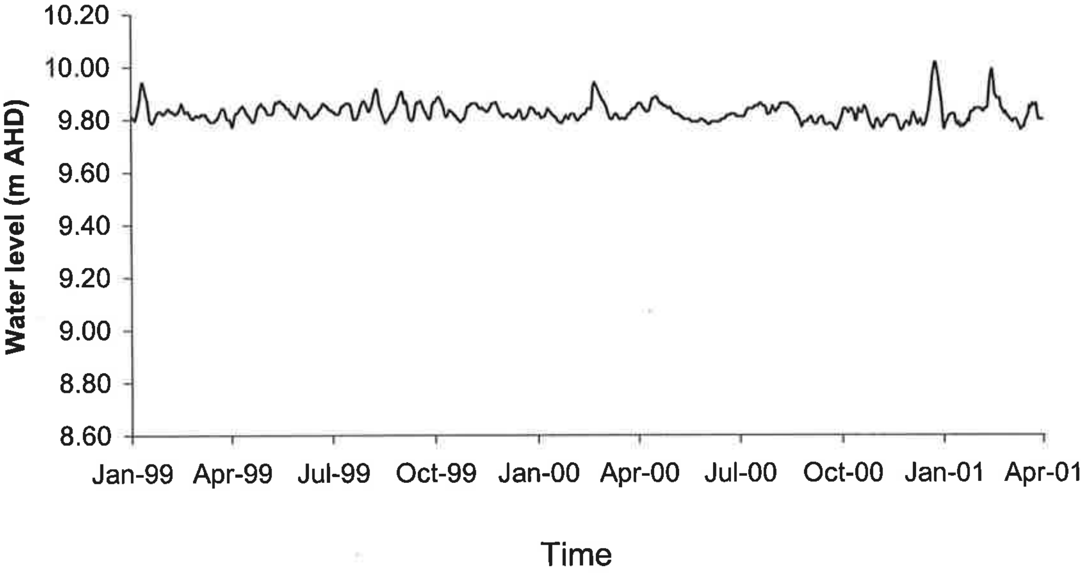

New South Wales
Renmark
BA CC
PI
Wentworth
LD
BM OP
Victoria
River Murray
N
Adelaide
State border
South Australia
0
100 km

Figure 2.2. The hydrograph for Chambers Creek (CC) and Old Petes (OP) for January 1999 through to April 2001. The base elevation at CC was 8.77 m AHD and at OP 9.41 m AHD.

Figure 2.3. The hydrograph for Banrock Station (BA) for August 1999 to April 2001. Water level data prior to this date were not available. The water level staff at BA does not measure below 8.5 m AHD and the rate of water level drawdown below this level was estimated based on information supplied by B. Vagnarelli, Banrock Station (pers. comm.). The base elevation at BA was 8.04 m AHD.


Water level (m AHD)
10.20
10.00
9.80
9.60
9.40
9.20
9.00
8.80
8.60
Jan-99
Apr-99
Jul-99
Oct-99
Jan-00
Apr-00
Jul-00
Oct-00
Jan-01
Apr-01
Time

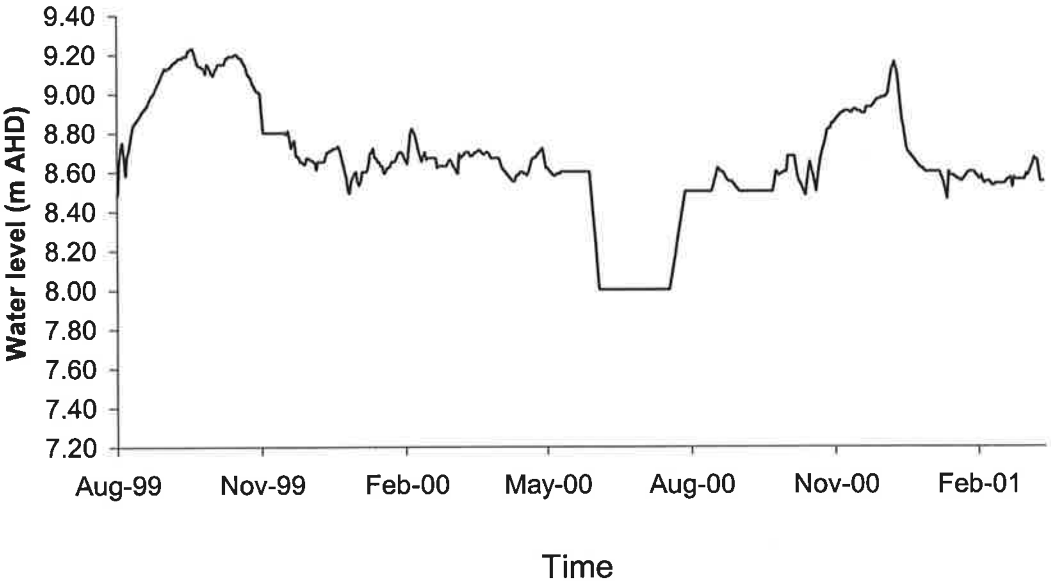
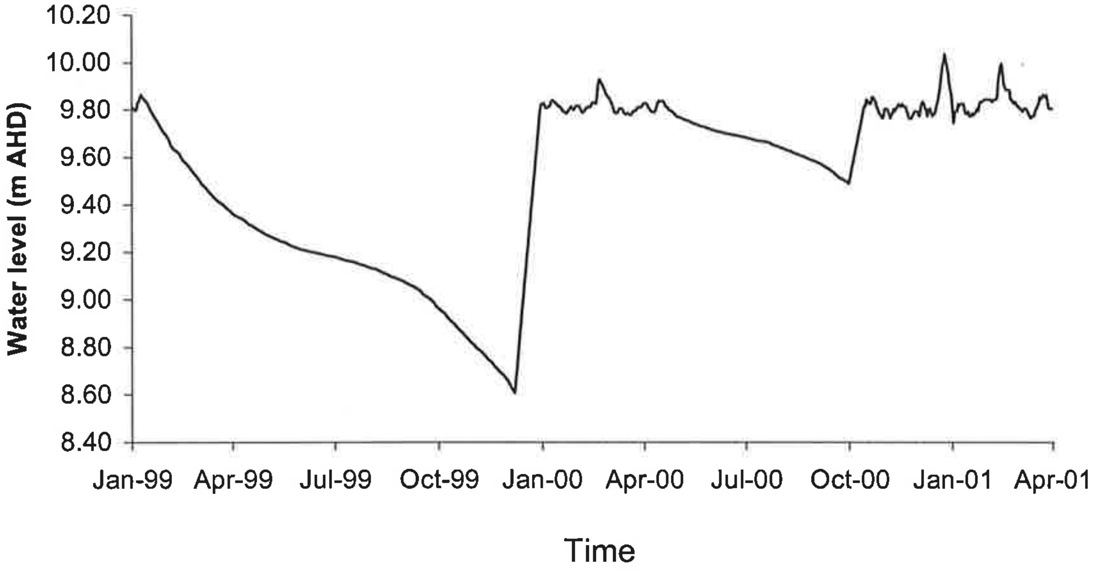

Water level (m AHD)
9.40
9.20
9.00
8.80
8.60
8.40
8.20
8.00
7.80
7.60
7.40
7.20
Aug-99
Nov-99
Feb-00
May-00
Aug-00
Nov-00
Feb-01
Time

Figure 2.4. The hydrograph for Big Mussel (BM) for January 1999 to April 2001. The base elevation was 8.80 m AHD.

Figure 2.5. The hydrograph for Little Duck for January 1999 to April 2001. Only three measurements of water level beneath the sediment surface were taken while the wetland was dry. The dotted line on the hydrograph is the estimated water level between readings taken on 11/11/99 and 23/8/00. The base elevation was 12.55 m AHD.


10.20
10.00
9.80
9.60
9.40
9.20
9.00
8.80
8.60
8.40
Water level (m AHD)
Jan-99
Apr-99
Jul-99
Oct-99
Jan-00
Apr-00
Jul-00
Oct-00
Jan-01
Apr-01
Time

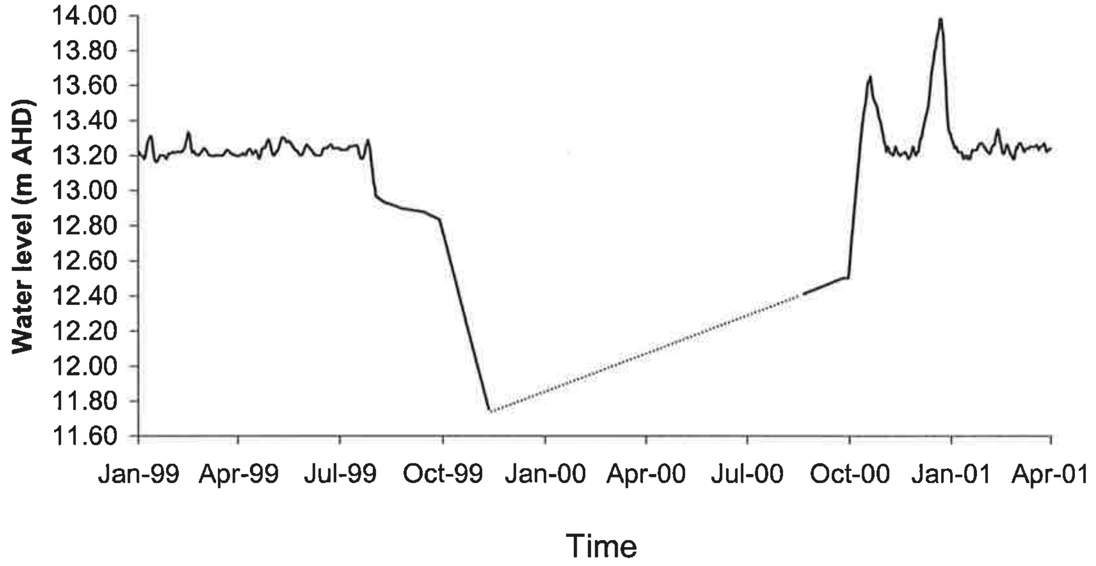

14.00
13.80
13.60
13.40
13.20
13.00
12.80
12.60
12.40
12.20
12.00
11.80
11.60
Water level (m AHD)
Jan-99
Apr-99
Jul-99
Oct-99
Jan-00
Apr-00
Jul-00
Oct-00
Jan-01
Apr-01
Time

Figure 2.6. The hydrograph for Pilby Creek for the period June 1999 to April 2001. The base elevation was 17.77 m AHD.

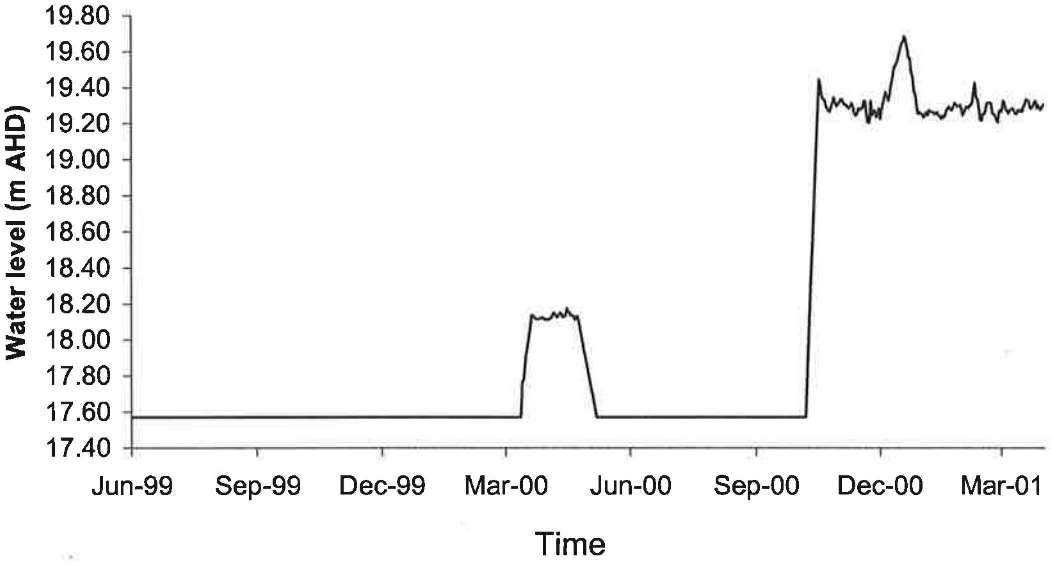

Water level (m AHD)
19.80
19.60
19.40
19.20
19.00
18.80
18.60
18.40
18.20
18.00
17.80
17.60
17.40
Jun-99
Sep-99
Dec-99
Mar-00
Jun-00
Sep-00
Dec-00
Mar-01
Time

Figure 2.7. NMS ordination plot of the floristic composition of transects from each wetland during November 1999 (r^2=0.70, stress=23.7%). Seven species, indicated by joint plots, had strong correlations with the 2D NMS ordination plot ($r^2 > 0.3$). Joint plots are represented by lines that radiate from the centroid of ordination scores. The angle and length of the lines indicate the direction and strength of the relationships. A single joint plot line represents *P. lapathifolia* and *C. minima*. Species codes are based on the first three letters of the generic and species names.

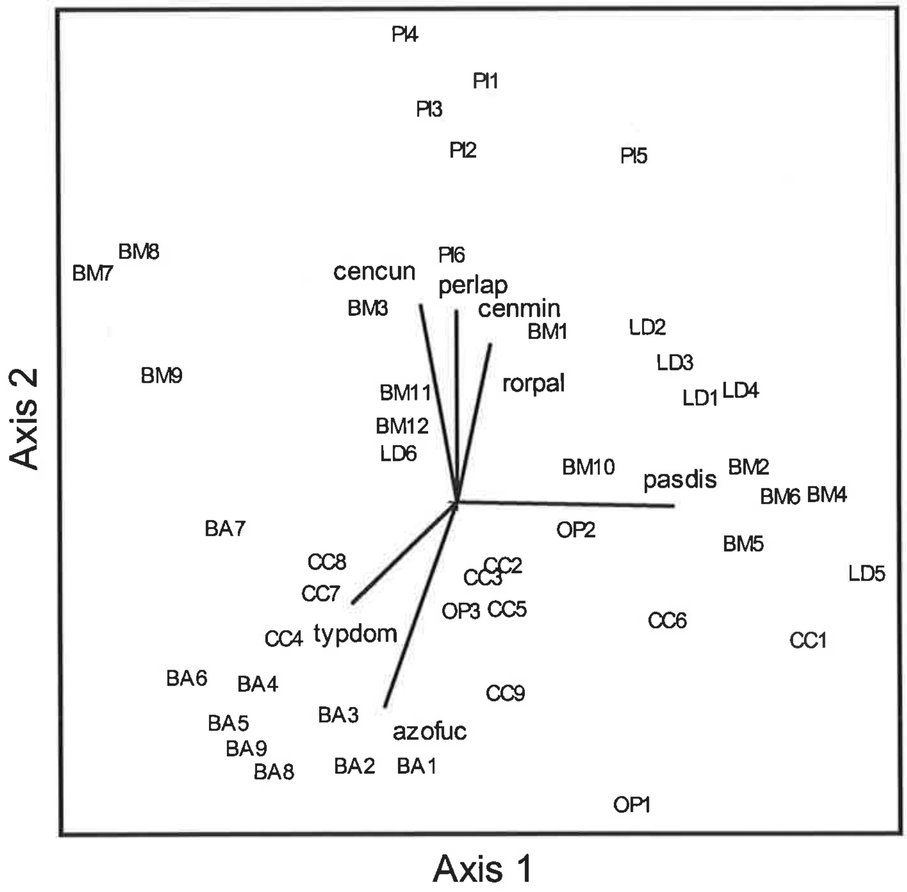

PI4
PI1
PI3
PI2
PI5
BM8
BM7
PI6
cencun
perlap
BM3
cenmin
BM1
LD2
LD3
BM9
rorpal
BM11
LD1
LD4
BM12
LD6
BM10
pasdis
BM2
BM6
BM4
BA7
OP2
BM5
CC8
CC2
CC3
LD5
CC7
OP3
CC5
CC6
CC4
typdom
CC1
BA6
BA4
CC9
BA5
BA3
azofuc
BA9
BA8
BA2
BA1
OP1
Axis 1
Axis 2

Figure 2.8. NMS ordination plot of the floristic composition of transects from each wetland during February 2000 (r^2=74, stress=21.6%). Six species, indicated by joint plots, had a strong correlation with the axes on the 2D NMS ordination plot ($r^2 > 0.25$). Joint plots are represented by lines that radiate from the centroid of ordination scores. The angle and length of the lines indicate the direction and strength of the relationships. Species codes are based on the first three letters of the generic and species names.

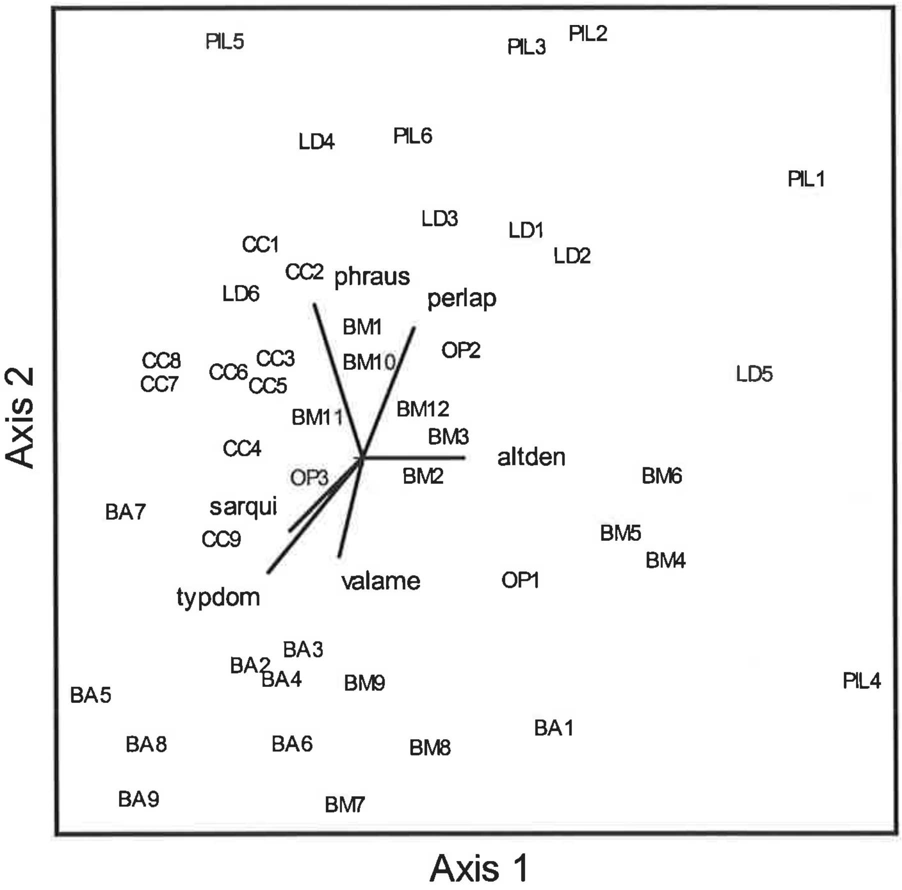

PIL5
PIL3
PIL2
LD4
PIL6
PIL1
LD3
LD1
LD2
CC1
CC2
phraus
perlap
LD6
BM1
OP2
CC8
CC7
CC6
CC3
CC5
BM10
LD5
BM11
BM12
BM3
CC4
altden
OP3
BM2
BM6
BA7
sarqui
CC9
BM5
BM4
typdom
valame
OP1
BA3
BA2
BA4
BM9
PIL4
BA5
BA1
BA8
BA6
BM8
BA9
BM7
Axis 2
Axis 1

Figure 2.9. NMS ordination plot of the floristic composition of transects from each wetland during May 2000 (r^2=0.73, stress=23.2%). Four species, indicated by joint plots, had strong correlations with the axes of the 2D NMS ordination plot ($r^2 > 0.25$). Joint plots are represented by lines that radiate from the centroid of ordination scores. The angle and length of the lines indicate the direction and strength of the relationships. Species codes are based on the first three letters of the generic and species names.

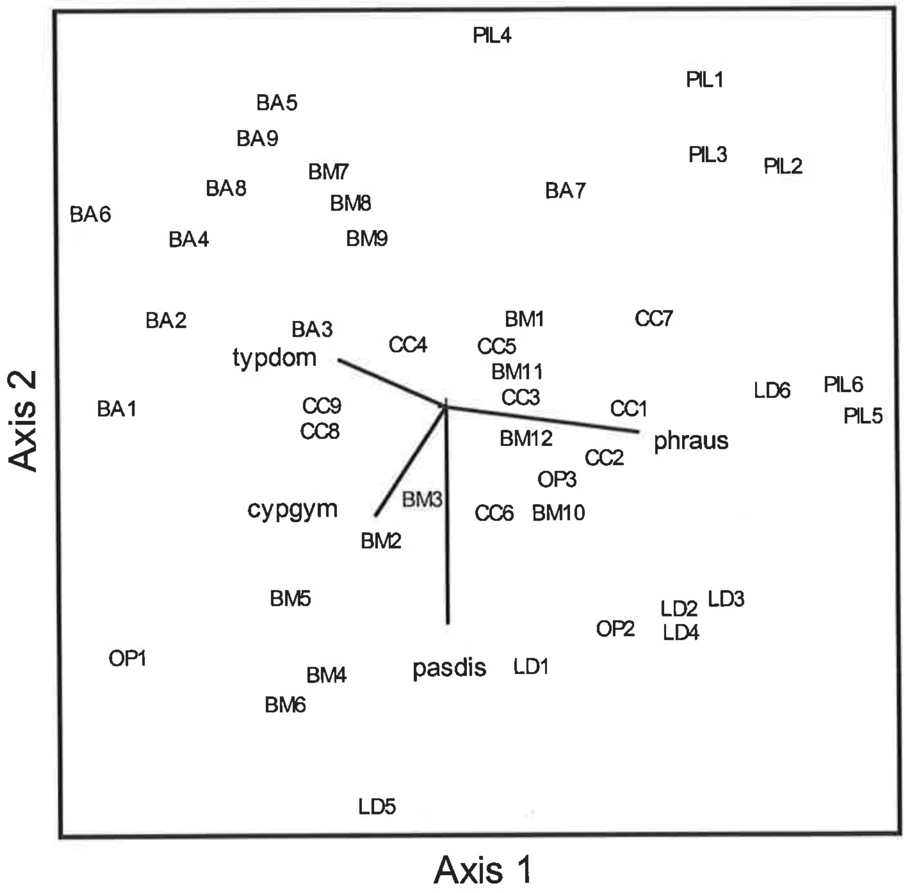

PIL4
PIL1
BA5
BA9
PIL3
PIL2
BM7
BA8
BA7
BM8
BA6
BA4
BM9
BM1
CC7
BA2
BA3
CC4
CC5
typdom
BM11
LD6
PIL6
CC3
BA1
CC9
CC1
PIL5
CC8
phraus
BM12
CC2
OP3
cypgym
BM3
CC6
BM10
BM2
LD3
BM5
LD2
OP2
LD4
OP1
pasdis
LD1
BM4
BM6
LD5
Axis 1
Axis 2

Figure 2.10. NMS ordination plot of the floristic composition of transects from each wetland during August 2000 (r^2=0.74, stress= 21.7%). Seven species, indicated by joint plots, were strongly correlated with the axes of the 2D NMS ordination plot ($r^2 >$ 0.3). Joint plots are represented by lines that radiate from the centroid of ordination scores. The angle and length of the lines indicate the direction and strength of the relationships. Species codes are based on the first three letters of the generic and species names.

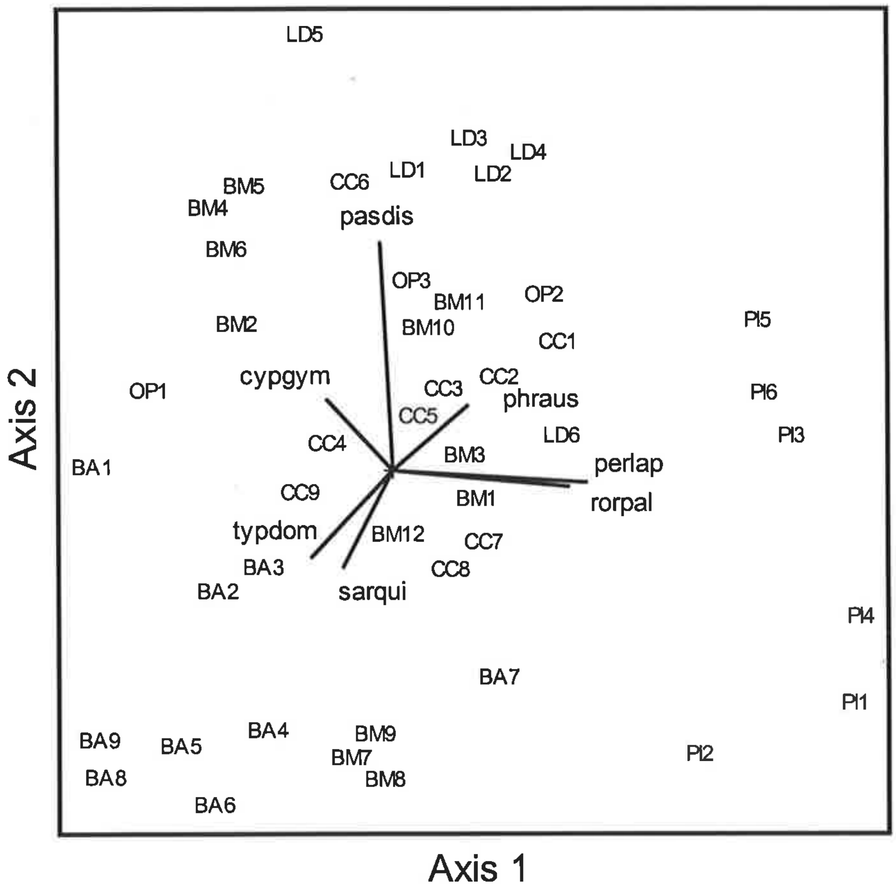

LD5
LD3
LD4
LD1
LD2
BM5
CC6
BM4
pasdis
BM6
OP3
BM11
OP2
BM10
PI5
BM2
CC1
cypgym
CC3
CC2
OP1
phraus
PI6
CC5
LD6
PI3
CC4
BM3
perlap
BA1
BM1
rorpal
CC9
typdom
BM12
CC7
BA3
CC8
BA2
sarqui
PI4
BA7
PI1
BA9
BA4
BM9
BA5
BM7
PI2
BA8
BM8
BA6
Axis 2
Axis 1

Figure 2.11. NMS ordination plot of the floristic composition of transects from each wetland during December 2000 (r^2=0.68, stress=29.9%). Three species were strongly correlated with the axes of the 2D NMS ordination plot ($r^2 > 0.3$). Joint plots are represented by lines that radiate from the centroid of ordination scores. The angle and length of the lines indicate the direction and strength of the relationships. Species codes are based on the first three letters of the generic and species names.

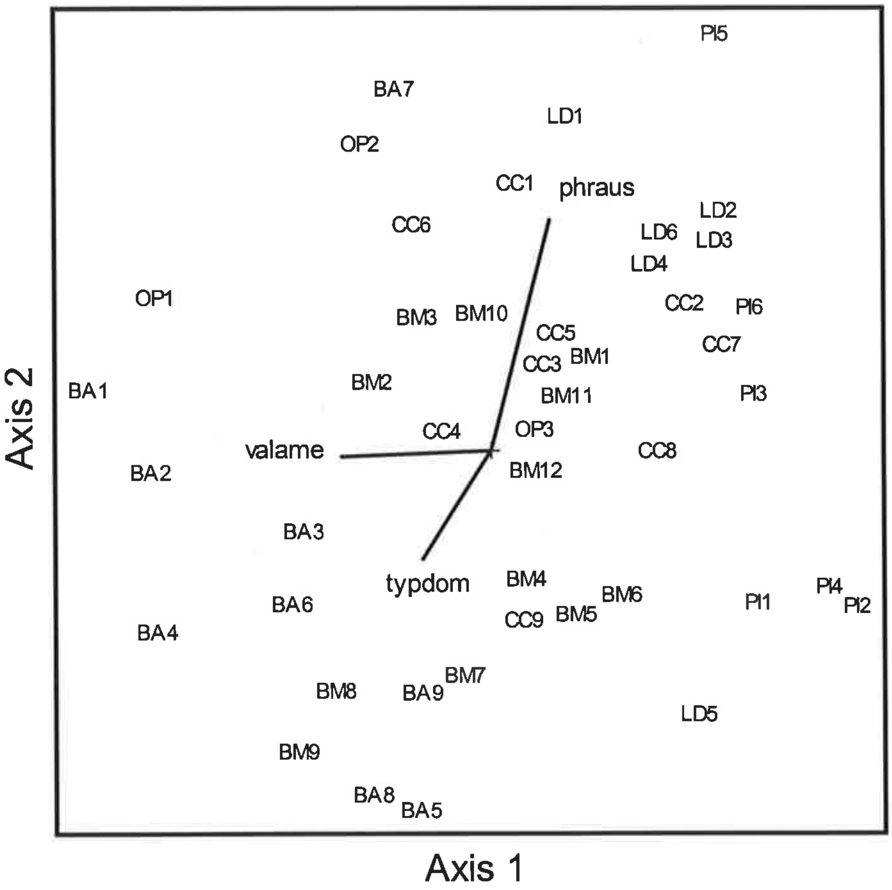
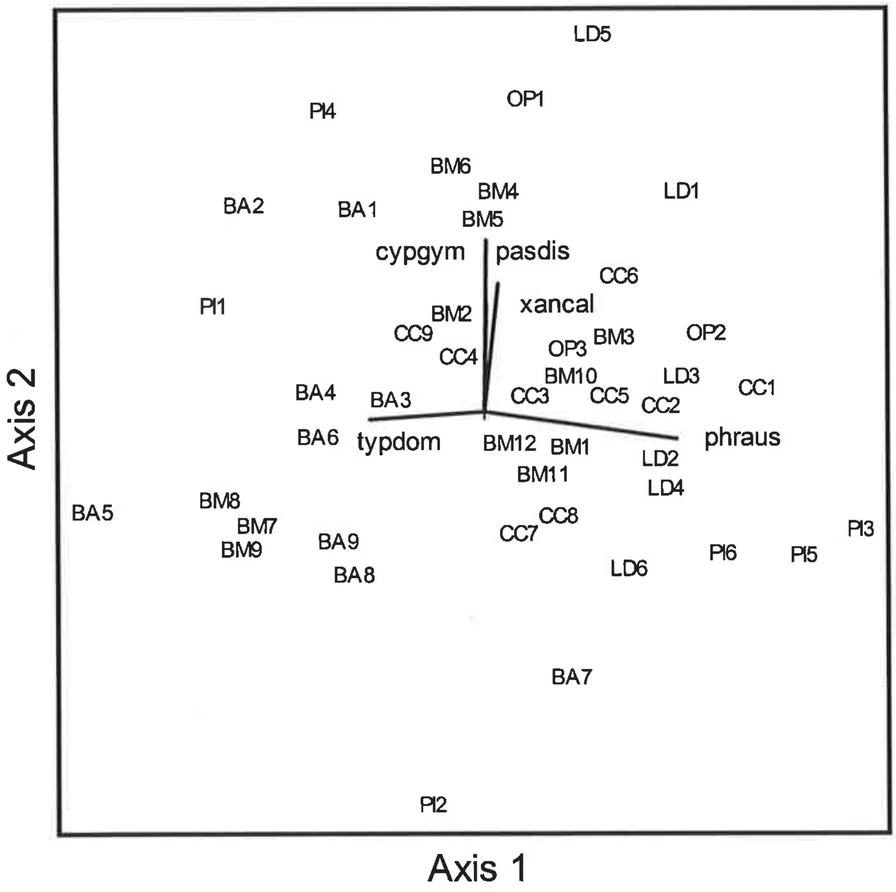

PI5
BA7
LD1
OP2
CC1
phraus
LD2
CC6
LD6
LD3
LD4
OP1
CC2
PI6
BM3
BM10
CC5
CC7
CC3
BM1
BA1
BM2
BM11
PI3
CC4
OP3
valame
CC8
BA2
BM12
BA3
typdom
BM4
BM6
PI4
BA6
PI1
PI2
CC9
BM5
BA4
BM7
BM8
BA9
LD5
BM9
BA8
BA5
Axis 2
Axis 1

Figure 2.12. NMS ordination plot of the floristic composition of transects from each wetland during March 2000 (r^2=0.75, stress=25.8%). Five species, indicated by joint plots, were strongly correlated with the axes of the 2D NMS ordination plot ($r^2 > 0.3$). Joint plots are represented by lines that radiate from the centroid of ordination scores. The angle and length of the lines indicate the direction and strength of the relationships. Species codes are based on the first three letters of the generic and species names.


LD5
OP1
PI4
BM6
BM4
LD1
BA2
BA1
BM5
cypgym
pasdis
CC6
PI1
xancal
BM2
CC9
OP2
BM3
OP3
CC4
BM10
LD3
BA4
BA3
CC3
CC5
CC1
CC2
BA6
typdom
BM12
BM1
phraus
LD2
BM11
LD4
BA5
BM8
CC8
PI3
BM7
CC7
BA9
PI6
PI5
BM9
LD6
BA8
BA7
PI2
Axis 2
Axis 1

CHAPTER 3

INFLUENCE OF FLOOD AND DRAWDOWN ON VEGETATION CHANGE

3.1 Abstract

The aim of this study was to determine how flood and drawdown influence the establishment and extirpation of wetland plants and thus promote vegetation change. This was examined in four Lower Murray wetlands monitored on six occasions between November 1999 and March 2001. The hydrograph for each wetland was divided into discrete flood and drawdown 'events'. Vegetation change, as a function of establishment and extirpation, was differentially influenced by a) the depth, duration, timing and rate of flood and drawdown, b) the vegetation present in the wetland prior to the event, which was influenced by c) the characteristics of previous flood and drawdown events. The extent of change was greatest during the initial phase of flood events because of the inability of mudflat annuals to persist, and in Big Mussel, the establishment of the submerged macrophyte *Vallisneria americana* and the emergent macrophyte *Typha domingensis*. The impact of drawdown on the extirpation of mature emergents was less than expected, presumably on account of their ability to maintain contact with groundwater. The establishment of *T. domingensis*, along with the inability of drawdown regimes to extirpate it and species such as *Paspalum distichum*, suggests that water regimes characterised by annual flood and drawdown have the potential to promote the establishment and spread of these nuisance species.

3.2 Introduction

Vegetation change in wetlands is influenced by flood and drawdown mediated extirpation and establishment. Drawdown exposes mudflats and promotes the establishment of mudflat annuals and emergent macrophytes (Galinato and van der Valk 1986; Deswart *et al.* 1994; ter Heerdt and Drost 1994; Brock and Casanova

1997). The rapid growth of mudflat annuals causes substantial changes in floristic composition (Kadlec 1962; Harris and Marshall 1963; Galinato and van der Valk 1986). Exposure of the wetland bed also leads to the dieback of desiccation intolerant submerged macrophytes (Cooke 1980). As drawdown continues, increased drought stress (*sensu* Grime 1979) can cause the dieback of mudflat annuals and ultimately emergent macrophytes (Harris and Marshall 1963).

Flooding reverses the effects of drawdown. Mudflat annuals possess few strategies for tolerating the stresses of flooding and die back quickly when totally immersed (van der Sman *et al.* 1993). Emergent macrophytes spread vegetatively in shallow water and may persist in deeper water (> 80 cm) for 2-3 years (Millar 1973; Squires and van der Valk 1992). Establishment opportunities are typically restricted to submerged macrophytes and a small number of emergent macrophytes. As for the growth of mature plants, characteristics of the underwater light climate such as intensity and spectral quality influence the germination of submerged macrophytes (Farmer and Spence 1987).

Vegetation change, however, is influenced by more than just whether an elevation is wet or dry. Instead, the species mixture that develops, and the extent of change, is influenced by the characteristics of flood and drawdown. Experimental and field studies have shown that the establishment and extirpation of individuals may be modified by the duration, depth, frequency and timing of flood and drawdown (Casanova and Brock (2000).

This chapter presents a further analysis of the study introduced in Chapter 2 and focuses on the response of vegetation to flood and drawdown in the four managed wetlands. Rather than assess the impact of a wetland's water regime as a whole, vegetation change was assessed in response to flood and drawdown 'events' and hence a more detailed description of hydrology is provided.

It was predicted that:

1) drawdown events would have a greater impact on vegetation change than flood events because of the establishment opportunities for emergent macrophytes and mudflat annuals and the extirpation of desiccation intolerant submerged macrophytes; and
2) as drawdown continued, drought stress would promote emergent macrophyte

dieback and further vegetation change.

An overarching aim of this analysis was to interrogate the response of individuals across the littoral zone to determine how variations in the characteristics of flood and drawdown modify vegetation responses. The implications of this study as they apply to the spread of nuisance species are explored.

A description of the four wetlands is provided in Section 2.3.

3.3 Methods

3.3.1 Event characterisation

Each wetland's hydrograph was divided into flood and drawdown events. The start of a drawdown event was recorded when regulation structures were closed and water levels commenced falling. Flood events were periods during which at least partial filling occurred in the wetland and water levels rose above the previous drawdown event's low water mark. The only exception to the dissection of the hydrograph into flood and drawdown events was for the managed floods in BA that resulted in overbank flooding (above normal pool level). These were treated as single 'managed' flood events.

The method of hydrograph determination for each wetland is described in Section 2.4.3.

3.3.2 Vegetation sampling

The method of vegetation sampling is described in full in section 2.4.1.

Quadrats were placed at the highest point on the littoral zone, the lowest point and at elevation changes of 25%, 50% and 75%. Littoral zone morphology changed across the basin and this method led to sampling at a range of elevations across each wetland: Banrock Station (BA) = 35 elevations, Big Mussel (BM) = 50, Little Duck (LD) = 27, Pilby Creek (PI) = 27.

For PI, LD and BM the drawdown event that intercepted the November 1999 survey began prior to the collection of any floristic data. Vegetation composition and changes during this period are described from observations made during June and September 1999.

3.3.3 Analysis

There were 44 species across all wetlands with a % total cover/abundance (TCA) for all surveys combined of greater than 0.1%. Each species was analysed using a repeated measures non-parametric Friedman ANOVA (Statistica for Windows, StatSoft 1997) to identify those that experienced a change in cover during the survey. Each transect within a wetland was used as a replicate measure of cover (maximum cover score per transect = 5 (number of elevations per transect) × 5 (number of cells per elevation) × 6 (maximum score per cell) = 150).

A range of statistical tests were then considered, including contingency table analyses, general linear models and a Friedman multiple comparison tests, to determine the surveys between which a significant change in cover occurred, but all were found inappropriate (A. Verbyla and A. Kiermeier, BiometricsSA, pers. comm.). This was because species distribution and abundance in the study wetlands was patchy and data contained a high number of 0 values with comparatively few larger values.

Changes in cover between surveys were instead assessed on the basis of the number of elevations occupied between surveys and differences in cover at each of these elevations. At each elevation, cover scores in the five individual 1m × 1m cells were summed for comparison. Summed scores were then assigned to groups for graphical analysis; 0-5 = 1, 6-10 = 2, 11-15 = 3, 16-20 = 4, 21-25 = 5, 25-30 = 6.

Azolla filiculoides and *Lemna minor* were excluded from the analysis because they are floating species and their presence is determined by the presence or absence of surface water rather than, for example, the depth or rate of inundation.

3.4 Results

3.4.1 Description of flood and drawdown events

The description of flood and drawdown events in this section is based on the hydrographs presented in Chapter 2.

Banrock Station

The wetland was emptied in May 1999. In August 1999 it was refilled and a managed flood was initiated where water levels rose at 1.4 cm d^{-1} peaking at 1.23 m above the bottom of the wetland on 5 October 1999 (Figure 2.3). During the flood, water levels were above the managed pool level for 123 days. Levels dropped at 2.2 cm d^{-1} in November and then stabilised for a brief period before eventually reaching the operational pool level range in late December 1999 (Figure 2.3). Levels then fluctuated between 8.49 and 8.80 m AHD (m Australian Height Datum) until the end of May 2000 when a drawdown event commenced during which water levels fell by 60 cm in about one week. Although the wetland was empty for 42 days, most of the sediment remained saturated and a small number of residual pools persisted. This was due to low evaporation rates (1.2 mm d^{-1}) resulting from low ambient temperatures (mean daily maximum temperature for June/July 2000 = 15-18°C: Figure 3.1).

BA was re-filled at 3.8 cm d^{-1} in early August. Water levels then fluctuated within the operational pool level range until early November 2000 when a managed flood commenced and levels rose at 0.5 cm d^{-1} to 8.90 m AHD (25 November 2000: Figure 2.3). This flood was augmented by high flows in the river and raised the peak to 9.16 m AHD on 26 December (Figure 2.3). Water levels receded at 2.6 cm d^{-1} until 16 January 2001 and then fluctuated within the operational pool level range until the end of the study (Figure 2.3).

Big Mussel

In November 1999, BM was at the end of a drawdown event that had started in January 1999. Drawdown was governed by evaporation and thus varied in accordance with temperature fluctuations (0.1-1.1 cm d^{-1}; Figure 3.1). Seepage would also have contributed to drawdown, however, rates of seepage were not available. This applies for all wetlands.

Prior to re-filling water levels were 1.2 m below operational pool level (Figure 2.4). Re-filling took place in two stages. The removal of the first series of drop boards from regulation structures resulted in filling at ~7 cm d^{-1} between 8 and 19 December 1999. The remaining boards were then removed and the wetland filled at ~3 cm d^{-1} until it reached the pool level of Lock 3 (Figure 2.4). Water levels then fluctuated about the operational pool level for 14 weeks.

Another drawdown event commenced in late April 2000 at 0.2 cm d^{-1} and lasted until late September 2000 (Figure 2.4). Refilling was from higher flows in October 2000 at 2.6 cm d^{-1} over approximately 20 days. The wetland remained full until the end of the study in March 2001. During the final flood event water level peaks of 10.03 and

9.99 m AHD were recorded on 25 December 2000 and 14 February 2001, respectively, because of higher flows (Figure 3.2).

Little Duck

Drawdown commenced in late August; water levels were initially drawndown by pumping at 4.6 cm d^{-1} and then by evaporation (Figure 2.5). No surface water was present by early October 1999 and the wetland bed remained dry until October 2000. During this period water levels varied from 80 cm (11 November 1999) to < 20 cm (21 August 2001 and 25 September 2001) beneath the sediment surface (Figure 2.5).

Re-filling was from high flows in October 2000 at about 4.5 cm d^{-1}, after which, the wetland remained full for the remainder of the study. High river flows occurred twice in this period (Figure 3.2) and water levels peaked at 13.65 and 13.98 m AHD on 20 October and 23 December 2000, respectively (Figure 2.5).

Pilby Creek

Water levels were drawn down in May 1999 (Figure 2.6). Although precise rates of drawdown were not recorded, the method of drawdown (via hydraulic gradient) ensured a rate of at least 1 m per week. There was no surface water by late June and water levels were at least 20 cm beneath the sediment surface at the lowest elevation in the basin by late July 1999 and at least 1 m below by November 1999.

A partial re-fill occurred in March 2000 when water levels rose at 6.3 cm d^{-1} for 6 days and then remained between 18.12 and 18.15 m AHD for about one month before falling in May/June 2000 at 4 cm d^{-1} (Figure 2.6). Despite the absence of surface water the sediment in the previously inundated lower portion of the basin remained saturated until at least August, presumably because of low ambient temperatures and net evaporation rates (Figure 3.1). PI was empty until a flood event in October 2000 during which when water levels rose from 17.77 to 19.44 m AHD in < 10 days (Figure 2.6). The wetland was full for the remainder of the study and water levels peaked at 19.66 m AHD on 20 December 2000 (Figure 2.6) as a consequence of high river flows (Figure 3.2).

3.4.2 Vegetation response

Banrock Station

Forty seven species were recorded; six had changes in cover and accounted for 41.9%

TCA in BA for all surveys. In November 1999, seedlings of *Myriophyllum verrucosum* (8.62-8.97 m AHD), *Typha domingensis* (8.83-9.07 m AHD) and *Vallisneria americana* (8.66-8.70 m AHD) were recorded at elevations above the operational pool level, inundated by the managed flood event that had started in August 1999 (Plate 3.1, Figure 3.3). All plants were estimated to be less than four weeks old. The flood receded in late November and by February 2000 no seedlings were found at the previously inundated elevations. The presence of *T. domingensis* seedlings in November 1999 periodically increased its overall cover, which then remained constant until the study's completion (Figure 3.3).

Between November 1999 and February 2000 *Sporobolus mitchellii* increased the number of elevations it occupied, from two to 11, at sites that had been inundated during the managed flood (Figure 3.3). Similarly, *Cyperus gymnocaulos* increased cover at two elevations occupied in November 1999 and spread to an additional two (8.68 and 8.79 m AHD); all elevations were inundated during the managed flood (Figure 3.3).

Between February and May 2000 there was little water level variability and with the exception of *C. gymnocaulos*, which declined in cover at five of 11 sites at or above the operational pool level, there was no vegetation change (Figure 3.3).

Despite drawdown, *V. americana* declined in cover at only four of seven elevations between May and August (Figure 3.3). *S. mitchellii* declined over the same period and was found at five elevations in August compared to 12 in May, with most of the reductions occurring at lower elevations (Figure 3.3). In contrast, *M. verrucosum* and *Sonchus* sp., both absent in May, were present in August 2000, with juveniles of the former found on areas exposed during the drawdown (Figure 3.3).

Between August and December 2000, *S. mitchellii* increased cover at two of five elevations and spread to an additional two elevations. Both of the additional elevations were inundated during the managed flood in late November to early December by 9-13 cm (Figure 3.3). Other changes between August and December were the loss of *M. verrucosum* at two of three elevations and the dieback of *Sonchus* sp. at the lowest elevation of its range in August that was inundated by at least 20 cm in the managed flood (Figure 3.3). Both species declined further by March 2001 with *M. verrucosum* extirpated from its only elevation and *Sonchus* sp. dying back at the three lowest elevations of its distribution that were flooded for 13 to 46 days to depths of 19-35 cm. However, *Sonchus* sp. did persist at elevations flooded for five days to a maximum depth of 9 cm (Figure 3.3).

From August 2000 to March 2001 there was a decline in the distribution of *V. americana* from 10 to seven elevations. Plants contracted to 8.17-8.33 m AHD placing them at an average water depth for the period December 2000 to March 2001 of 27-42 cm. The cover of *V. americana* fluctuated at all of the remaining elevations for this period (Figure 3.3).

Big Mussel

Forty eight species were recorded, of which 15 had changes in cover (Figure 3.4) and accounted for 40.4 % TCA in BM for all surveys. Of these, five species were recorded in all of the surveys - *Aster subulatus*, *Bolboschoenus caldwellii*, *Cynodon dactylon*, *Heliotropium curassavicum* and *T. domingensis*.

The drawdown event in 1999, which commenced prior to the study, exposed mudflats that were colonised by mudflat annuals and emergent macrophytes. The most common emergent macrophytes were *B. caldwellii* and *Juncus aridicola*. Establishment only occurred at elevations greater than 8.93 m AHD, even though water levels fell to 8.61 m AHD.

During the flood event between December 1999 and April 2000, 10 species declined in cover. All were recorded in November 1999 at exposed elevations, but after the flood event were in depths of at least 19 cm. Six of the 10 species, all mudflat annuals – *Alternanthera denticulata*, *Centipeda cunninghamii*, *Mimulus repens*, *Persicaria lapathifolia*, *Polygonum aviculare* and *Rorippa palustris* - were not observed again after February (Figure 3.4). *A. subulatus*, *C. dactylon* and *H. curassavicum* also declined in cover (Figure 3.4) but were present in May 2000, persisting at elevations that were not flooded or in reduced abundances at elevations that were flooded (Figure 3.4).

B. caldwellii increased cover from November 1999 to February 2000 through colonising additional elevations as well as expanding at elevations already occupied (Figure 3.4). However, as flooding continued it died back at low elevations between February and May 2000 (Figure 3.4).

V. americana, which was absent at the start of the study, germinated and established on re-flooded mudflats between November and February (Figure 3.4). Plants then increased cover at all occupied sites and spread to five additional elevations by May 2000 (Figure 3.4). *T. domingensis* also established on re-flooded mudflats (Plate 3.2), with juveniles recorded at 17 elevations previously (Figure 3.4). Between February and May juveniles flooded to > 60 cm died back (Figure 3.4). Cover did not decrease though because plants at higher, shallow flooded elevations increased abundance. *Schoenoplectus validus* also established at sites inundated during the flood event but recruits were few.

No establishment of mudflat annuals or emergent macrophytes was recorded during the drawdown event between May and October 2000. In addition, there was no response from extant vegetation and water levels did not fall below elevations occupied by fringing stands of *T. domingensis*.

By December 2000, the wetland had re-filled and *T. domingensis* increased its abundance at 13 elevations and spread to an additional three. This trend continued toward March when it was recorded at an additional six elevations and recorded its maximum % TCA for a single survey (25%: Figure 3.4). *V. americana* reached its maximum distribution and abundance in December after increasing cover at six of the seven elevations at which it was recorded in August. It then spread to a further six, mainly shallow flooded elevations, by March (Figure 3.4).

X. californicum was not observed until December 2000 and March 2001, when seedlings were recorded at elevations above the operational pool level that were inundated during periods of high river flow (Figure 3.4).

Little Duck

Twenty four species were recorded, of which six had significant changes in cover and accounted for 40.6% TCA in LD for all surveys. The most dominant species to experience changes in cover was *Paspalum distichum* that accounted for 30.5% TCA for the study at LD. In contrast, other dominant species maintained cover despite changing water levels, e.g. *Phragmites australis* (33.9% TCA), *C. gymnocaulos* (7.5% TCA) and *T. domingensis* (5.2% TCA).

Drawdown commenced in June 1999, however, establishment of mudflat annuals and emergent species was not observed until October 1999. *P. lapathifolia* increased its distribution and abundance during the early months of drawdown but was present in only one sampling cell by August (Figure 3.5). In contrast, *P. distichum* more than doubled its cover across at least 10 of 16 elevations between November 1999 and August 2000 (Figure 3.5). This represented an increase in cover from 32.1% to 40.7%.

The initial period of flooding between August and December 2000 had the greatest impact upon vegetation change. *A. denticulata* and *A. subulatus*, which established during the drawdown event prior to November 1999, were extirpated from flooded elevations with only the former re-establishing at elevations approximately level with the operational pool level by March 2001 (Figure 3.5).

No *P. distichum* flooded to > 35 cm persisted through to December with distribution declining from 16 to 10 elevations (Figure 3.5). Furthermore, all plants flooded from 13 to 36 cm had a decline in cover. Plants were 20-40 cm tall. Some individuals had recovered by March 2001 and increased at sites exposed by 6 cm through to those flooded to 29 cm. These represent median depths calculated for the duration of the flood event prior to March.

X. californicum established after re-filling, with seedlings recorded at elevations flooded to 32 cm in early December (Figure 3.5). By March, *X. californicum* increased its abundance and was recorded at six elevations at or above the operational pool level. No submerged macrophytes were observed after re-filling (Figure 3.5).

Pilby Creek

Thirty eight species were recorded, of which nine had changes in cover and accounted for 51.3% TCA in PI for all surveys. The most dominant species to change cover was *P. lapathifolia* (21.8% TCA). However, the cover of *P. australis* (35.9% TCA), the most dominant plant in PI, was unaffected by the flood and drawdown events.

Water levels were drawndown in June 1999 and establishment of mudflat annuals occurred in August. For most species substantial vegetative growth was not observed until the warmer months of October and November 1999 (mean daily temperature > 20°C). *P. lapathifolia* grew from ~50 cm to over 180 cm during this period.

Between November 1999 and February 2000, *C. cunninghamii*, *C. minima*, *C. pumilio*, *P. lapathifolia* and *R. palustris* all declined in distribution and abundance (Figure 3.6). This period was one of the warmest during the study with 42% of the daily maximum temperatures ≥ 30°C.

The flood event in April 2000 caused the partial die back of *C. cunninghamii*, *C. minima*, *C. pumilio* and *R. palustris* at flooded elevations by May 2000 (Figure 3.6). As a consequence *R. palustris* declined from a TCA of 16.0% in November to 2.6% in May. In contrast, *P. lapathifolia* survived flooding to 35 cm for 60 days (Figure 3.6). Most of the *P. lapathifolia* in May were at least 150 cm tall and had developed adventitious roots on the main stem below the water surface.

Although not intercepted by any transects, seedlings of the submerged macrophytes *Potamogeton ochreatus* and *V. americana* were observed at low elevations between April and May 2000 (depth 30-40 cm). The mean daily temperature during the flood event was 23.1°C and the water clarity was high with the wetland bed clearly visible.

During the drawdown that followed the partial fill, *P. lapathifolia* colonised two additional areas of the wetland bed and by August 2000 had increased cover at four of the previously occupied elevations (Figure 3.6). *R. palustris* spread from one to 10 elevations between May and August 2000 and *C. cunninghamii* from one to four. Establishment occurred at elevations that were inundated or near the high water mark during the partial fill (Figure 3.6).

PI filled rapidly from high river flows during early October 2000 (Figure 3.6). *C. cunninghamii*, *C. minima*, *C. pumilio* and *R. palustris* were completely inundated and none were recorded for the remainder of the study. *P. lapathifolia* also died back and was recorded at only one elevation during December in comparison to nine in August (Figure 3.6), representing a decline in TCA from 31.1% to 2.7%. With the exception of some plants higher on the elevation gradient in shallow water – predominantly *P. australis* - there were no rooted plants, including submerged species, found alive in the inundated part of the basin in March 2001.

3.5 Discussion

The general establishment and extirpation response observed for emergent macrophytes, mudflat annuals and submerged macrophytes was in keeping with classical models of vegetation change in wetlands subject to periodic drawdown (e.g. Segal 1971; van der Valk and Davis 1980). However, the mixture of species present at any one time, and the extent of change, was influenced by a) the characteristics of the event (depth, duration, timing and rate), b) the vegetation present in the wetland prior to the event, which was influenced by c) the characteristics of previous flood and drawdown events.

It was hypothesised that drawdown events would have a greater impact upon vegetation change because of the establishment opportunities for emergent macrophytes and mudflat annuals and because of the desiccation stress imposed on submerged macrophytes. This was found to be incorrect with the greatest impact on vegetation change caused by the flood event in BM from November 1999 to February 2000. Change was driven by extensive dieback of mudflat annuals and the establishment of submerged and emergent macrophytes. Although extirpation was also substantive in LD and PI, it was the establishment of submerged macrophytes in BM that differentiated their response.

3.5.1 Flood events - establishment

There are few reports of the establishment of submerged plants from seed in Lower Murray wetlands, presumably on account of the turbid water column which typically varies from 50-100 Nephelometric Turbidity Units (NTU). This restricts even mature individuals of common species such as *V. americana* to depths of ~1 m (Blanch *et al.* 1998). Most stands of submerged vegetation are thought to establish from vegetative fragments or asexual propagules such as turions. However, re-filling after drawdown provides an opportunity for seedlings to germinate and establish in shallow water under improved light conditions.

The filling phase (December 1999) of the flood event that led to the establishment of submerged vegetation in BM occurred in two stages: a rapid fill (~7 cm d^{-1}) followed by a slower fill (3 cm d^{-1}). By February 2000, *V. americana*, which was not present in November 1999, was recorded at depths of 54-70 cm with 1-3 leaves at the water surface. Assuming that germination occurred soon after re-filling (between mid to late December), this suggests leaf extension rates of 0.9-1.5 cm d^{-1}, which are comparable to the maximum extension rates recorded by Blanch *et al.* (1998) for this species (1.1 cm d^{-1}).

Flooding in BM also promoted the establishment of *T. domingensis*. When water levels reached operational pool level seedlings were in depths of 33-87 cm. *T. domingensis* can germinate and photosynthesise when submerged but ultimately survival depends upon leaves reaching the water surface (Nicol and Ganf 2000).

Observations of juveniles indicate that plants at higher elevations had produced emergent leaves by February 2000 (Plate 3.2) but that some at lower elevations were yet to do so. For *T. domingensis* and *V. americana*, it is hypothesised that the initial filling phase promoted germination and that the second was slow enough to enable plants to extend their leaves and maintain access to suitable light conditions.

The managed flood in BA had a similar effect as re-flooding in BM with *T. domingensis*, *V. americana* and *M. verrucosum* germinating in shallow water at elevations above the operational pool level. A key to germination at these higher elevations was the absence of plants such as *P. australis* and *C. gymnocaulos* that in the other study wetlands would have limited access to space. The higher elevations of BA are sandy and thus turbidity from resuspension remained low, perhaps aiding germination.

No germination of submerged species was observed in PI and LD in October 2000. This was despite dense stands previously occupying both wetlands suggesting a viable seed bank (e.g. 1998: P. Tucker, Australian Landscape Trust, pers. comm.). The presence of seeds from submerged plants (*V. americana* and *Nitella* sp.) in LD is also supported by a seed bank study by Stone (2001).

The absence of germination in PI may have been a function of rapid filling, an average turbidity of 63 NTU (J. Brookes, Australian Water Quality Studies Centre, pers. comm.) and high colour (colour: 60-100 HU for October-December 2000) all contributing to a poor underwater light climate. In LD the absence of submerged plant germination was probably attributable to a 5-10 cm thick layer of decomposing *P. distichum*, which also reduced dissolved oxygen levels (near zero from October 2000 to March 2001: S. Nichols, Australian Landscape Trust, pers. comm.).

3.5.2 Flood events - extirpation

The characteristics of flooding and the type of vegetation already present in the wetland influenced extirpation during flood events. If previous drawdown intercepted cooler months, then few species colonised the wetland bed and flooding promoted minimal extirpation, e.g. in BA (June-August 1999). In BM, the flood event that commenced in December 1999 followed a period of drawdown during which a suite of mudflat annuals and emergent macrophytes colonised the wetland bed.

Even though most mudflat annuals found in the wetlands, such as *A. denticulata*, *C. minima* and *R. palustris*, are capable of growing on waterlogged soil (Brock and Casanova 1997), they possess few adaptations for tolerating even shallow flooding (Grace 1993; Blom 1999). The extent of mudflat annual dieback was thus influenced by the depth and duration of flooding.

The influence of flood duration was demonstrated in BM. For instance, many of the mudflat annuals that established during the preceding drawdown event survived the first six weeks of inundation. This included *C. cunninghamii*, which supports the observations of Blanch *et al.* (1999) who found it at elevations across the riverine littoral flooded to 0-20 cm for 95 days. However, continued flooding through to May resulted in the loss of this and all other mudflat annuals (except *A. subulatus*) from flooded elevations, regardless of depth. A similar outcome was recorded for PI where all except one mudflat annual, *P. lapathifolia*, were extirpated within 10 weeks of the flood event that commenced in October 2000.

In BM and PI, most plants were totally immersed once the operational pool height was reached. The impact of incomplete plant submersion was demonstrated in a partial fill in PI (April-May 2000) where the depth did not exceed 40 cm. This enabled *P. lapathifolia*, which was 1.5-2 m tall, to maintain emergent photosynthetic tissue. Although studies espousing the importance of emergent photosynthetic tissue for flooded mudflat annuals are limited, it is well established for emergent macrophytes (e.g. Coops *et al.* 1996; Siebentritt and Ganf 2000). Persistence was presumably aided by the production of adventitious roots on the main stem.

The significance of the relationship between flooding depth and plant height was also illustrated in LD. *P. distichum*, which had grown to a height of 20-40 cm on the exposed wetland bed, only died back at elevations flooded to > 35 cm. This contrasts with Blanch *et al.* (1999) who found that *P. distichum* occurred at elevations across the Lower Murray littoral zone flooded to 20-60 cm for a median of 65 days. Although dieback occurred in deeper water, viable (leafless) stem fragments persisted at these elevations for at least the first three months of the flood event.

The only other examples of emergent species responding negatively to flooding were *B. caldwellii* and *C. dactylon* in BM and juvenile *T. domingensis* in BM and in BA. Notably, mature emergent macrophytes such as *P. australis* and *T. domingensis* did not experience reductions in cover when flooded in any wetland. This was to be expected: the depth distribution of many plants would have been determined by pre-management water levels which were re-instated when levels were returned to operational pool.

3.5.3 Drawdown events - establishment

Wetland species typically require temperatures, day lengths and light intensities akin to those of warmer spring/summer periods (Galinato and van der Valk 1986; Britton and Brock 1994). For example, germination is generally increased under high soil moisture and alternating high to moderate temperatures (alternating 15/25˚C and 20/30˚C) and decreased under lower temperatures and decreasing photoperiod (Galinato and van der Valk 1986; Welling *et al.* 1988b). The consequences of winter drawdown were demonstrated in BA (June-August 1999) and BM (April-October 2000) where no establishment was observed. The winter drawdown in both wetlands coincided with mean daily maximum temperatures of 16ºC. This suggests that drawdown events restricted to cooler, winter months have limited potential for promoting the establishment of emergent macrophytes and mudflat annuals.

Another factor that may inhibit germination is shading from extant vegetation and leaf litter. In BM water levels did not drop below the bottom of *T. domingensis* stands in the April-October 2000 drawdown event. This meant that the only exposed sediment was shaded and within *T. domingensis* stands. Even then, a thick mat of roots covered most of the sediment within stands.

The influence of the rate of initial drawdown can be inferred from the vegetation that developed on BM, LD and PI; rapid drawdown in LD and PI resulted in the establishment of predominantly mudflat annuals. In contrast, slow drawdown in BM stimulated the establishment of mudflat annuals as well as emergent macrophytes such as *B. caldwellii* and *J. aridicola.* Few studies have examined the influence of rapid drawdown on establishment. Some suggest that early drawdown (spring) favours emergent macrophytes while annuals are more prevalent after a late drawdown (summer) where hot weather accelerates mudflat drying (Harris and Marshall 1963; Salisbury 1970; ter Heerdt and Drost 1994). Applying the same rationale, accelerated mudflat drying from rapid drawdown may have the same affect on the relative abundances of mudflat annuals and emergent macrophytes.

3.5.4 Drawdown events - extirpation

Submerged macrophytes are usually the first plants to die back during drawdown because of their desiccation intolerant tissue (Cooke 1980; Briggs and Maher 1985). However, they can persist if below ground tissue remains viable in moist sediment (van Wijck 1989). The winter drawdown in BA induced no *V. americana* extirpation, with plants surviving caked in moist clay in the wetland bed. Low daily maximum temperatures (16°C) and low mean evaporation rates (1.2 mm d^{-1}) facilitated the maintenance of moist sediment.

As drawdown continues (months to years), extirpation is thought to be driven by species-specific drought tolerances. This would be true where groundwater is beyond the rooting depth of plants on the wetland bed. For example, the groundwater at the base of PI was at least 1 m below the sediment surface. As a consequence, shallow rooted mudflat annuals such as *C. cunninghamii* and *R. palustris* (root depth < 40cm: MAS, pers. obs.) were unable to access it and presumably died back as moisture levels close to the sediment surface were exhausted.

A feature of drawdown was the lack of extirpation of emergent macrophytes. Access to groundwater is one possible explanation, as illustrated by a number of examples:

- *P. distichum* normally grows on wet mud or in shallow water (Middleton 1990; Middleton *et al.* 1991; Blanch *et al.* 1999b). Its ability to persist and increase its cover at LD despite the absence of surface water, implies that it was able to maintain contact with groundwater that was less than 80 cm beneath the sediment surface.

- In BM and LD water levels did not fall below the operational pool level by more than 1.2 and 1.45 m respectively. *P. australis*, whose cover was unaffected by drawdown, has rhizomes capable of penetrating 1.5-2 m down the soil profile (Haslam 1970) suggesting that plants at elevations of up to 50 cm above pool level could maintain access to groundwater.

- Roberts and Marston (2000) report that *T. domingensis* has a high water requirement and can tolerate at most 3-4 months of dry conditions outside the growing season. The ability of *T. domingensis* to persist in LD throughout the 14-month drawdown event implies access to groundwater. Maintaining root contact with groundwater was probable given that groundwater below *T. domingensis* was never more than 1-1.5 m and that its roots can extend to at least 1 m (G.G. Ganf, pers. comm.).

Field studies that observe the dieback of emergent macrophytes commonly employ drought tolerance as an explanatory mechanism for vegetation change. However, this has only been examined experimentally by Kirkman and Sharitz (1993) who considered stomatal control. The role of groundwater access and thus drought avoidance through mechanisms such as root extension has received apparently no consideration for wetland species. This mechanism is explored in Chapter 7.

3.5.5 Potential for the spread of nuisance species

When flood and drawdown promote the establishment and growth of wetland plants without imposing alternating periods of stress, some species may become dominant. The genus *Typha* is well known for this and because of its ability to form monotypic stands that out-compete other species (Wilcox *et al.* 1985; Froend *et al.* 1993; Reinartz and Warne 1993) is recognized worldwide as a freshwater weed (e.g. North America: Odum 1988).

T. domingensis became dominant in BM towards the end of the study because of the establishment of juveniles following the December 1999 re-filling and the subsequent lack of extirpation of mature plants. Species of *Typha* can periodically persist at depths of 2 m for 2-3 years (Grace 1989; Squires and van der Valk 1992) but the optimal depth range of *T. domingensis*, the species common in Lower Murray wetlands, is closer to 20-60 cm (Blanch *et al.* 1999b).

I propose that drawdown at intervals of less than 12 months reduces the duration of deep flooding stress and enables plants to persist at lower elevations than would be possible if water levels were static. This enables greater dominance of *T. domingensis* across the littoral zone and means that water levels must fall below *T. domingensis* stands to expose bare mudflats and provide germination opportunities for other species.

T. domingensis did not expand to the same extent in BA, LD and PI as it did in BM. In LD and PI, this was probably for the same reasons that submerged species failed to establish, i.e. rapid filling, coloured water and the presence of a layer of decaying organic material on the sediment. Seed burial is of particular significance for *T. domingensis* (van der Valk 1986).

In BA the only opportunities for establishment were during managed floods and winter drawdowns. As previously described, the managed flood did lead to the germination of *T. domingensis* at BA, but the saline conditions that developed once water levels receded (evident from salt scalds) most likely prevented establishment given that this species prefers low soil salinities (Froend *et al.* 1993).

Another possible nuisance in Lower Murray wetlands is *P. distichum*. The potential for it to dominate was demonstrated in LD in August 2000 where it covered most of the exposed wetland bed. Although it had significant reductions in abundance when flooded, it was able to persist for at least four months as leafless stem fragments. One proposed management regime in LD is to drawdown 4-5 months after re-filling. It is hypothesised that this would enable surviving stem fragments to rapidly re-colonise the wetland bed and inhibit the establishment of species from the seed bank (e.g. *A. denticulata* and *A. subulatus*).

3.5.6 Implications for restoration

Controlling the abundance of potentially dominant species requires water regimes that periodically impose stress (*sensu* Grime 1979). Annual regimes appear to encourage the spread and persistence of potential nuisance species by more frequently relieving the stresses associated with deeper flooding. Annual flood and drawdown events have also been observed in North American wetlands to encourage invasive vegetation which comes to dominate the littoral zone and exclude annuals during drawdown (e.g. Payne 1998).

To counter the effect of annual water regime cycles, it is proposed that wetland managers increase the depth and duration of flood and/or drawdown. However, this may only be feasible in some wetlands. For example, partial drawdown may only be possible because a) groundwater remains close to the sediment surface (e.g. LD) or b) drawdown below a certain depth may result in undesirable groundwater saline intrusions (e.g. BM: B. Weir, South Australian Field and Game Association, Barmera-Moorook Branch, pers. comm.). Imposing stress through drawdown in these types of wetlands is unlikely to be a practical tool.

The alternate is to keep wetlands flooded. This would see wetlands flooded at normal operational level for extended periods. Although this may not remove emergent macrophytes from shallow water it should restrict their distribution at lower elevations. A period of at least 2-3 years would appear to be sufficient for this purpose (Millar 1973; Squires and van der Valk 1992).

The objective of wetland managers to maintain and enhance biodiversity carries with it an implicit desire to increase establishment opportunities. The results of this study suggest that while flood and drawdown events may be managed to provide opportunities for establishment, they should also be managed to impose periods of stress to initiate periodic extirpation.

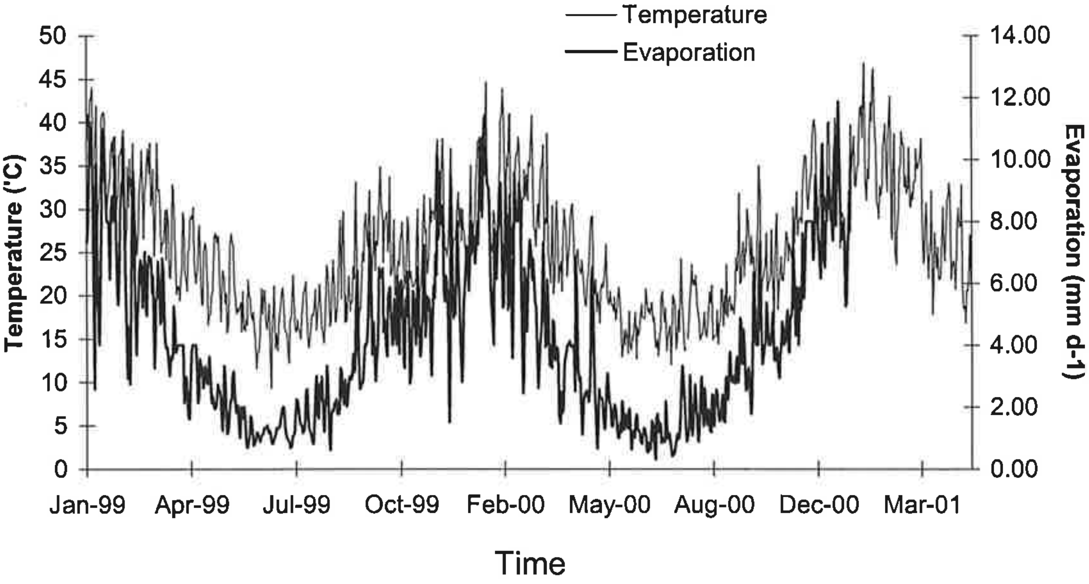
Plate 3.1. Seedlings of *M. verrucosum*, *T. domingensis* and *V. americana* inundated to ~10 cm at Banrock Station wetland. These plants germinated on exposed mudflats above the managed pool level at elevations inundated by a managed flood from August to December 1999.

Plate 3.2. Seedlings of *T. domingensis* with a stand of adult plants in the background at Big Mussel lagoon. Lower elevations in front of the mature stand were exposed during the drawdown event in 1999. Upon re-flooding of the mudflats *T. domingensis* germinated and seedlings were growing in water > 60 cm during February 2000. Many plants at lower elevations did not survive through to May 2000.


19 10 '99

Figure 3.1. The evaporation rate and daily maximum temperature measured at Lock 5 and Renmark, respectively, between January 1999 and April 2001.

Figure 3.2. Flow to the South Australian border (ML/day) between January 1999 and April 2001. Higher flows traversed the lower River Murray in the latter half of 2000, with peak flows at the border of 41, 572 ML/day on 13 October and 63,427 ML/day on 17 December 2000.


Temperature
Evaporation
50
45
40
35
30
25
20
15
10
5
0
Temperature (°C)
14.00
12.00
10.00
8.00
6.00
4.00
2.00
0.00
Evaporation (mm d-1)
Jan-99
Apr-99
Jul-99
Oct-99
Feb-00
May-00
Aug-00
Dec-00
Mar-01
Time

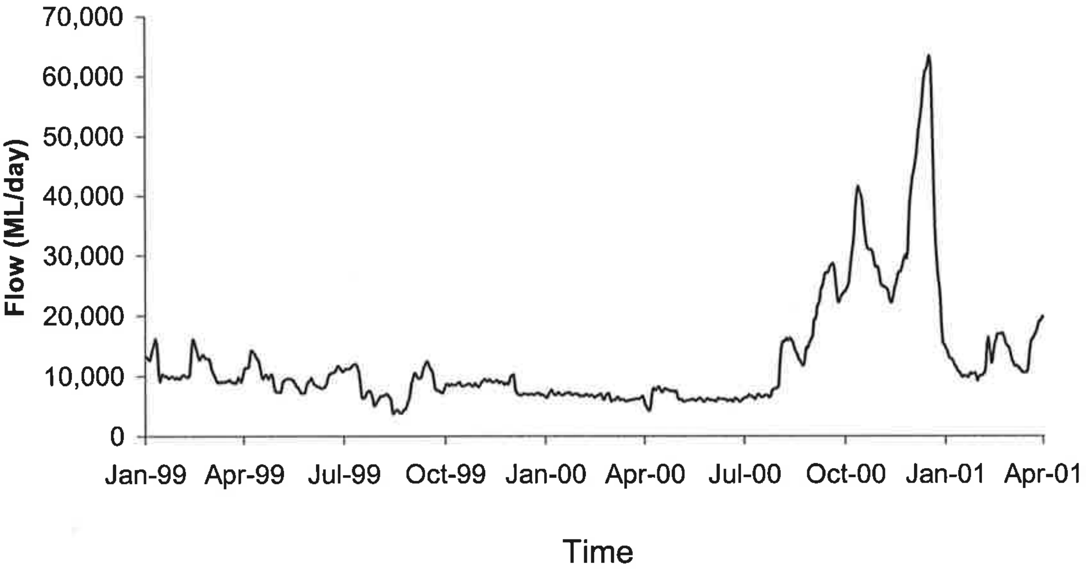

70,000
60,000
50,000
40,000
30,000
20,000
10,000
0
Flow (ML/day)
Jan-99
Apr-99
Jul-99
Oct-99
Jan-00
Apr-00
Jul-00
Oct-00
Jan-01
Apr-01
Time

Figure 3.3. The cover/abundance of six species across the elevation gradient in Banrock Station for each of the six surveys. Species are presented alphabetically from top left to bottom right. The scores at each elevation represent the summed score of the five individual 1m × 1m quadrats. 0-5 =1, 6-10 =2, 11-15= 3, 16-20= 4, 21-25= 5, 25-30= 6. The height and width of bars on the plots represents different summed cover/abundance groups.

- 1 – 2 ▬ 3 ▬ 4 ▬ 5 ▬ 6

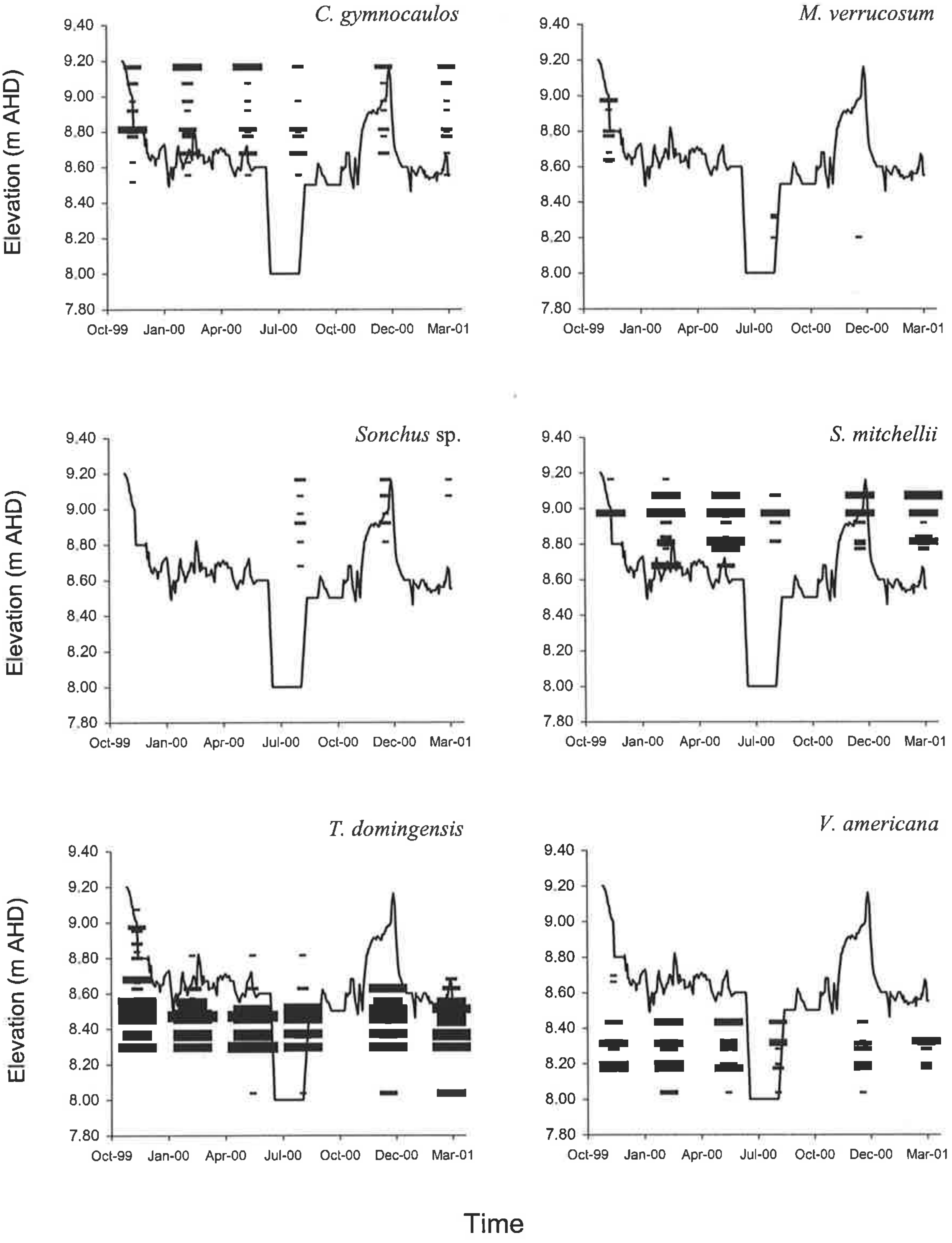

C. gymnocaulos
M. verrucosum
Sonchus sp.
S. mitchellii
T. domingensis
V. americana
Elevation (m AHD)
9.40
9.20
9.00
8.80
8.60
8.40
8.20
8.00
7.80
Oct-99
Jan-00
Apr-00
Jul-00
Oct-00
Dec-00
Mar-01
Time

Figure 3.4. The cover abundance of 13 species across the elevation gradient in Big Mussel for each of the six surveys. Species are presented alphabetically from top left to bottom right. The scores at each elevation represent the summed score of the five individual 1m × 1m quadrats. 0-5 =1, 6-10 =2, 11-15= 3, 16-20= 4, 21-25= 5, 25-30= 6. The height and width of bars on the plots represents different summed cover/abundance groups.

- 1 – 2 ━ 3 ▬ 4 ▬▬ 5 ▬▬ 6

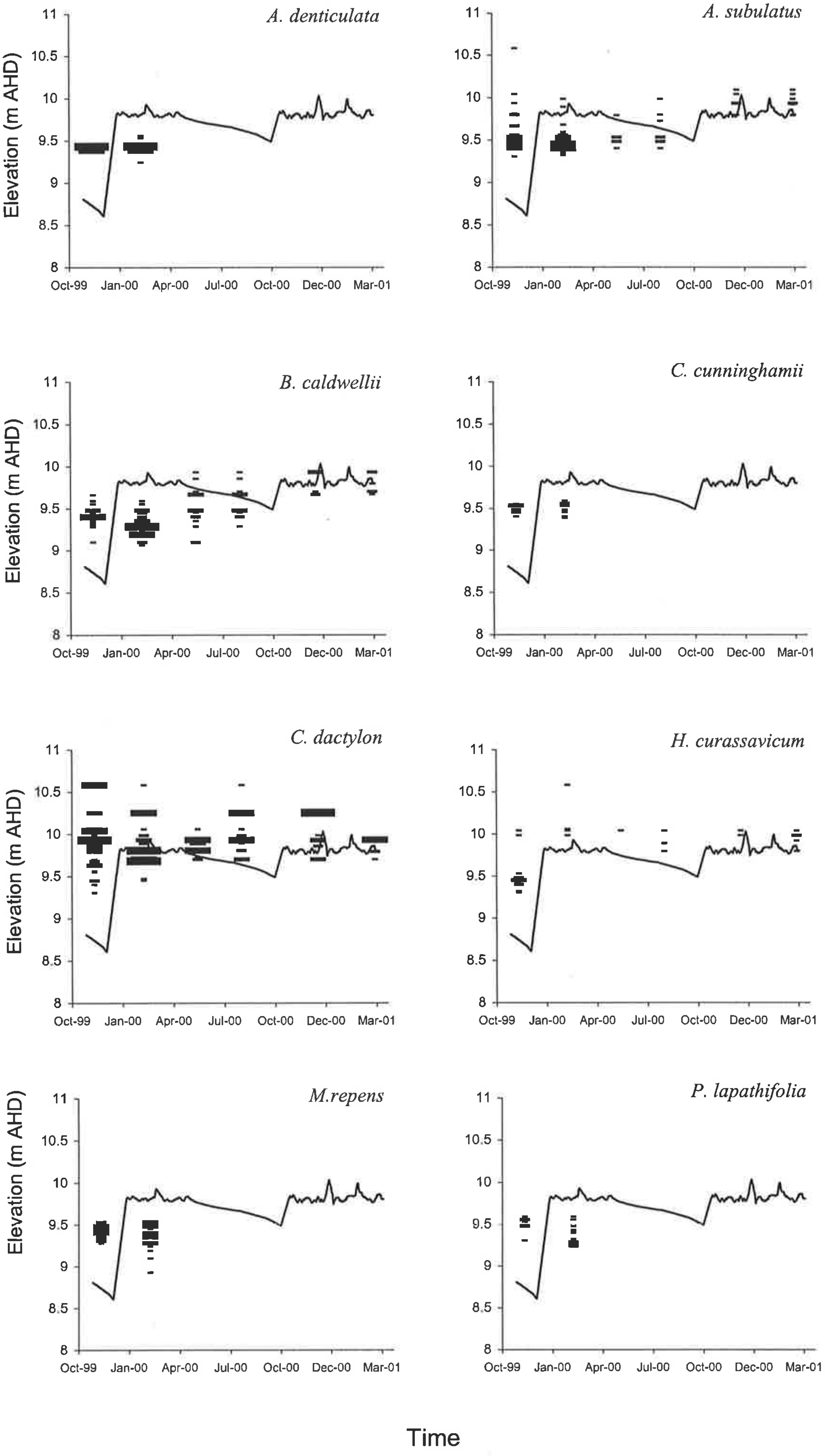

A. denticulata
A. subulatus
B. caldwellii
C. cunninghamii
C. dactylon
H. curassavicum
M.repens
P. lapathifolia
Elevation (m AHD)
11
10.5
10
9.5
9
8.5
8
Oct-99
Jan-00
Apr-00
Jul-00
Oct-00
Dec-00
Mar-01
Time

Figure 3.4. (continued).

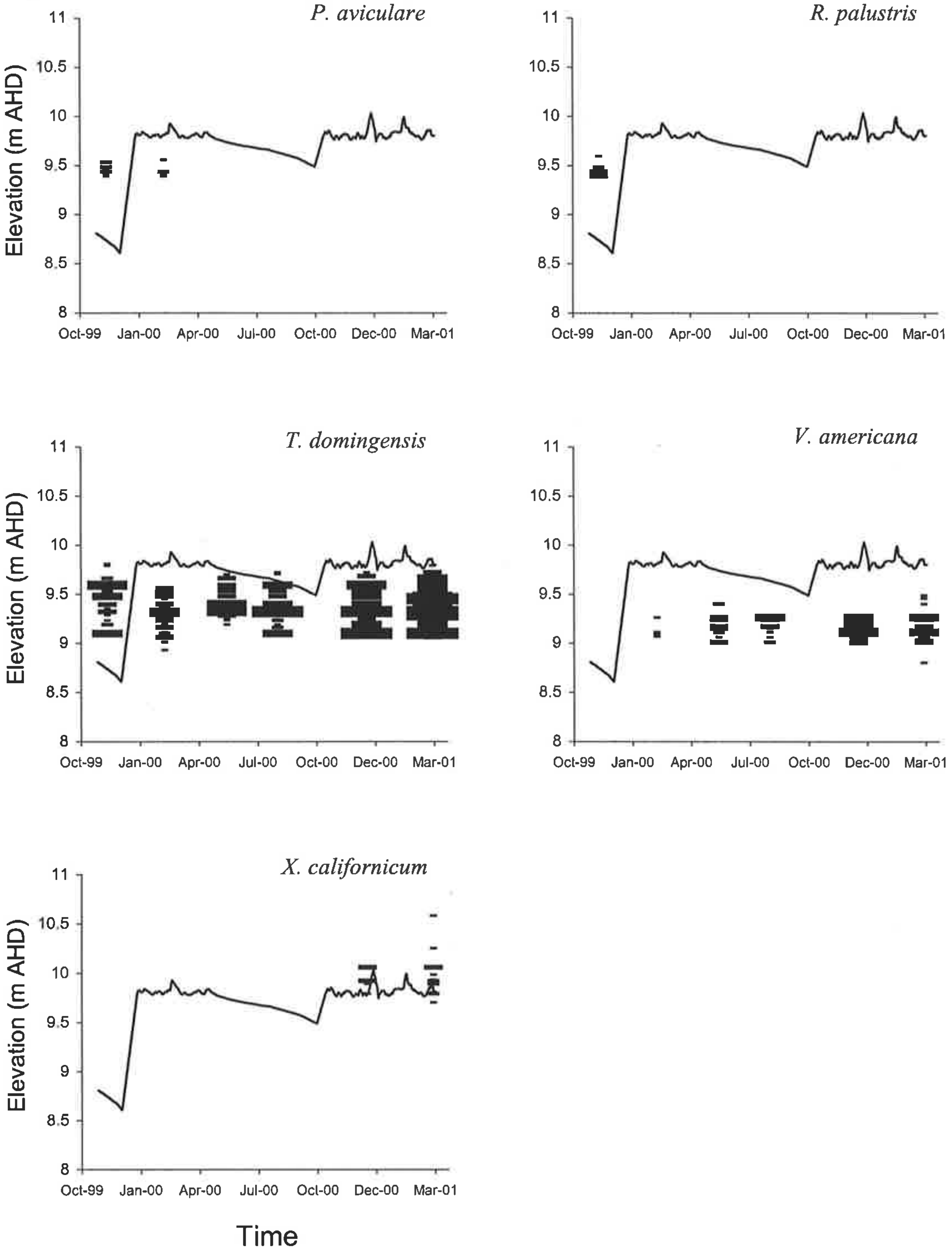

P. aviculare
R. palustris
T. domingensis
V. americana
X. californicum
Elevation (m AHD)
11
10.5
10
9.5
9
8.5
8
Oct-99
Jan-00
Apr-00
Jul-00
Oct-00
Dec-00
Mar-01
Time

Figure 3.5. The cover abundance of five species across the elevation gradient in Little Duck for each of the six surveys. Species are presented alphabetically from top left to bottom right. The scores at each elevation represent the summed score of the five individual 1m × 1m quadrats. 0-5 =1, 6-10 =2, 11-15= 3, 16-20= 4, 21-25= 5, 25-30= 6. The height and width of bars on the plots represents different summed cover/abundance groups.

- 1 - 2 ▬ 3 ▬ 4 ▬ 5 ▬ 6

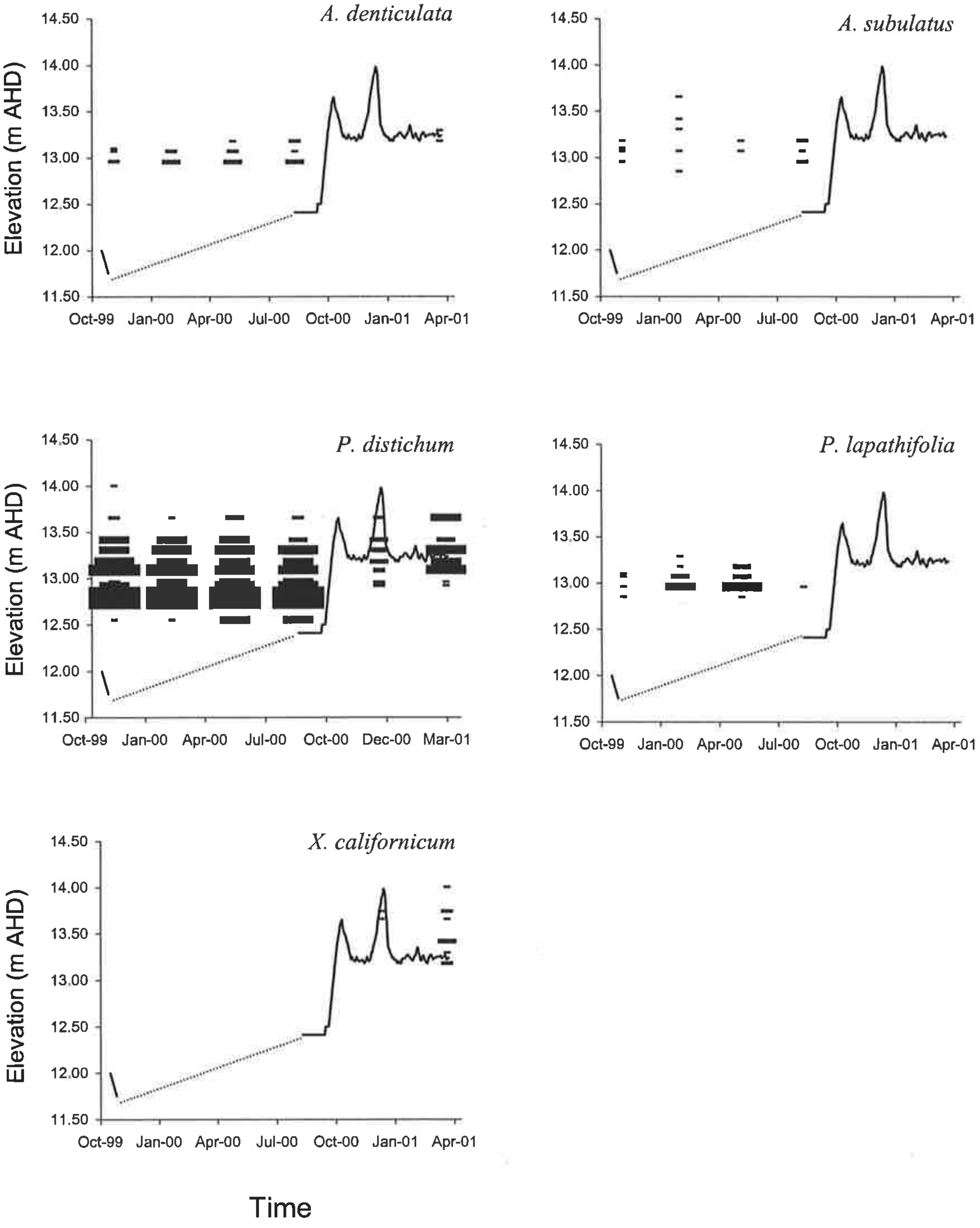
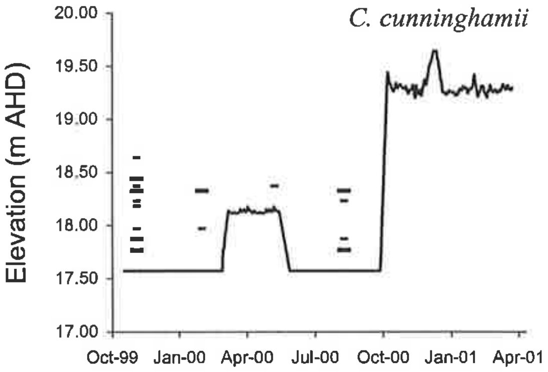
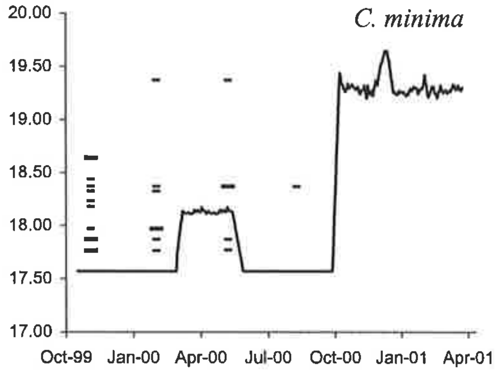
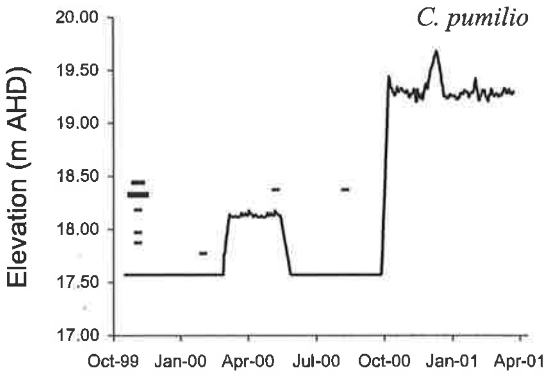

A. denticulata
A. subulatus
P. distichum
P. lapathifolia
X. californicum
Elevation (m AHD)
14.50
14.00
13.50
13.00
12.50
12.00
11.50
Oct-99
Jan-00
Apr-00
Jul-00
Oct-00
Jan-01
Apr-01
Dec-00
Mar-01
Time

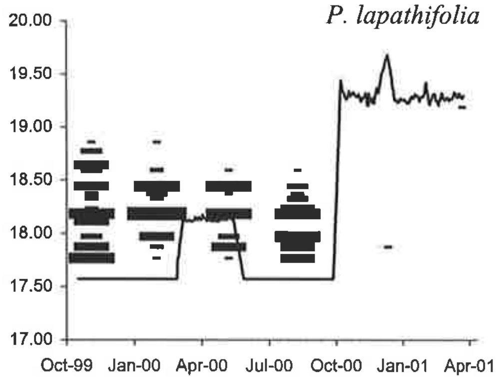
Figure 3.6. The cover abundance of five species across the elevation gradient in Pilby Creek for each of the six surveys. Species are presented alphabetically from top left to bottom right. The scores at each elevation represent the summed score of the five individual 1m × 1m quadrats. 0-5 =1, 6-10 =2, 11-15= 3, 16-20= 4, 21-25= 5, 25-30= 6. The height and width of bars on the plots represents different summed cover/abundance groups.

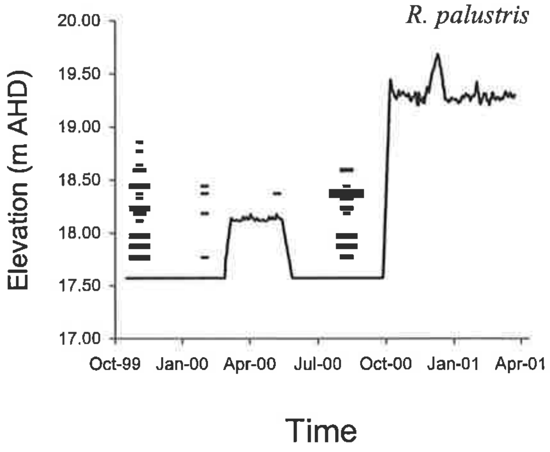
- 1 – 2 ▬ 3 ▬ 4 ▬ 5 ▬ 6


C. cunninghamii
Elevation (m AHD)
20.00
19.50
19.00
18.50
18.00
17.50
17.00
Oct-99
Jan-00
Apr-00
Jul-00
Oct-00
Jan-01
Apr-01


C. minima
20.00
19.50
19.00
18.50
18.00
17.50
17.00
Oct-99
Jan-00
Apr-00
Jul-00
Oct-00
Jan-01
Apr-01


C. pumilio
Elevation (m AHD)
20.00
19.50
19.00
18.50
18.00
17.50
17.00
Oct-99
Jan-00
Apr-00
Jul-00
Oct-00
Jan-01
Apr-01


P. lapathifolia
20.00
19.50
19.00
18.50
18.00
17.50
17.00
Oct-99
Jan-00
Apr-00
Jul-00
Oct-00
Jan-01
Apr-01


R. palustris
Elevation (m AHD)
20.00
19.50
19.00
18.50
18.00
17.50
17.00
Oct-99
Jan-00
Apr-00
Jul-00
Oct-00
Jan-01
Apr-01
Time

CHAPTER 4

PREDICTING THE FLORISTIC COMPOSITION OF LOWER RIVER MURRAY WETLANDS

4.1 Abstract

The strength of the relationship between water regime and floristic composition was tested by constructing a model to predict the presence and absence of species and functional groups in Lower Murray wetlands. The species pool was filtered using water regimes of 3, 4, 5 and 6 months in length and species and functional group water regime preferences. Overall, predictions of species were more accurate (76-86%) than predictions of functional groups (64-74%). Species predictions became more accurate as the length of hydrograph increased. This was because fewer predictions were made of annuals that tolerated < 100 days of flood or drawdown. A hydrograph of six months in length should prove to be generally useful in differentiating the response of annual from perennial species. In general, the accuracy of the model was a function of more accurate predictions of absence than presence. Although the model is based on Lower Murray wetland plants, the design and method of water regime preference estimation should yield accurate species predictions for most wetlands with minimum water level variability.

4.2 Introduction

Keddy (1999) advocates an 'assembly rules' approach to predicting floristic composition where a species pool is filtered by the local environment to create a predicted community. To filter the species pool requires knowledge of a wetland's water regime and the species' life history traits that indicate tolerance to the chosen filters. Predictions can then be made for individual species or functional groups, i.e. 'a group of taxa that show a similar response to a defined perturbation' (*sensu* Noble and Gitay 1996).

Life history traits can be estimated via controlled screening experiments (e.g.

germination at different soil moistures) or by relating the distribution of field populations to environmental factors (Noble and Slatyer 1980; McIntyre *et al.* 1995; Noble and Gitay 1996). An example of the latter is the use of repeated monitoring of plant distributions in wetlands that experience variable water levels to develop estimates of a water regime preference.

This chapter provides a preliminary assessment of a model that predicts the presence, absence and establishment of a species or functional group derived from an initial species pool. The physical data used by the model are elevation and varying lengths of the wetland hydrograph. The initial pool is filtered on the basis of species and functional group water regime preferences. Preferences were determined by repeated monitoring of five wetlands with different water regimes over an 18-month period. The model is based upon four different hydrograph lengths (3, 4, 5 and 6 months) and was independently tested using water regime and vegetation data from a permanently flooded wetland.

The model was interrogated to determine:

1) to what degree the accuracy of the model outcome was influenced by the presence or absence of species;

2) whether the model was better at predicting species or functional groups;

3) the sensitivity of the model to different lengths of hydrograph; and

4) whether the model predictions favoured annual above perennial species.

The limitations, assumptions and methods of improving the model are discussed along with the prospect of using the model for wetland management and field studies.

4.3 Methods

4.3.1 Species water regime preferences

Data collection

The collection of vegetation data and the source of water level and temperature data are described in Chapters 2 and 3. The data used to construct the model were taken from Banrock Station (BA), Big Mussel (BM), Chambers Creek (CC), Little Duck (LD) and Pilby Creek (PI). The remaining wetland, Old Petes (OP), was used to test the model.

Construction of water regime preferences

Water regime preferences were determined only for species with a total cover/abundance score for all surveys of > 0.1% (44). Preferences were calculated by reference to individual wetland hydrographs for 1 September 1999 to 31 March 2001 (Figures 2.2 – 2.6). The starting date of 1 September 1999 was chosen because it was approximately 3 months before the first survey, which is the approximate interval between surveys.

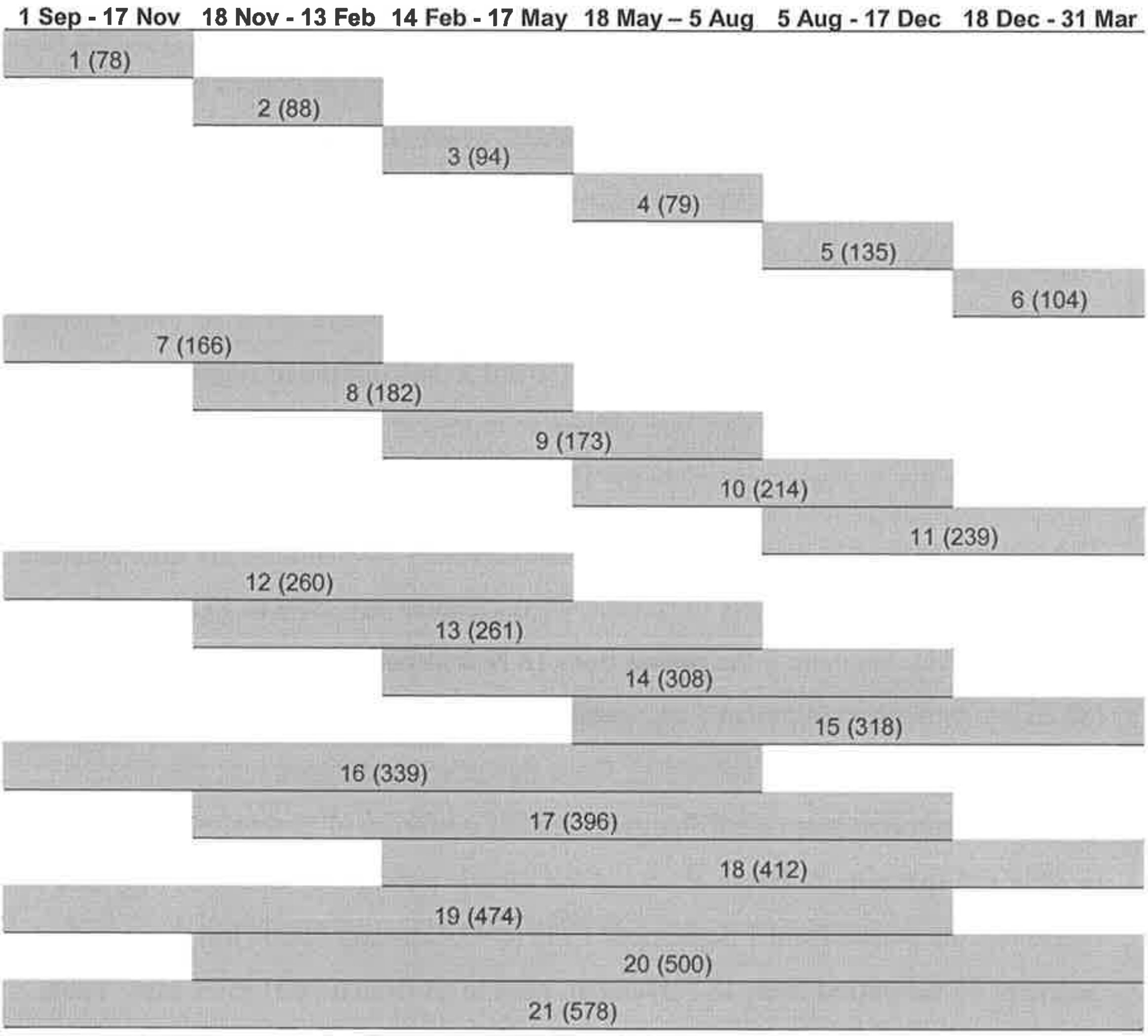
The sample period from 1 September 1999 to 31 March 2001 was split into 'segments' based upon wetland survey dates. Wetland surveys occurred over a period of 5-6 days e.g. 15-20 November 1999. To avoid re-calculation of segments for each wetland, the middle survey date was chosen to represent all survey dates. For example, for the November surveys the 17 November 1999 was selected.

The number of days in each segment was calculated by determining the time between surveys. Segment 1 represents the period from 1 September 1999 to 17 November 1999 (78 days), Segment 2 the period from 18 November 1999 to 13 February 2000 (88 days), through to Segment 6 representing the period from 18 December 2000 to 31 March 2001 (104 days: Table 4.1). Once this primary division was complete, a further 15 segments were identified representing multiples of approximately three months and spanning different blocks of the sample period. For example, Segment 7 represents the period from 1 September 1999 to 13 February 2000 (166 days) and Segment 20 the period from 18 November 1999 to 31 March 2001 (500 days: Table 4.1).

The next step was to identify the spatial and temporal location for individuals of each species. Individuals were assigned a segment of the sample period based upon the surveys during which they were recorded. An individual recorded only during August 2000 would be assigned Segment 4, whereas an individual recorded at the same location in a wetland in the February 2000, May 2000 and August 2000 surveys would be assigned Segment 13.

Following this allocation, the elevation dependent hydrograph of correct length (as determined by the respective segment) was identified for individuals and used to determine the number of days they were exposed or flooded within particular depth

Table 4.1. The sample period for the entire study (1 September 1999 to 31 March 2001) split into 21 segments based on wetland survey dates. The number of days in each segment was determined by the time span between survey dates and is indicated in brackets.



ranges (Table 4.2). Depth ranges were selected to reflect the predicted tolerances of Lower Murray wetland species (e.g. Blanch *et al.* 1998; Blanch *et al.* 1999a; Siebentritt and Ganf 2000).

The data for individuals of each species was pooled and the 25th, 50th and 75th percentiles for each of the ten depth ranges calculated. The 75th percentile was selected to describe the species tolerance and used in the model. For a species to be included in the model, at least five individuals had to be recorded. Individuals found

Table 4.2. Water regime indices and the corresponding depth ranges used to determine species preferences. A negative sign (–) indicates where water levels are below the sediment surface.

Water Regime Indices	Depth range	Water Regime Indices	Depth range
1	≥ 0 cm	6	< 0 cm
2	0 to 20	7	0 to –20 cm
3	20 to 60 cm	8	-20 to –60 cm
4	60 to 100 cm	9	-60 to –100 cm
5	> 100 cm	10	<-100 cm

at the same location for two or more consecutive surveys are treated as one record only. This reduced the size of the species pool for the model to 33 species. Five observations was an arbitrary selection and was anticipated to represent the minimum data required to make accurate predictions of water regime preference.

4.3.2 Functional group water regime preferences

Noble and Gitay (1996) recognize five categories of functional classification. Their fourth category describes 'a group of taxa that show a similar response to a defined perturbation'. It is with respect to this definition that the term 'functional group' is used throughout this chapter.

Similarities between species were determined using the Relative Sorensen distance measure (equivalent to the Bray-Curtis metric) and clusters were assigned using the Group Average Linkage method (equivalent to Unweighted Paired Groups Means Analysis, UPGMA; PC-ORD ver. 4.21, McCune and Mefford 1999). Once group membership was determined, water regime preferences for groups were quantified using the 75th percentile for each water regime indice.

4.3.3 Model description and assumptions

The model predicts species presence/absence and establishment at elevations based upon water regime preferences and water level data. It commences by assuming that all recorded species are present and proceeds to filter those that cannot tolerate the user-supplied water regime – Step 1. Establishment for a sub-set of the species pool occurs in Step 2. Model outcomes are the sum of Step 1 and Step 2.

Steps 1 and 2 were repeated for both species and functional group water regime preferences.

The model was constructed using multiple worksheets in Microsoft Excel 2000 (Microsoft Corporation). The model operations were performed using macros and multiple IF functions.

Step 1 – Persistence of mature plants

For each user-defined elevation the model takes the wetland hydrograph and determines how many days are spent in each water regime indice (Table 4.2). The species water regime preferences are then compared to the days spent in each indice. To be recorded as present, the number of days an elevation is in each indice must be ≤ that tolerated by the species.

Four sub-models were constructed to test for the effect of different hydrograph lengths on the accuracy of predictions - 3 (MOD 3), 4 (MOD 4), 5 (MOD 5) and 6 months (MOD 6). Three months was anticipated to be the minimum time required to observe a change in vegetation and six months the time needed to distinguish between responses of annuals and perennials.

Step 2 – Establishment scenarios

Establishment rules were determined for species that established during the sample period. This included most annuals in the species pool but few perennials. No provision was made for predicting establishment from vegetative propagules.

As each scenario has a different influence on establishment, the model first determines if the hydrograph meets the criteria for any of four scenarios (described in detail below). To engage a scenario requires a specific combination of wet (water levels above sediment surface) and dry periods (water levels below sediment surface). Even if a scenario is engaged, the species that establish are still subject to the same procedure as in Step 1. Water regime preferences for most seedlings are unknown and it is assumed that they respond in the same way as mature plants. The validity of this assumption is considered in the discussion. The ACTIVE period refers to the time over which establishment conditions are met for establishment scenarios 2-4.

The rules for engagement of each scenario are presented below. The method used by the model to select different scenarios is outlined in Figure 4.1.

Establishment scenario 1 (ESTAB 1)

This scenario only engages Step 1 and applies to elevations that remain either permanently wet or dry or where water level fluctuations are ≤ 20 cm. It describes the conditions in unmanaged wetlands on the Lower Murray directly above weirs where water levels are approximately static under normal operational conditions. The banks in most Lower Murray wetlands are approximately vertical at the water's edge and at least 20 cm high. This means that fluctuations of ≤ 20 cm rarely expose bare mudflats.

Establishment scenario 2 (ESTAB 2)

This scenario relates to elevations that are exposed to drawdown after an initial period of inundation. To engage this scenario there must be an initial wet period followed by a dry period. There can be a period of fluctuating water levels with alternating wet and dry (up to five periods of wet/dry) but the ACTIVE drawdown period does not commence until the difference in water height between the wet and dry periods is at least 20 cm and there is a dry period of at least 14 days. If drawdown occurs within 14 days of the end of the hydrograph the scenario will not be engaged. Seventeen species may establish under ESTAB 2, 13 of which are mudflat annuals (Table 4.3).

For establishment to occur the temperature during the drawdown phase must exceed 20°C for at least 75% of the time. This prevents germination in cooler months.

Establishment scenario 3 – ESTAB 3

This scenario identifies elevations that are a) re-flooded for at least 14 days after a drawdown and b) not followed by another dry phase. It is the only scenario under which the submerged macrophyte *Vallisneria americana* can establish since seedlings are desiccation intolerant. The only other species that establish during ESTAB 3 are *Myriophyllum verrucosum* and *Typha domingensis* (Table 4.3).

There is an additional set of conditions for the establishment of *T. domingensis* and *V. americana*.

- *T. domingensis*: For the first 14 days water depth must remain between 0-20 cm to ensure that seedlings remain in an adequate light environment but must not exceed 60 cm for a period of 28 in the first 42 days to ensure that water depth does not exceed the tolerances of juvenile plants.

Table 4.3. An asterisk indicates under which scenario a species can establish. Species are presented in their respective functional groups. Full species names are provided in Appendix 1.

	ESTAB 2	ESTAB 3	ESTAB 4		ESTAB 2	ESTAB 3	ESTAB 4
Group 1				Group 4			
A. avenaceae	*			*A. semibaccata*			
B. medianus	*			*E. dielsii*			
P. distichum				*E. australis*	*		*
C. dactylon				*H. curassavicum*	*		*
A. denticulata	*			*X. californicum*			*
A. subulatus	*			*S. diandra*			*
B. caldwellii	*						
L. peploides				Group 5			
M. repens	*			*C. gymnocaulos*			
				P. australis			
Group 2				*S. quinqueflora*			
C. cunninghamii	*			*S. mitchellii*			
C. minima	*						
P. aviculare	*			Group 6			
P. lapathifolia	*			*J. aridicola*	*		
P. luteo-album	*		*	*P. decipiens*			
R. palustris	*			*S. validus*			
Group 3				Group 7			
B. basaltica				*M. verrucosum*	*	*	
C. pumilio	*			*T. domingensis*		*	
				V. americana		*	

- *V. americana*: For the first 14 days water depth must remain between 0-20 cm to ensure seedlings remain in an adequate light environment. After the first 28 days water levels must rise above 20 cm to reduce the impact of wave action and waterfowl grazing on seedling mortality.

Establishment scenario 4 – ESTAB 4

ESTAB 4 applies to elevations that are at, or just above, operational pool level and are inundated during periods of overbank flooding. The elevation is initially dry, then flooded for at least 7 days after which water levels fall and the site is dry for at least 14 days. Alternating wet/dry periods may occur both prior and after the ACTIVE period. For the ACTIVE period to commence there must be a difference of at least 20 cm between successive wet/dry periods and the temperature must remain above 20°C for at least 75% of the time.

4.3.4 Model testing

The model was tested on OP, an unmanaged, permanently inundated wetland with water levels regulated by operations at Lock 3. The hydrograph used for OP was based on water level data collected at Lock 3 for the 6 months prior to the final survey in March 2001. The model was tested by comparing vegetation presence/absence data from the March 2001 survey with the model predictions.

OP was monitored using three transects, each with five elevations. However, the elevations at transects 1 and 2 were identical and thus predictions were only made for 10 elevations. Codes describing transects and elevations are, for example, T1 – transect 1, E1 – elevation 1. Elevations are in m AHD (m Australian Height Datum).

The accuracy of predictions is described as follows:

- O_p observed present;
- O_a observed absent;
- P_p predicted present; and
- P_a predicted absent.

If a species is observed at an elevation and was also predicted to occur at that elevation, then the code O_pP_p applies. If a species was not observed at an elevation but was predicted to occur, then the code O_aP_p applies. The remaining combinations are O_aP_a and O_pP_a.

4.4 Results

4.4.1 Species water regime preferences

Species water regime preferences are presented in Appendix 2.

Water regime preferences were calculated for 33 species. The greatest number of records of individual species was for *Cyperus gymnocaulos* (61), *Paspalum distichum* (96), *Phragmites australis* (80) and *T. domingensis* (92). A number of species barely exceeded the minimum threshold of five e.g. *Atriplex semibaccata* (5), *Eragrostis dielsii* (6), *Spergularia diandra* (6) and *Bolboschoenus medianus* (8).

Species had wide tolerances to the rise and fall of water levels. Annuals tolerated a median of < 100 days of flood (≥ 0cm) or drawdown (< 0 cm) whereas perennials tolerated > 100 days of one or both. The greatest median number of days of drawdown tolerated was by *Sporobolus mitchellii* (439), *P. australis* (430), *C. gymnocaulos* (350) and *Sarcocornia quinqueflora* (327) and of flooding by *V. americana* (412), *Schoenoplectus validus* (372) and *T. domingensis* (182).

4.4.2 Functional groups

Cluster analysis identified seven groups based upon species water regime preferences (Figure 4.2). The group water regime preferences are presented in Appendix 3.

The cluster analysis separated species tolerant of wetter conditions (Groups 6 and 7) from those occupying temporarily to infrequently flooded elevations (Groups 1-5: Figure 4.2). Although Groups 6 and 7 tolerated a similar number of days flooded, Group 6 occupied shallower flooded elevations while Group 7, more deep flooded sites.

The remaining species were divided between Groups 1-3, primarily annual species that established during drawdown and were tolerant of an equivalent number of days flooded and drawndown. Groups 4-5 consisted of annual and perennial species tolerant of a greater proportion of days drawndown than flooded. Groups 1-3 included perennial species that commonly grew at or near the water's edge e.g. *P. distichum*, *Cynodon dactylon* and *Bolboschoenus caldwellii*.

4.4.3 Model predictions for species at OP

Predictions based upon species water regime preferences are presented under the functional groups within which species occur (model predictions for functional groups are presented in Section 4.4.6).

Group 1

MODs 3 to 6 did not predict seedling establishment of species from Group 1.

All MODs predicted the presence of *C. dactylon* and *Ludwigia peploides* but the former declined from T1/2E1-E4 and T3E1 for MOD 3 to T1E4 and T3E1 for MODs 5 and 6 (Tables 4.4-4.7). *L. peploides* was predicted at T3E4 and T3E5 by MODs 5 and 6 at elevations that remained inundated by at least 20 cm.

P. distichum, was predicted to occur at more elevations than any other species by MOD 3 (8; Table 4.4) but was absent from MOD 5 and 6 (Tables 4.6-4.7).
B. medianus, *Aster subulatus* and *B. caldwellii* were only predicted by MOD 3 (Table 4.4).

Group 2

None of the MODs predicted the seedling establishment of any of the Group 2 species. From the initial pool of six species, only MOD 3 predicted the occurrence of *Centipeda minima* (Table 4.4). None of the other species were predicted by any model (Tables 4.5-4.7).

Group 3

MOD 3 predicted the presence of *Brassica basaltica* and *Chenopodium pumilio* at a range of elevations (Table 4.4), but only *B. basaltica* was predicted at a subset of these elevations by MOD 4 (Table 4.5). Neither was predicted by the remaining MODs.

Group 4

All MODs predicted the establishment of *Epaltes australis*, *S. diandra*, *Xanthium californicum* and *Heliotropum curassavicum* via ESTAB 4.

The section of hydrograph used by MOD 3 contained only one establishment event, which started on 11 February when the water level was above 9.85 m for 11 days (Figure 4.3). The establishment of the four species was restricted to T1E4, which was flooded for 7 days, the minimum necessary to initiate establishment. In contrast, two

Table 4.4. The predicted distribution of species across the elevation gradient at OP for MOD 3. Elevations in m AHD were the same across T1 and T2 hence predictions were combined (T1,2). Black boxes indicate the presence of adults and grey boxes seedling establishment.

	T1/2E1	T1/2E2	T1/2E3	T1/2E4	T1/2E5	T3E1	T3E2	T3E3	T3E4	T3E5
Group 1	10.43	10.25	10.07	9.89	9.73	9.92	9.74	9.71	9.56	9.50
A. avenaceae										
B. medianus				■		■				
P. distichum	■			■	■	■	■	■	■	■
C. dactylon	■	■	■	■		■				
A. subulatus	■									
B. caldwellii	■									
A. denticulata										
L. peploides	■								■	■
M. repens										
Group 2										
C. cunninghamii										
C. minima	■									
P. aviculare										
P. lapathifolia										
P. luteo-album										
R. palustris										
Group 3										
B. basaltica		■	■		■		■	■		
C. pumilio	■				■		■	■		
Group 4										
A. semibaccata		■	■							
E. dielsii	■	■	■							
E. australis	■	■	■	▨						
S. diandra		■	■	▨						
X. californicum		■	■	■ ▨	■	■	■	■		
H. curassavicum				■ ▨		■				
Group 5										
P. australis	■	■	■	■	■	■	■	■	■	■
C. gymnocaulos	■	■	■	■		■				
S. quinqueflora	■	■	■	■		■				
S. mitchellii	■	■	■	■		■				
Group 6										
J. aridicola	■				■		■	■	■	■
P. decipiens					■		■	■		
S. validus				■	■	■	■	■	■	■
Group 7										
M. verrucosum										
T. domingensis	■				■		■	■	■	■
V. americana									■	■

Table 4.5. The predicted distribution of species across the elevation gradient at OP for MOD 4. Elevations in m AHD were the same across T1 and T2 hence predictions were combined (T1,2). Black boxes indicate the presence of adults and grey boxes seedling establishment.

	T1/2E1	T1/2E2	T1/2E3	T1/2E4	T1/2E5	T3E1	T3E2	T3E3	T3E4	T3E5
Group 1	10.43	10.25	10.07	9.89	9.73	9.92	9.74	9.71	9.56	9.50
A. avenaceae										
B. medianus										
P. distichum	■				■		■	■		
C. dactylon			■	■		■				
A. subulatus										
B. caldwellii										
A. denticulata										
L. peploides									■	■
M. repens										
Group 2										
C. cunninghamii										
C. minima										
P. aviculare										
P. lapathifolia										
P. luteo-album										
R. palustris										
Group 3										
B.basaltica			■		■		■	■		
C. pumilio										
Group 4										
A. semibaccata			■							
E. dielsii		■	■							
E. australis		■	■	▨						
S. diandra				▨						
X. californicum			■	▨		▨				
H. curassavicum				■ ▨		■ ▨				
Group 5										
P. australis	■	■	■	■	■	■	■	■	■	■
C. gymnocaulos	■	■	■	■		■				
S. quinqueflora		■	■	■		■				
S. mitchellii		■	■	■		■				
Group 6										
J. aridicola					■		■	■	■	■
P. decipiens										
S. validus				■	■	■	■	■	■	■
Group 7										
M. verrucosum										
T. domingensis					■		■	■	■	■
V. americana									■	■

Table 4.6. The predicted distribution of species across the elevation gradient at OP for MOD 5. Elevations in m AHD were the same across T1 and T2 hence predictions were combined (see T1,2). Black boxes indicate the presence of adults and grey boxes seedling establishment.

	T1/2E1	T1/2E2	T1/2E3	T1/2E4	T1/2E5	T3E1	T3E2	T3E3	T3E4	T3E5
Group 1	10.43	10.25	10.07	9.89	9.73	9.92	9.74	9.71	9.56	9.50
A. avenaceae										
B. medianus										
P. distichum										
C. dactylon				■		■				
A. subulatus										
B. caldwellii										
A. denticulata										
L. peploides									■	■
M. repens										
Group 2										
C. cunninghamii										
C. minima										
P. aviculare										
P. lapathifolia										
P. luteo-album										
R. palustris										
Group 3										
B. basaltica										
C. pumilio										
Group 4										
A. semibaccata										
E. dielsii		■	■							
E. australis		■	■	▨						
S. diandra				▨						
X. californicum				▨		▨				
H. curassavicum				■ ▨		▨				
Group 5										
P. australis	■		■	■		■				
C. gymnocaulos		■	■	■		■				
S. quinqueflora		■	■	■		■				
S. mitchellii		■	■	■		■				
Group 6										
J. aridicola									■	■
P. decipiens										
S. validus				■		■	■	■	■	■
Group 7										
M. verrucosum										
T. domingensis									■	■
V. americana									■	■

Table 4.7. The predicted distribution of species across the elevation gradient at OP for MOD 6. Elevations in m AHD were the same across T1 and T2 hence predictions were combined (see T1,2). Black boxes indicate the presence of adults and grey boxes seedling establishment.

	T1/2E1	T1/2E2	T1/2E3	T1/2E4	T1/2E5	T3E1	T3E2	T3E3	T3E4	T3E5
Group 1	10.43	10.25	10.07	9.89	9.73	9.92	9.74	9.71	9.56	9.50
A. avenaceae										
B. medianus										
P. distichum										
C. dactylon				■		■				
A. subulatus										
B. caldwellii										
A. denticulata										
L. peploides									■	■
M.repens										
Group 2										
C. cunninghamii										
C. minima										
P. aviculare										
P. lapathifolia										
P. luteo-album										
R. palustris										
Group 3										
B.basaltica										
C. pumilio										
Group 4										
A. semibaccata										
E. dielsii		■	■							
E. australis		■	■	▒						
S. diandra				▒						
X. californicum				▒		▒				
H. curassavicum				▒		▒				
Group 5										
P. australis				■		■				
C. gymnocaulos		■	■							
S. quinqueflora		■	■							
S. mitchellii		■	■	■						
Group 6										
J. aridicola										
P. decipiens										
S. validus					■		■	■	■	■
Group 7										
M. verrucosum										
T. domingensis									■	■
V. americana									■	■

establishment events were initiated in MODs 4-6 with the additional one occurring in late December when water levels rose above 9.89 m AHD for 8 days and peaked at 10.02 m AHD. The establishment of *X. californicum* and *H. curassavicum* at an additional elevation (T3E1) was predicted for the second flood event.

The occurrence of all Group 4 species was predicted by MODs 3 and 4, especially at higher elevations (Tables 4.4-4.5). However, species predictions were reduced under MODs 5 and 6 and in the latter, only *E. dielsii* and *E. australis* were predicted at the highest two elevations at T1/2.

Group 5

MODs 3 and 4 predicted *P. australis* at all elevations and the remaining species at T1/2E1-E4 and T3E1 (Tables 4.4-4.5). Most species persisted at T1/2E2-E4 for MOD 5 and all were present at T3E1 (Table 4.6). In contrast, *P. australis* was restricted to T1/2E4 and T3E1 for MOD 6 and the remaining species to the middle range of elevations for T1/2 (Table 4.7).

Group 6

None of the MODs predicted the establishment of *J. aridicola*.

Persicaria decipiens was predicted only by MOD 3 and was restricted to T1/2E5 and T3E2-E3. In contrast, *J. aridicola* and *S. validus* were predicted to occur across a range of lower elevations, especially at T3 (Table 4.4). The effect of alternative MODs was to reduce the distribution of *J. aridicola* across the elevation gradient, whereas *S. validus* persisted at lower elevations (Tables 4.5-4.7).

Group 7

No establishment was predicted for *T. domingensis* and *V. americana*.

T. domingensis and *V. americana* were predicted across a range of predominantly lower elevations for MODs 3 and 4 (Tables 4.4-4.5) and were restricted to T3E4-E5 for MODs 5 and 6 (Table 4.6-4.7). *M. verrucosum* was not predicted for any MODs.

4.4.4 General model accuracy for species at OP

The overall accuracy of the model improved as the length of hydrograph used increased from MOD 3 to MOD 6. However, gains in accuracy diminished progressively from MOD 3 to MOD 6 (Table 4.8).

Table 4.8. The accuracy of the four models based upon different periods of the hydrograph for individuals species. Each model made 495 predictions. O_p – observed present, O_a – observed absent, P_p - predicted present, P_a – predicted absent.

	Model 3	Model 4	Model 5	Model 6
O_pP_p	47	38	25	21
O_aP_p	107	64	41	29
Total predictions	154	102	66	50
% correct	31%	37%	38%	42%
O_pP_a	13	22	35	39
O_aP_a	328	371	394	406
Total predictions	341	393	429	445
% correct	96%	94%	92%	91%
Total correct	375 (76%)	409 (83%)	419 (85%)	427 (86%)
Total incorrect	120 (24%)	86 (17%)	76 (15%)	68 (14%)

The source of accuracy differed between models. MOD 3 accurately predicted 96% of absences (O_aP_a) but only 31% of plant presence (O_pP_p) whereas MOD 6 predicted 91% of absences and 43% of presences (Table 4.8). Contributing to this result was that MOD 3 made more predictions of presence, resulting in more over-predictions of presence, while the more conservative MOD 6 made more predictions of absence, leading to more over-predictions of absence (Table 4.8).

4.4.5 Model accuracy for species

Group 1

Most predictions for Group 1 species were for *P. distichum* and *C. dactylon.* All models over-predicted *C. dactylon* (Table 4.9). *P. distichum* was predicted accurately in MOD 3 at least 50% of the time but was predicted less frequently in MOD 4 and not at all in MODs 5 and 6 leaving it under-predicted. *L. peploides,* did not occur at any of the elevations surveyed and was over predicted. *A. subulatus* was predicted accurately only once for MOD 3 and not at all in the other MODs (Table 4.9).

Group 2

Other than one prediction by MOD 3, all other models predicted the absence of Group

Table 4.9. The accuracy of species predictions for MODs 3-6. The maximum score in a model was 15 (3 transects × 5 elevations). O_p - observed present, O_a - observed absent, P_p - predicted present and P_a predicted absent.

	MOD 3				**MOD 4**				**MOD 5**				**MOD 6**			
	O_pP_p	O_aP_p	O_aP_a	O_pP_a	O_pP_p	O_aP_p	O_aP_a	O_pP_a	O_pP_p	O_aP_p	O_aP_a	O_pP_a	O_pP_p	O_aP_p	O_aP_a	O_pP_a
Group 1																
A. avenaceae	0	0	15	0	0	0	15	0	0	0	15	0	0	0	15	0
B. medianus	0	3	12	0	0	0	15	0	0	0	15	0	0	0	15	0
P. distichum	6	5	3	1	2	4	4	5	0	0	8	7	0	0	8	7
C. dactylon	2	7	6	0	1	4	9	1	1	2	11	1	1	2	11	1
A. subulatus	1	1	8	5	0	0	9	6	0	0	9	6	0	0	9	6
B. caldwellii	0	2	12	1	0	0	14	1	0	0	14	1	0	0	14	1
A. denticulata	0	0	15	0	0	0	15	0	0	0	15	0	0	0	15	0
L. peploides	0	4	11	0	0	2	13	0	0	2	13	0	0	2	13	0
M. repens	0	0	15	0	0	0	15	0	0	0	15	0	0	0	15	0
Total	9	22	97	7	3	10	109	13	1	4	115	15	1	4	115	15
Group 2																
C. cunninghamii	0	0	15	0	0	0	15	0	0	0	15	0	0	0	15	0
C. minima	0	2	13	0	0	0	15	0	0	0	15	0	0	0	15	0
P. aviculare	0	0	15	0	0	0	15	0	0	0	15	0	0	0	15	0
P. lapathifolia	0	0	15	0	0	0	15	0	0	0	15	0	0	0	15	0
P. luteo-album	0	0	15	0	0	0	15	0	0	0	15	0	0	0	15	0
R. palustris	0	0	15	0	0	0	15	0	0	0	15	0	0	0	15	0
Total	0	2	88	0	0	0	90	0	0	0	90	0	0	0	90	0
Group 3																
B. basaltica	0	8	7	0	0	6	9	0	0	0	15	0	0	0	15	0
C. pumilio	0	6	9	0	0	0	15	0	0	0	15	0	0	0	15	0
Total	0	14	16	0	0	6	24	0	0	0	30	0	0	0	30	0
Group 4																
A. semibaccata	2	2	10	1	1	1	11	2	0	0	12	3	0	0	12	3
E. dielsii	0	6	9	0	0	4	11	0	0	4	11	0	0	4	11	0
E. australis	2	6	7	0	1	3	10	1	1	3	10	1	1	3	10	1
S. diandra	0	6	9	0	0	0	15	0	0	0	15	0	0	0	15	0
X. californicum	3	4	8	0	3	2	10	0	1	2	10	2	1	2	10	2
H. curassavicum	0	3	9	3	0	3	9	3	0	3	9	3	0	3	9	3
Total	7	27	52	4	5	13	66	6	2	12	67	9	2	12	67	9
Group 5																
P. australis	9	6	0	0	9	6	0	0	5	2	4	4	3	0	6	6
C. gymnocaulos	5	4	5	1	5	4	5	1	4	3	6	2	3	1	8	3
S. quinqueflora	2	7	6	0	2	5	8	0	2	5	8	0	2	2	11	0
S. mitchellii	7	2	6	0	5	2	6	2	5	2	6	2	5	1	7	2
Total	23	19	17	1	21	17	19	3	16	12	24	8	13	4	32	11

Table 4.9. (continued).

Group 6																
J. aridicola	2	6	7	0	2	4	9	0	0	2	11	2	0	0	13	2
P. decipiens	0	4	11	0	0	0	15	0	0	0	15	0	0	0	15	0
S. validus	4	5	6	0	4	5	6	0	4	5	6	0	3	3	8	1
Total	6	15	24	0	6	9	30	0	4	7	32	2	3	3	36	3
Group 7																
M. verrucosum	0	0	15	0	0	0	15	0	0	0	15	0	0	0	15	0
T. domingensis	2	6	7	0	2	4	9	0	1	1	12	1	1	1	12	1
V. americana	0	2	12	1	0	2	12	1	0	2	12	1	0	2	12	1
Total	2	8	34	1	2	6	36	1	1	3	39	2	1	3	39	2

2 species (Table 4.9). This was accurate as none were recorded in OP.

Group 3

C. pumilio and *B. basaltica* were over-predicted in MODs 3 and 4, but the more conservative MODs 5 and 6 accurately predicted their absence at all elevations (Table 4.9).

Group 4

MOD 3 over-predicted the presence of species with seven of 34 predictions correct while MODs 5 and 6 predicted the presence of two of 14. The most accurate predictions of presence were for *X. californicum*, the least were for *E. dielsii* and *S. diandra*. The number of accurate predictions of absence was high for all species across MODs (Table 4.9). The number of predictions of presence declined for MODs 5 and 6, with *A. semibaccata*, recorded in OP at three elevations, not predicted at all.

Group 5

All MODs accurately predicted the presence of species in Group 5 more often than not; this was the only group of species for which this occurred (Table 4.9). The ratio of correct: incorrect remained at 9:6 for *P. australis* for all MODs but the source of accuracy (O_pP_p versus O_aP_a) changed from MOD 3 to MOD 6 (Table 4.9).
S. quinqueflora had the greatest increase in correct predictions from 8/15 in MOD 3 to 13/15 in MOD 6 due to the increase in O_aP_a. The presence of *S. mitchellii* was the most accurately predicted for all species.

Group 6

MOD 3 accurately predicted the presence of *J. aridicola* at two elevations in OP, but subsequent models were more accurate as fewer predictions were made of *J. aridicola*, which led to an increase in O_aP_a (Table 4.9).

All MODs performed moderately at predicting the presence of *S. validus*, with the number of accurate predictions ranging from four out of nine to three of six (Table 4.9). MOD 3 inaccurately predicted the presence of *P. decipiens* at four elevations, but the remaining MODs all accurately predicted its absence (Table 4.9).

Group 7

None of the MODs accurately predicted *V. americana*. The presence of *T. domingensis* was over predicted for MOD 3, due mainly to predictions at higher elevations (Table 4.9). Both MODs 4 and 5 predicted *T. domingensis* presence at only the lower elevations of T3, which resulted in greater overall accuracy.

4.4.6 Model predictions for functional groups at OP

Functional group water regime preferences are presented in Appendix 3.

MOD 3 predicted the presence of all functional groups across T1/2 and all bar Group 2 for T3 (Table 4.10). The widest distribution was for Groups 1 and 5. Establishment was predicted only for Group 4 at T1/2E4. While the outputs of MOD 4 were similar to MOD 3, there was a substantial reduction in the number of predictions of species presence from MOD 4 to 5 (Table 4.10).

Groups 2 and 3 were not predicted by MOD 5 or 6 and Group 7 was restricted to the lowest two elevations for T3. In contrast, Groups 1, 5 and 6 were predicted at four or more elevations (Table 4.10). In addition, MODs 4-6 consistently predicted the establishment of Group 4 species at T1/2E4 and T3E1.

4.4.7 General model accuracy for functional groups at OP

The overall accuracy was greatest for MOD 4 (70%) and lowest for MOD 6. Although MOD 3 accurately predicted a greater % of absences, MOD 4 was more accurate at predicting the presence of species (Table 4.11). The greatest discrepancy in model performance was the accuracy of predicting species absence, with the highest for MOD 3 (91%) and the lowest for MOD 6 (68%: Table 4.11).

Table 4.10. The predicted distributions of water regime preference groups for MODs 3-6 across the elevation gradient at OP. Elevations (indicated below transect/elevation code) were the same across T1 and T2 hence predictions were combined (see T1/2). Black boxes represent the presence of adults and grey boxes seedling establishment.

	T1/2E1	T1/2E2	T1/2E3	T1/2E4	T1/2E5	T3E1	T3E2	T3E3	T3E4	T3E5
MOD 3	10.43	10.25	10.07	9.89	9.73	9.92	9.74	9.71	9.56	9.50
Group 1	■	■	■	■	■	■	■	■	■	■
Group 2	■									
Group 3	■	■	■		■		■	■		
Group 4	■	■	■	■ ▨		■				
Group 5	■	■	■	■	■	■	■	■	■	■
Group 6	■			■	■	■	■	■	■	■
Group 7					■		■	■	■	■
MOD 4										
Group 1	■		■	■	■	■	■	■	■	■
Group 2										
Group 3			■		■		■	■		
Group 4		■	■	■ ▨		■ ▨				
Group 5	■	■	■	■	■	■	■	■	■	■
Group 6				■	■	■	■	■	■	■
Group 7					■		■	■	■	■
MOD 5										
Group 1				■		■			■	■
Group 2										
Group 3										
Group 4		■	■	■		■				
Group 5	■	■	■	■		■				
Group 6				■	■	■	■	■	■	■
Group 7									■	■
MOD 6										
Group 1				■		■			■	■
Group 2										
Group 3										
Group 4		■	■	■		■				
Group 5		■	■	■		■				
Group 6					■		■	■	■	■
Group 7									■	■

Table 4.11. The accuracy of the four models based on different periods of the hydrograph for groups. Each model made 105 predictions. O_p – observed present, O_a – observed absent, P_p - predicted present, P_a – predicted absent.

	MOD 3	MOD 4	MOD 5	MOD 6
O_pP_p	36	32	18	14
O_aP_p	34	24	15	13
Total predictions	70	56	33	27
% correct	51%	57%	55%	52%
O_pP_a	3	7	21	25
O_aP_a	32	42	51	53
Total predictions	35	49	72	78
% correct	91%	86%	71%	68%
Total correct	68 (65%)	74 (70%)	69 (66%)	67 (64%)
Total incorrect	37 (35%)	31 (30%)	36 (34%)	38 (36%)

4.4.8 Model accuracy for functional groups at OP

MOD 3 predicted the presence of Group 1 accurately on 11 occasions. MODs 4-6 made fewer accurate predictions of presence and along with an increase in the predictions of absence, which were mostly incorrect, resulted in a decline in overall accuracy (Table 4.12).

Group 2 was never present in OP and this was accurately predicted by MODs 4-6 (Table 4.12). Group 3 was present at only one elevation, which was predicted for MODs 3 and 4, although this coincided with a high number of over predictions (Table 4.12).

All MODs predicted the presence and absence of Group 4 more accurately than inaccurately, with MOD 3 the most accurate (Table 4.12). The greatest number of accurate predictions of presence for Group 5 was by MODs 3 and 4 (Table 4.12). MODs 5 and 6 were more conservative and made more predictions of absence, resulting in a reduction in overall accuracy.

MOD 3 was least accurate in predicting presence and absence for Group 6 (Table 4.12). MODs 4 and 5 accurately predicted presence and absence four and five times,

Table 4.12. Predictions of species presence for MODs 3-6. The maximum score for a group in a model is 15 (3 transects × 5 elevations). O_p – observed present, O_a – observed absent, P_p - predicted present, P_a – predicted absent.

	MOD 3				MOD 4				MOD 5				MOD 6			
	O_pP_p	O_aP_p	O_aP_a	O_pP_a	O_pP_p	O_aP_p	O_aP_a	O_pP_a	O_pP_p	O_aP_p	O_aP_a	O_pP_a	O_pP_p	O_aP_p	O_aP_a	O_pP_a
Group 1	11	4	0	0	9	4	0	2	2	3	1	9	2	3	1	9
Group 2	0	2	13	0	0	0	15	0	0	0	15	0	0	0	15	0
Group 3	1	9	5	0	1	5	9	0	0	0	14	1	0	0	14	1
Group 4	6	4	4	1	4	4	4	3	4	4	4	3	4	4	4	3
Group 5	12	3	0	0	12	3	0	0	8	2	1	4	6	2	1	6
Group 6	4	7	3	1	4	5	5	1	4	5	5	1	2	3	7	3
Group 7	2	5	7	1	2	3	9	1	0	1	11	3	0	1	11	3

respectively, compared to MOD 6 that accurately predicted presence and absence two and seven times respectively.

For Group 7, MOD 3 predicted presence and absence accurately on nine occasions, compared to the remaining MODs with 11 correct. The source of accuracy (O_pP_p vs. O_aP_a) changed between MOD 4 and 5 with the former making more predictions of presence than the latter (Table 4.12).

4.4.9 Accuracy of species versus groups predictions

Predictions for species and groups did not differ for Group 2 and 3 species (Table 4.13).

The greatest difference in accuracy was for the prediction of absences of Group 1 species which ranged from 93 to 88% for MOD 3 to MOD 6 for species predictions but did not exceed 10% for group predictions (Table 4.13).

Species predictions of presence for Group 5 and 6 species increased from MODs 3 to 6 but remained approximately the same for group predictions (Table 4.13). For Group 7, species predictions of presence remained approximately the same whereas group predictions declined from 29 to 0% (Table 4.13).

The only major difference in change of absences was for Group 4, where species predictions remained constant but group predictions declined from 80 to 57%.

4.5 Discussion

4.5.1 Model performance

The accuracy of model predictions when tested using the hydrograph and floristic composition of Old Petes was greater for species (76-86%) than functional groups (64-74%). The difference in accuracy was influenced mostly by predictions of absence for Group 1, that were 88-93% accurate (O_aP_a) across all MODs for species predictions, compared to 0 to 10% for groups. In addition, species predictions for Groups 5 and 6 had a much greater increase in accuracy for predictions of presence O_pP_p as the length of hydrograph increased.

For species predictions, the model became more conservative as the length of hydrograph increased, with MOD 3 through to MOD 6 making progressively fewer predictions of species presence and more of absence. As a result the proportion of predictions of presence that were correct increased making MOD 6 the most accurate. The overall accuracy of the model was attributable more to correct predictions of absence. This implies that by using the water regime preferences it is easier to predict where a plant will not persist, rather than where it will.

Using a shorter length of hydrograph led to more predictions of annual species, which tolerate shorter periods of flood and drawdown. As the length of hydrograph increased, predictions were restricted more to perennial species capable of tolerating extended periods of flood and drawdown. This improved the accuracy of the model as few annuals were recorded in OP. Over-prediction of annuals is one of the weaknesses of the model.

Some perennial species were still filtered out by the hydrograph, these were species that favour an equivalent number of days flooded and drawndown e.g. *B. caldwellii* and *P. distichum*. In contrast, the perennial species whose presence was accurately predicted and observed in the wetland were those either tolerant of long periods of dry with short periods of wet (e.g. *C. gymnocaulos*, *S. quinqueflora* and *S. mitchellii*) or short periods of dry and long periods of wet (*S. validus* and *T. domingensis*) and were found at higher and lower elevations respectively.

Table 4.13. The percentage of correct predictions for each MOD is presented for presence and absence. The upper half of the table relates to species predictions, summarised into groups and is based on the results from Table 4.9. The bottom half of the table relates to group predictions and is based on the data presented in Table 4.12. Data is absent where all predictions and observations were entirely of presence or absence.

	MOD 3				MOD 4				MOD 5				MOD 6			
	O_pP_p	O_aP_p	O_aP_a	O_pP_a	O_pP_p	O_aP_p	O_aP_a	O_pP_a	O_pP_p	O_aP_p	O_aP_a	O_pP_a	O_pP_p	O_aP_p	O_aP_a	O_pP_a
Species																
Group 1	0.29	0.71	0.93	0.07	0.23	0.77	0.89	0.11	0.20	0.80	0.88	0.12	0.20	0.80	0.88	0.12
Group 2	0.00	1.00	1.00	0.00			1.00	0.00			1.00	0.00			1.00	0.00
Group 3	0.00	1.00	1.00	0.00	0.00	1.00	1.00	0.00			1.00	0.00			1.00	0.00
Group 4	0.21	0.79	0.93	0.07	0.28	0.72	0.92	0.08	0.14	0.86	0.88	0.12	0.14	0.86	0.88	0.12
Group 5	0.55	0.45	0.94	0.06	0.55	0.45	0.86	0.14	0.57	0.43	0.75	0.25	0.76	0.24	0.74	0.26
Group 6	0.29	0.71	1.00	0.00	0.40	0.60	1.00	0.00	0.36	0.64	0.94	0.06	0.50	0.50	0.92	0.08
Group 7	0.20	0.80	0.97	0.03	0.25	0.75	0.97	0.03	0.25	0.75	0.95	0.05	0.25	0.75	0.95	0.05
Groups																
Group 1	0.73	0.27			0.69	0.31	0.00	1.00	0.40	0.60	0.10	0.90	0.40	0.60	0.10	0.90
Group 2	0.00	1.00	1.00	0.00			1.00	0.00			1.00	0.00			1.00	0.00
Group 3	0.10	0.90	1.00	0.00	0.17	0.83	1.00	0.00			0.93	0.07			0.93	0.07
Group 4	0.60	0.40	0.80	0.20	0.50	0.50	0.57	0.43	0.50	0.50	0.57	0.43	0.50	0.50	0.57	0.43
Group 5	0.80	0.20			0.80	0.20			0.80	0.20	0.20	0.80	0.75	0.25	0.14	0.86
Group 6	0.36	0.64	0.75	0.25	0.44	0.56	0.83	0.17	0.44	0.56	0.83	0.17	0.40	0.60	0.70	0.30
Group 7	0.29	0.71	0.88	0.13	0.40	0.60	0.90	0.10	0.00	1.00	0.79	0.21	0.00	1.00	0.79	0.21

All MODs made predictions of establishment, but only via Scenario 4. The section of hydrograph used for MOD 3 encountered only one period where water levels were elevated above the normal operational pool level (early February 2001). This resulted in the predicted establishment of *E. australis*, *H. curassavicum*, *S. diandra* and *X. californicum*. Another flood that occurred in late December was within the hydrograph of MODs 4-6 and also engaged ESTAB 4, but only led to the prediction of two species, *H. curassavicum* and *X. californicum*.

Of all the species for which establishment was predicted, only seedlings of *X. californicum* were recorded in survey transects in OP. It was not possible to determine which flood event triggered germination given that survey dates were either side of the two floods (mid-December 2000 and March 2001). Seedlings of *H. curassavicum* were also observed, but outside the area of surveyed transects. This suggests that factors other than water regime, such as dispersal, may influence the species that establish.

For group predictions, a four month segment of hydrograph (MOD 4) was most accurate because of high accuracy for predictions of absence (86%) and the most accurate predictions of group presence (57%). The number of correct predictions increased for Groups 2, 3, 6 and 7 with an increase in the length of hydrograph, but decreased for Groups 1, 4 and 5. This pattern does not represent a trend for perennial and/or annual species or those more or less tolerant of flood or drawdown.

The use of 'functional groups' is common for describing groups of species with similar environmental tolerances or life history strategies (Noble and Slatyer 1980; Boutin and Keddy 1993; Brock and Casanova 1997) and has been proposed as a useful method for predicting change in community structure (Noble and Gitay 1996). Summarising species water regime preferences to construct functional group preferences appeared to reduce the sensitivity of the model to individual species. This was demonstrated for Group 1 in MOD 3, where three species were unable to tolerate the water regime experienced across all elevations (as predicted by species predictions), yet functional group predictions suggested that Group 1 would occupy every elevation.

4.5.2 Limitations, assumptions and proposed modifications to the model

The accuracy of the model is influenced by the accuracy of species water regime preferences. Intuitively, the more observations that preferences are based on, both spatially and temporally, the more accurate they should be. However, this was not evident from the results of this analysis, where species with preferences based upon a high number of observations (e.g. *C. gymnocaulos* and *P. australis*) were not predicted anymore accurately than those based on a low number of observations (e.g. *A. semibaccata* and *S. diandra*).

The model used the 75-percentile to describe the days tolerated by species within each water regime indice and thus characterise the water regime preference. This value was chosen as an estimate of the upper tolerance limits of plants. However, to determine if this is the best estimate of species tolerances, other estimates of tolerance should be trialled e.g. median up to maximum days spent in each water regime indice.

Another check of the validity of the water regime preferences would be to recalculate indices using different depth ranges. Other studies have described water regime using depth ranges with 5 cm (Brownlow *et al.* 1994) through to 20-100 cm intervals (Blanch *et al.* 1999b). Investigation of narrower depth intervals about 0 cm may yield more accurate predictions for annual species that are low growing and presumably more sensitive to depths from 0 to 20 cm.

There were a number of examples where the model inaccurately predicted the water regimes known to be tolerated by a species. For example, *V. americana* was observed in OP at elevations flooded for at least 6 months from 0 to 20 cm, yet the model predicted it could tolerate only 51 days in this depth range. This result is a function of wetland monitoring not intercepting elevations flooded from 0-20 cm where mature *V. americana* occurred.

The water regime preferences for the model assume that there is no difference in the depth tolerated by mature versus juvenile plants. Although this assumption is invalid for tolerance to a number of water regime indices, especially those relating to deep flooding, it was accepted because of the lack of data relating to the water regime tolerances of seedlings. The response of developing plants is also influenced by whether the initial propagule was a seed or portion of a perennating organ. Hence, the model would benefit from more intensive monitoring of establishment or experimental studies to examine the success of establishment from sexual versus vegetative propagules.

Establishment requirements were deduced from observations made during repeated sampling. The establishment rules undoubtedly under-predicted the range of conditions under which species could establish in the field because a limited number of observations of establishment were made. For example, the model predicts that *A. subulatus* can only establish on the bed of wetlands during drawdown because this was the only location at which establishment was observed. Yet at OP it was growing above the height of where water levels peaked suggesting that it can establish at times other than during drawdown e.g. following rainfall.

One pre-requisite for establishment was that temperature in the ACTIVE period was > 20°C for 75% of the time, which in practice prevented establishment during winter months. However, the rule does allow gemination to proceed in summer months. This is in contrast to the conclusions of Britton and Brock (1994) who found that germination of wetland seed banks from northern New South Wales, Australia, was restricted most by summer conditions. A rule for maximum temperatures was not included because monitoring recorded establishment of at least some plants during summer months. Controlled, experimental studies would prove useful in further eliciting the temperature and moisture conditions under which plants from the species pool germinate.

Measurements of accuracy were based entirely upon the proportion of true compared to total predictions and allowed for a comparison of the relative accuracy of the four MODs. Another method of measuring the accuracy of the model would be to use various statistical approaches, such as contingency tables.

4.5.3 Applicability of the model

The accuracy of the model is likely to change when applied to wetlands subject to drawdown because the opportunity for annuals to establish is greater. The response of annuals to drawdown is generally difficult to predict because numerous species can colonise and survive the moist conditions present during the initial stages of drawdown. As such, composition is driven more by dispersal and colonisation (Seabloom *et al.* 1998; Seabloom *et al.* 2001) and seedling recruitment (Poiani and Johnson 1993; Leck and Simpson 1995). A trial using data from a wetland subject to drawdown is the next stage in the development of this model.

Although the model is based upon species from the Lower Murray, the design should be applicable to wetlands from other regulated river systems or from aquatic systems where water levels lack variability (e.g. lakes). A hydrograph of six months in length should prove to be generally useful in differentiating the response of annual from perennial species. Underlying such an application would be the calculation of water regime preferences based upon the same depth ranges used in this study. Although the depth ranges were selected with Lower Murray species in mind they should also be appropriate for wetland species from elsewhere in the world.

Figure 4.1. Engagement of the different establishment scenarios in Step 2 of the model: Scenario 2 – ESTAB 2; Scenario 3 – ESTAB 3; Scenario 4 - ESTAB 4.

The hydrograph for each elevation was divided into wet (water level above the sediment surface) and dry (water level below the sediment surface) periods. On the flow diagram of the model (opposite page) wet periods are indicated by circled odd numbers and dry periods by circled even numbers. ① > 0 indicates that the initial period is wet. If ① = 0 and ② > 0, then the initial period is dry. Combinations of wet and dry periods can engage an establishment scenario provided fluctuations are ≥ 20 cm.

For example, to engage ESTAB 2 requires a wet period followed by a dry period e.g. ① > 0, ② > 0, ① = 0. If this combination occurs, then the rules for ESTAB 2 are applied i.e. temperature, the duration of the wet and dry periods.

If the rules of the scenario are adhered to, as indicated by Y, then the species that may establish under that scenario (Table 4.2) are subjected to the same procedure outlined for Step 1. If the rules are not adhered to then no establishment may occur and the model only operates according to Step 1.

The model can tolerate 5 wet and 5 dry periods, i.e. up to ⑨ and ⑩. The dashed line leading to **A** and **B** indicate a continuation of alternating wet and dry periods beyond ⑤ and ⑥. The possible outcomes illustrated in the boxes (dashed outline) on the left and right side of the diagram indicates what would follow at points **A** and **B** respectively.

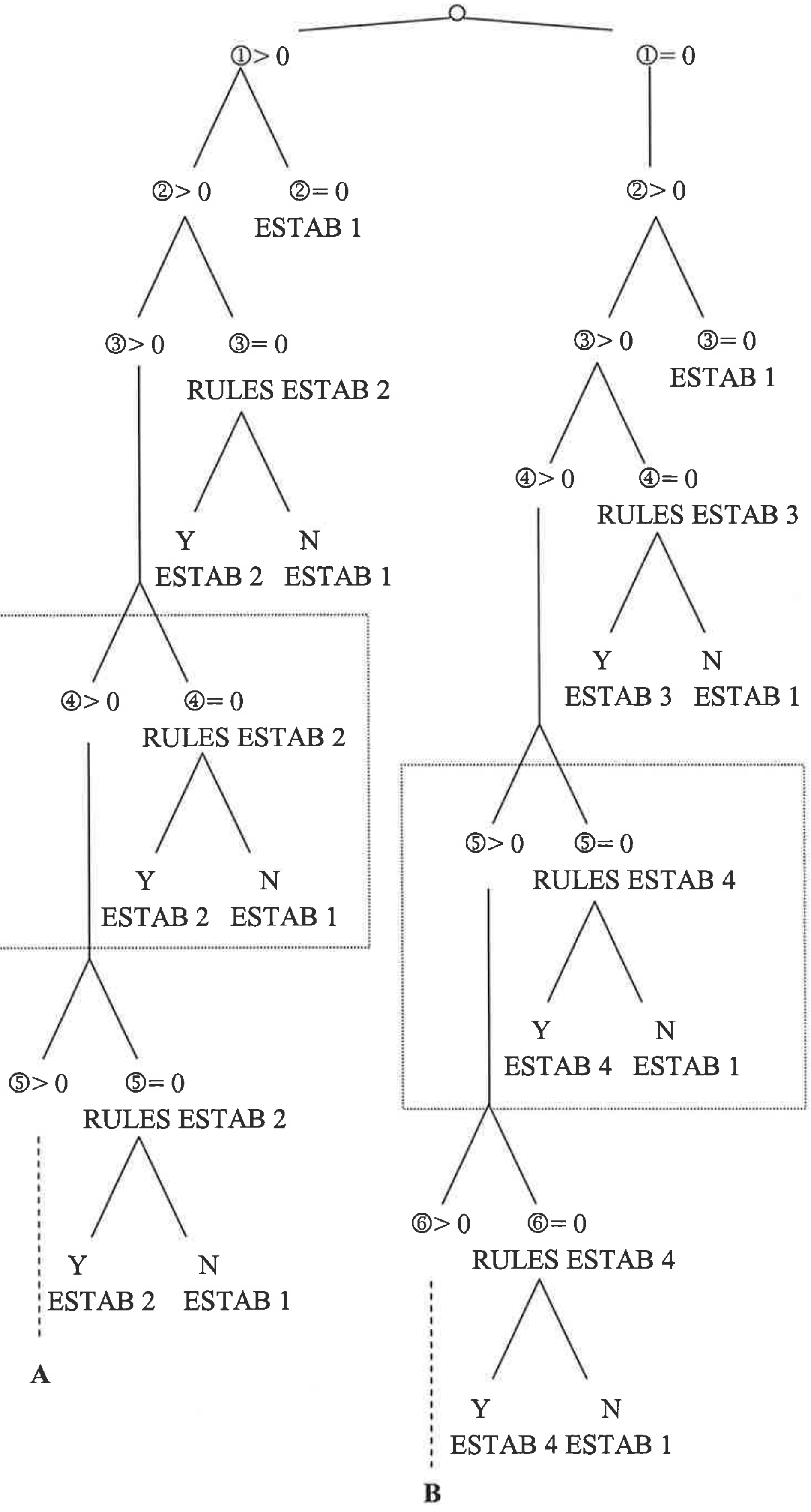

①> 0
①= 0
②> 0
②= 0
ESTAB 1
②> 0
③> 0
③= 0
RULES ESTAB 2
Y
N
ESTAB 2
ESTAB 1
③> 0
③= 0
ESTAB 1
④> 0
④= 0
RULES ESTAB 3
Y
N
ESTAB 3
ESTAB 1
④> 0
④= 0
RULES ESTAB 2
Y
N
ESTAB 2
ESTAB 1
⑤> 0
⑤= 0
RULES ESTAB 4
Y
N
ESTAB 4
ESTAB 1
⑤> 0
⑤= 0
RULES ESTAB 2
Y
N
ESTAB 2
ESTAB 1
A
⑥> 0
⑥= 0
RULES ESTAB 4
Y
N
ESTAB 4
ESTAB 1
B

Figure 4.2. Cluster analysis of species based on water regime preferences for the ten water regime indices. Seven groups were identified. Species codes are based on the first three letters of the genus and specific epithet (see Appendix 1 for full species names).

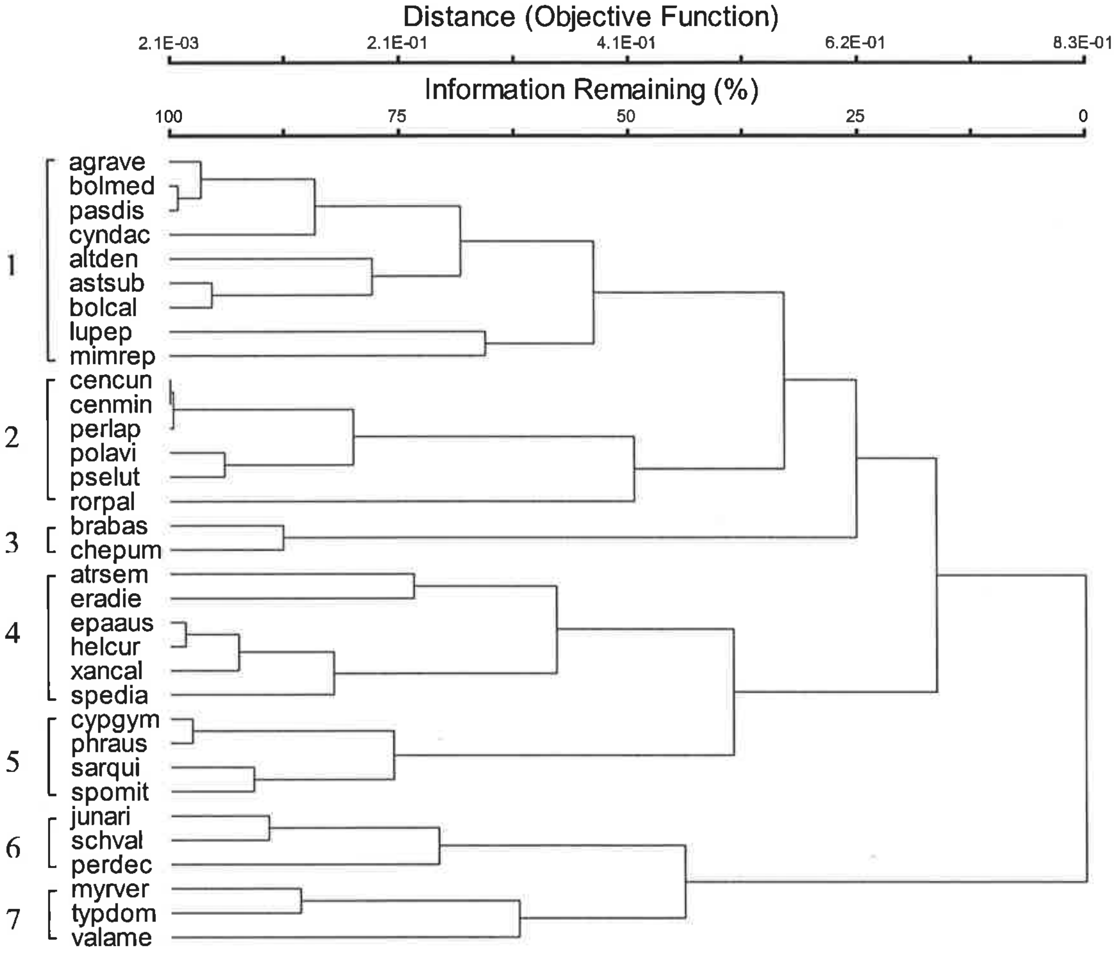
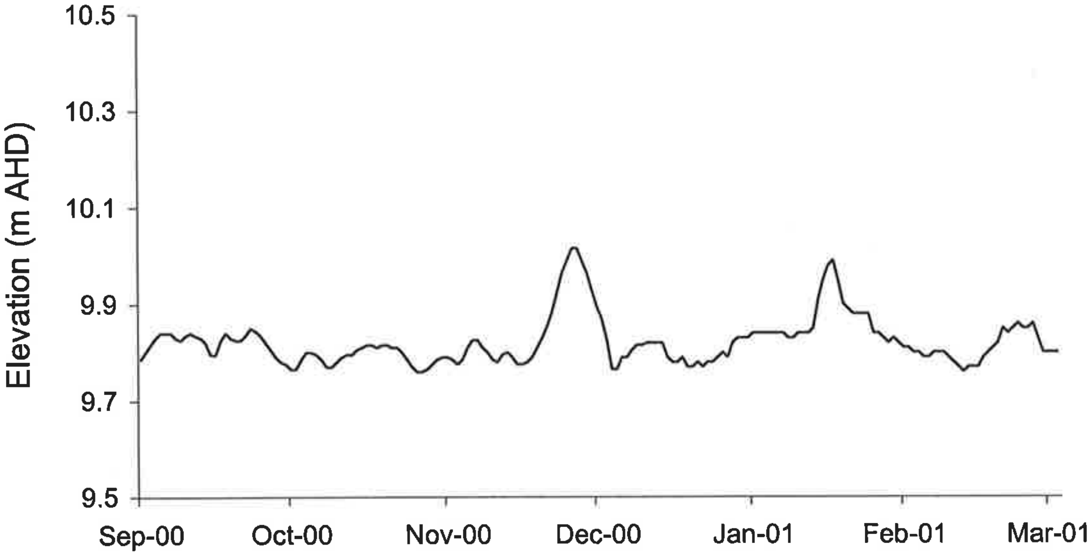

Distance (Objective Function)
2.1E-03
2.1E-01
4.1E-01
6.2E-01
8.3E-01
Information Remaining (%)
100
75
50
25
0
1
agrave
bolmed
pasdis
cyndac
altden
astsub
bolcal
lupep
mimrep
2
cencun
cenmin
perlap
polavi
pselut
rorpal
3
brabas
chepum
4
atrsem
eradie
epaaus
helcur
xancal
spedia
5
cypgym
phraus
sarqui
spomit
6
junari
schval
perdec
7
myrver
typdom
valame

Figure 4.3. The hydrograph at Old Petes from 1 September 2000 to 31 March 2001. Water levels are regulated by weir operations at Lock 3 (data supplied by B. Porter, SA Water).


Elevation (m AHD)
10.5
10.3
10.1
9.9
9.7
9.5
Sep-00
Oct-00
Nov-00
Dec-00
Jan-01
Feb-01
Mar-01

CHAPTER 5

EFFECTS OF AN ENHANCED FLOOD ON RIPARIAN PLANTS

5.1 Abstract

In October 2000, the flow of the River Murray entering South Australia was increased from 32,000 to 42,050 ML d^{-1} by release of water from an offstream reservoir, and a downstream weir was raised by 500 mm to impound the flood and enhance local floodplain inundation. The flood was maintained for about two weeks, although the duration of inundation was longer at low elevations on the floodplain. Vegetation at three sites was surveyed before and after the flood to examine the impact of inundation on the growth and germination of flood-tolerant, flood-dependent and flood-intolerant species. Among 32 recorded species, *Atriplex vesicaria* (bladder saltbush, Chenopodiaceae), *Sporobolus mitchellii* (rats tail couch, Graminae) and *Sarcocornia quinqueflora* (samphire, Chenopodiaceae) accounted for nearly 82% of the total cover/abundance. Flood-tolerant and flood-dependent species (e.g. *S. mitchellii*) grew and germinated and flood-intolerant species (e.g. *A. vesicaria*) senesced. No aquatic plants germinated or established, despite favourable conditions, suggesting an impoverished seed bank or grazing. Based on the growth but lack of germination of flood-tolerant and dependent species, the value of small, occasional interventions in environmental flow management may be to maintain existing communities rather than restore degraded ones.

5.2 Introduction

Flooding promotes the growth and reproduction of some riparian plants (e.g. Lenssen *et al.* 2000; Robertson *et al.* 2001) and activates the sexual and asexual propagules of aquatic and semi-aquatic species (Brock and Rogers 1998; Casanova and Brock 2000). It may also eliminate flood-intolerant species that have colonised the floodplain during dry periods (e.g. van der Valk and Davis 1976). The balance between these responses is influenced by the depth, duration, frequency and timing of wetting and drying (e.g. Rea and Ganf 1994; Blanch *et al.* 1999; Nicol and Ganf 2000).

The floodplain of the River Murray once experienced regular periods of wetting and drying associated with a naturally variable flow regime (e.g. Maheshwari *et al.* 1995), but over the last 100 years regulation and diversions have markedly changed the frequency, duration, magnitude and timing of river flows (e.g. Walker 1992; Walker and Thoms 1993). These changes have adversely affected the flora and fauna (e.g. Blanch *et al.* 1999, 2000; Walker 2001), and state and federal governments are actively promoting environmental flow management as a strategy to maintain and restore habitats. One such initiative occurred in October 2000, when the South Australian Department for Water, Land and Biodiversity Conservation (DWLBC) negotiated a flow release from Lake Victoria, an offstream water storage in New South Wales, to augment a natural high flow in the Murray entering South Australia. To prolong the flood and increase the area and depth of floodplain inundation, albeit in a restricted area, a 3 m weir on the Murray at Lock 5 (near Renmark, South Australia) was raised by 500 mm for about two weeks. The area had not been flooded for four years.

I anticipated that the enhanced flood would promote the growth and germination or sprouting of propagules of a variety of flood-tolerant and flood-dependent species, and that the responses would be greatest at those elevations flooded deepest and for longest. In contrast, flood-intolerant species were expected to senesce or die. This chapter focuses on describing the status of three dominant species during and after the recession of the flood, and considers the moderating effects of the depth and duration of flooding and other abiotic and biotic factors. In addition, the value of the enhanced flood as a model for future trials is considered.

5.3 Methods

5.3.1 Sites and sampling

The study region has a semi-arid climate with an annual average rainfall 250 mm y^{-1} and an average annual potential evaporation 2000 mm y^{-1} (Jolly *et al.* 1993). The floodplain soil is alluvial grey cracking clay up to 5 m deep (Hollingsworth *et al.* 1990).

Three sites were selected to represent the flooded area (Figure 5.1): two at Bulyong Island (Ninkle Nook, NN: 480000 E, 6225000 N; Jane Eliza, JE: 478500 E, 6220500 N) and one at Reny Island (Wide Waters, WW: 475000 E, 6230500 N). Wide Waters is adjacent to Ral Ral Creek, an anabranch of the Murray, and is influenced by weir manipulations at Lock 5. The likely extent of the flood at each site was predicted by a local natural resources manager (M. Harper, Australian Landscape Trust, Renmark, pers. comm.).

At each site, three transects were established perpendicular to the river and 100 m apart (thus, transects T1-T3 at NN, T4-T6 at JE, T7-T9 at WW). On each transect, 5×1 m quadrats (five contiguous 1×1 m 'cells') were placed at five elevations (see section 5.3.2). E1 was located just above the predicted maximum flood height, E5 at the lowest elevation that would be submerged, and E2-E4 at 25, 50 and 75%, respectively, of the difference between E1 and E5. Intermediate elevations were determined using a theodolite. Each site therefore was represented by single quadrats at five elevations on three transects.

Surveys were conducted prior to the flood (8-10 October 2000) and after recession (8-10 November 2000, 3-5 December 2000, 5-7 February 2001). The sites were visited also on 24 October 2000, seven days after the flood peak, but no plant responses were evident.

Plant cover in each quadrat was visually assessed and scored from 0-6, where 0 = absent, 1 = rare and 6 = continuous cover (Blanch *et al.* 1999). Species were identified following Jessop and Toelken (1986) and classified as 'flood-tolerant', 'flood-dependent' or 'flood-intolerant' (cf. Sainty and Jacobs 1994; Brock and Casanova 1997).

Incidental measurements of soil conductivity and pH were made in 1:5 suspensions of air-dried soil samples (surface 15 cm) in deionised water (Rayment and Higginson 1992). Measurements were made for all elevations at WW in the pre-flood, November and December surveys.

5.3.2 Water regime

River height (m AHD = Australian Height Datum) was monitored using Dataflow 392 loggers attached to 0-5 m differential pressure sensors and 3 m capacitance probes located in the river near each site. Water levels at each site were measured by sensors from 5 October to 7 November 2000 (JE) or 1 December (NN, WW), or otherwise estimated from backwater curves (longitudinal profiles of water surface elevation in relation to discharge) and daily river heights recorded at Lock 5. At the flood peak, depths across the floodplain were recorded and combined with the known river height to determine the actual heights of the sampling elevations. These data were combined with site hydrographs to indicate water level fluctuations and 10 water regime classes (above: 0, 5, 10, 20 and 40 cm; below: 0, -5, -10, -20 and -40 cm). At JE, floodplain topography prevented surface outflow from E2-E5, so that water there must have receded due to evaporation and seepage. Net evaporation was recorded at Lock 5 (data supplied by B. Porter, SA Water). No data were available for seepage rates.

5.3.3 Analysis

As three of 32 recorded plant species accounted for 78% of total cover, and all but one of the remainder had scores < 2%, ordination analysis was precluded. Rather, scores for the dominant species at each site were compared by ANOVA (factors elevation and time, transects as randomized blocks; no replication). One of the three transects at JE proved to have a different flooding regime from its two neighbours and was excluded from analysis. Missing data (T2 in the first survey, E3 at T3 and E5 at T8 in the second survey) caused the analytical program (SPSS for Windows 11.0.1: SPSS Inc., Illinois) to substitute approximate values (fractional degrees of freedom).

5.4 Results

5.4.1 Flood hydrograph

The diversion from Lake Victoria increased flow in the Murray from 32,000 to 42,050 ML d^{-1} (DWLBC 2001), and the raised weir at Lock 5 ensured that the flood peak covered about 11% of the floodplain (924 ha) between Locks 5-6 (I. Overton, CSIRO Land and Water, pers. comm.). Under normal operating conditions, this requires a flow of 70,000 ML d^{-1}. The flooded reach is little affected by levees or flood runners, so that rates of rise and fall were governed mainly by the slope of the floodplain.

From 6 October, the weir pool rose at 3 cm d^{-1} above its normal level of 16.3 m AHD, and was maintained above 16.7 m AHD for 11 days (Figure 5.2). The river level peaked at 16.8 m AHD on 17 October, and flow peaked at 42,300 ML d^{-1} on 18 October. The river thereafter receded at 3 cm d^{-1} and returned to pool level on 5 November. To ease pressure on the weir at Lock 5, the weir at Lock 4, 47 km downstream, was raised by 400 mm for the duration.

The lowest elevations at NN and WW were flooded for 31 days. At JE there was surface water at all elevations, but receding water in some areas was trapped in depressions and flooding persisted for up to 90 days. Table 5.1 shows the periods when the water level was within intervals above and below the sediment surface.

The Murray rose again in December 2000 (Figure 5.2). This second flood (peak 45,914 ML d^{-1}) was larger than the enhanced flood, but flooding was limited to the lower elevations at NN and WW because the weir at Lock 5 was not raised.

5.4.2 Plant responses

Prior to the flood, *Atriplex vesicaria* (bladder saltbush, Chenopodiaceae), *Sporobolus mitchellii* (rats tail couch, Gramineae) and *Sarcocornia quinqueflora* (samphire, Chenopodiaceae) accounted for 82% of total cover among 32 recorded species (Appendix 4). Seven days after the flood peak (17 October 2000) there were no seedlings or other apparent responses within quadrats, although flooded *A. vesicaria* lost some leaves and shoots from rhizomes of *Eleocharis acuta* (common spike rush, Cyperaceae) occurred between elevations E4–E5 at NN. In post-flood surveys, the same three species were predominant and *Wilsonia rotundifolia* (round-leaved wilsonia, Convolvulaceae) occurred sporadically (5.9% of total cover).

Ninkle Nook

At its peak, the flood at NN inundated the lowest quadrats (E4 0.19 m, E5 0.42 m) and approached the sediment surface at E3 (-0.04 m). Water levels remained below the sediment surface at E1 (-0.50 m) and E2 (-0.27 m) (Table 5.1). Only E5 was re-wetted in December. *S. quinqueflora* was absent at this site.

There was a significant interaction between elevation and time for the response of *S. mitchellii* at NN (Table 5.2). This arose because plants lower on the elevation gradient (E3-E5) increased their median score by 1 when there was no change at E2

Table 5.1. Numbers of days when water was above or below the sediment surface at five elevations (E1–E5) at three floodplain sites (Ninkle Nook, NN; Jane Eliza, JE; Wide Waters, WW), from 1 October 2000 to 12 February 2001 (135 days). Topography at JE precluded some estimates.

Site: Elevation	Days Above					Days Below				
	0 cm	5 cm	10 cm	20 cm	40 cm	0 cm	5 cm	10 cm	20 cm	40 cm
NN:E1	0	0	0	0	0	135	135	135	135	135
NN:E2	0	0	0	0	0	135	135	135	135	122
NN:E3	0	0	0	0	0	135	133	126	121	99
NN:E4	14	13	10	0	0	121	115	110	94	53
NN:E5	44	36	29	18	3	91	83	75	53	27
JE:E1	14	11	7	0	0	121	120	117	109	70
JE:E2	48	46	39	10	0	87	...	...	...	...
JE:E3	61	59	52	40	0	74	...	...	...	...
JE:E4	75	71	66	53	14	60	...	...	...	...
JE:E5	90	89	81	66	41	45	...	...	...	...
WW:E1	0	0	0	0	0	135	135	135	128	115
WW:E2	0	0	0	0	0	135	128	125	120	92
WW:E3	13	10	7	0	0	122	121	115	104	67
WW:E4	25	20	14	10	0	110	104	94	79	50
WW:E5	49	40	30	19	5	86	80	68	53	11

and a reduction in cover at E1 (Table 5.3). The effect at E1 was due to grazing by grey kangaroos (*Macropus giganteus*).

The response of *A. vesicaria* was also influenced by the interaction between time and elevation (Table 5.2). This was reflected in October and February by losses of cover at E4-E5, but a stable score at E3 (Table 5.3). At E5, the median score of 3 before inundation fell to 0 in February, although scores were not zero in all quadrats because some seeds germinated after the flood's recession. At E1-E2, kangaroos again caused an apparent decline.

Jane Eliza

At JE, all elevations were flooded (Table 5.1). E1 was flooded to > 10 cm for seven days and E5 was flooded to > 20 cm for 66 days. At this site, time had a significant

Table 5.2. Analyses of variance in cover of the three plant species at each site (Ninkle Nook, NN; Jane Eliza, JE; Wide Waters, WW). The decimal degrees of freedom (df) for site NN are approximations produced by SPSS for Windows to overcome missing data (T2 in the first survey, E3 at T3 and E5 at T8 in the second survey). The analysis for *S. quinqueflora* at site WW also was affected by missing data, but the values for df remain as integers.

Site	Source	*A. vesicaria*		*S. quinqueflora*		*S. mitchellii*	
		F (df)	*P*	*F* (df)	*P*	*F* (df)	*P*
NN	Elevation	9.27 (4,7.9)	0.002	...	...	12.10 (4,7.9)	0.002
	Time	33.95 (3,4.8)	0.001	...	...	4.50 (3,4.9)	0.071
	Elevation×Time	2.35 (12,19)	0.047	...	...	2.44 (12,19)	0.040
JE	Elevation	0.19 (4,4)	0.933	0.38 (4,4)	0.815	0.656 (4,4)	0.653
	Time	52.43 (3,3)	0.004	9.48 (3,3)	0.049	16.83 (3,3)	0.022
	Elevation×Time	0.14 (12,12)	0.999	0.43 (12,12)	0.921	0.68 (12,12)	0.746
WW	Elevation	3.56 (4,8)	0.060	0.46 (4,8)	0.764	4.25 (4,8)	0.039
	Time	4.31 (3,6)	0.061	2.79 (3,6)	0.127	6.51 (3,6)	0.026
	Elevation×Time	2.31 (12,24)	0.039	1.72 (12,23)	0.127	3.03 (12,24)	0.010

Table 5.3. Median cover (range 0-6; 25-75 percentiles in parentheses) of *S. mitchellii* and *A. vesicaria* at five elevations (E1-E5) at Ninkle Nook.

		E1	E2	E3	E4	E5
S. mitchellii	October	1 (0-2)	2 (2-2)	3 (2-3)	3 (3-3)	2 (2-2)
	November	1 (0-2)	2 (2-3)	3 (2-3)	3 (2-4)	2 (2-3)
	December	0 (0-1)	2 (1-2)	4 (3-4)	3 (2-4)	3 (2-3)
	February	0 (0-1)	2 (1-3)	4 (3-4)	4 (3-5)	3 (2-4)
A. vesicaria	October	3 (3-4)	3 (3-3)	0 (0-1)	1 (1-1)	3 (3-3)
	November	3 (2-3)	2 (2-2)	0 (0-1)	1 (0-1)	0 (0-1)
	December	2 (2-3)	2 (1-2)	0 (0-0)	1 (0-2)	0 (0-1)
	February	2 (2-2)	2 (1-2)	0 (0-0)	0 (0-1)	0 (0-1)

effect on the responses of the three species (Table 5.2), and depth and duration did not. *S. mitchellii* responded positively, especially at E3, where the median score rose from 1 to 3, and at E5. The status of plants at E2 in February was less variable than prior to the flood, suggesting that some grew after the recession (Table 5.4). Plants at

Table 5.4. Median cover (range 0-6; 25-75 percentiles in parentheses) of *S. mitchellii*, *A. vesicaria* and *S. quinqueflora* at five elevations (E1-E5) at Jane Eliza.

		E1	E2	E3	E4	E5
S. mitchellii	October	3 (1-3)	1 (0-3)	1 (0-3)	2 (1-5)	0 (0-0)
	November	3.5 (2-4)	1.5 (0-3)	1.5 (0-3)	1 (0-2)	0 (0-0)
	December	3 (2-4)	1.5 (1-3)	2 (1-3)	3 (3-3)	0 (0-1)
	February	3 (2-4)	3 (2-3)	3 (2-4)	3.5 (3-4)	1 (0-2)
A. vesicaria	October	0.5 (0-1)	1 (1-1)	0.5 (0-1)	0 (0-2)	1 (0-1)
	November	0 (0-0)	0.5 (0-1)	0 (0-0)	0 (0-0)	0 (0-0)
	December	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)
	February	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)
S. quinqueflora	October	0.5 (0-1)	0 (0-2)	1.5 (0-5)	0.5 (0-1)	2 (0-2)
	November	0 (0-1)	0 (0-2)	1.5 (0-4)	0 (0-0)	0 (0-2)
	December	0 (0-0)	0 (0-1)	1.5 (0-3)	0 (0-1)	0 (0-1)
	February	0 (0-1)	0 (0-2)	1 (0-3)	0 (0-0)	0 (0-0)

Table 5.5. Median cover (range 0-6; 25-75 percentiles in parentheses) of *S. mitchellii*, *A. vesicaria* and *S. quinqueflora* at five elevations (E1-E5) at Wide Waters.

		E1	E2	E3	E4	E5
S. mitchellii	October	2 (0-2)	3 (1-3)	2 (1-2)	0 (0-0)	-
	November	2 (0-2)	2 (1-3)	2 (2-3)	0 (0-0)	-
	December	2 (0-3)	2 (0-3)	2 (2-2)	0 (0-0)	-
	February	1 (0-2)	2 (0-2)	2 (2-3)	0 (0-0)	-
A. vesicaria	October	0 (0-1)	1 (0-1)	1 (0-1)	0 (0-0)	-
	November	0 (0-1)	0 (0-1)	0 (0-0)	0 (0-0)	-
	December	0 (0-1)	0 (0-1)	0 (0-0)	0 (0-0)	-
	February	0 (0-1)	0 (0-1)	0 (0-0)	0 (0-0)	-
S. quinqueflora	October	1 (0-2)	1 (0-2)	1 (1-2)	3 (2-3)	2 (2-3)
	November	0 (0-1)	2 (0-2)	1 (0-2)	1 (0-2)	0 (0-2)
	December	1 (0-1)	1 (0-2)	1 (0-2)	1 (0-2)	0 (0-2)
	February	1 (0-2)	1 (0-2)	1 (0-1)	1 (0-2)	0 (0-1)

E4-E5 did not respond until December. *A. vesicaria* declined at all elevations (Table 5.4). Reductions in cover of *S. quinqueflora* were greatest at E5, followed by E3 and E4.

Wide Waters

The flood hydrograph at WW was more like that at NN than at JE, as not all elevations were inundated (Table 5.1). Elevation E1 was the only elevation to remain dry; water rose to the sediment surface at E2 and E3-E5 were all submerged. E4-E5 were flooded again in December. *S. mitchellii* was sparse at this site. There was a significant interaction between time and elevation (Table 5.2), produced by a rise in median cover scores at E3 but no response at E4 (Table 5.5). Plants at E1 declined, due probably to grazing kangaroos. No plants occurred at E5.

A. vesicaria, like *S. mitchellii*, occurred sparsely at WW. Changes in cover between October and February were moderated by an interaction between elevation and time (Table 5.2), reflected in minor losses at E3 and no changes at E1 and E4 (Table 5.5). *S. quinqueflora* was widespread at WW (Table 5.5) and apparently was unaffected by changes in elevation and/or time (Table 5.2). Minor reductions were apparent, however, for deep-flooded plants (Table 5.5).

5.4.3 Soil conductivity and pH at Wide Waters

At WW, no changes in conductivity or pH were detected at E1-E2, suggesting that the rising floodwater did not affect the topmost 15 cm of soil. At the shallow-flooded E3, conductivity declined from the pre-flood survey (4.2 dS m^{-1}) to the post flood surveys (November: 1 dS m^{-1}; December: 0.6 dS m^{-1}; $F_{2,24} = 23.13$, $P < 0.0001$). At E4, conductivity decreased from 2.3 dS m^{-1} prior to the flood to 1.2 dS m^{-1} in November, then increased to 2.6 dS m^{-1} (December). At E5, conductivity did not change.

At E3-E5 there were no changes in soil pH (E3: pre-flood 6.0, November 6.5, December 6.4; $F_{2,24} = 3.33$, $P = 0.06$; E4: 6.0, 6.3, 6.0; $F_{2,21} = 1.41$, $P = 0.27$; E5: 6.1, 6.0, 6.3; $F_{2,17} = 2.14$, $P = 0.15$).

5.4.4 Uncommon species

Less common plants included *Alternanthera denticulata*, *Centipeda cunninghamii*, *Cotula coronopifolia*, *Eleocharis acuta*, *Marsilea drummondii*, *Mimulus repens* and *Myriophyllum verrucosum* (Table 5.6). *C. coronopifolia* (JE), *E. acuta* (NN) and *M. drummondii* (JE) appeared at flooded elevations after the recession in November. *C. cunninghamii* appeared at JE and WW in December, and *M. verrucosum* and

Table 5.6. Pooled cover scores for seven uncommon, flood-dependent plants at sites denoted by combinations of transect (T: Ninkle Nook T1-T3, Jane Eliza T5-T6, Wide Waters T7-T9) and elevation (E). None were recorded during the pre-flood survey (October 2000).

	October	November	December	February
A. denticulata				T3E5 2
C. cunninghamii			T5E2 2 T7E3 1 T8E3 3 T9E3 1	T5E2 2 T7E3 1
C. coronopifolia		T5E1 2 T6E1 1		
E. acuta		T1E3 4 T1E4 3 T1E5 3		
M. drummondii		T5E3 2		
M. repens			T5E5 2 T6E5 1	T5E5 5 T6E5 2
M. verrucosum				T5E5 1

Table 5.7. Sum cover scores of three exotic species at sites denoted by combinations of transect (T: Ninkle Nook T1-T3, Jane Eliza T5-T6, Wide Waters T7-T9) and elevation (E). Scores refer to juvenile plants, none of them present until after the flood recession.

	October	November	December	February
A. subulatus		T5E1 1	T5E1 1	
H. curassavicum		T7E2 1 T8E3 3	T7E2 1 T7E3 1 T8E3 3 T8E4 4	T7E5 3 T8E4 1
X. occidentale		T5E1 3	T5E1 1 T8E4 1	

A. denticulata in February. The combined total cover for these species was 1.4%. None occurred in samples prior to the flood.

Five exotic species had an aggregate 3.2% of total cover: *Aster subulatus*, *Heliotropium curassavicum*, *Lepidium campestre*, *Mesembryanthemum crystallinum*, *Spergularia diandra* and *Xanthium occidentale* (Table 5.7). Only three species (*A. subulatus*, *H. curassavicum*, *X. occidentale*) occurred at previously flooded elevations, and all germinated following recession in November. Only *H. curassavicum* survived beyond February.

5.5 Discussion

5.5.1 Plant responses

S. mitchellii was the only one of the three dominant species to respond positively to flooding. It is a spreading perennial grass, 20-45 cm high, with wiry stems running for 1-3 m and is common in occasionally inundated areas of the Murray-Darling Basin. Many plants were < 15 cm high (cf. Cunningham *et al.* 1999), and so were completely submerged at low elevations. At NN, *S. mitchellii* responded to 44 days' flooding in October and December. At JE, however, prolonged flooding at elevation E4 delayed the response relative to E3. The critical duration for top-flooding appears to be 50-60 days (cf. JE:E3), as plants declined after 70-75 days (cf. JE:E4). Nevertheless, sufficient individuals survived to enable the population to recover and expand by February. In areas along the Murray channel, *S. mitchellii* endures 20-60 cm flooding for up to 73 days (Blanch *et al.* 1999).

S. quinqueflora is a leafless, low-growing (20-100 cm), perennial chenopod shrub typical of saline areas (Cunningham *et al.* 1999). It declined at deep-flooded sites (e.g. JE:E5, WW:E4, WW:E5), but did not respond at sites that were shallow-flooded. The local distribution of *S. quinqueflora* was consistent with its tolerance of water-logged saline soils (Jessop and Toelken 1986). It may be unable to photosynthesize when top-flooded.

A. vesicaria is a perennial shrub that attains 70 cm height and diameter, and is distributed widely in semi-arid areas of south-eastern Australia, including alluvial plains (Jessop and Toelken 1986; Cunningham *et al.* 1999). Its cover was reduced at all inundated sites, suggesting intolerance of flooding. The four years without inundation prior to October 2000 probably had encouraged the local population to extend its range.

Among less-common species, flooding promoted *A. denticulata*, *M. verrucosum* and *M. repens* at the lowest elevations, *E. acuta* at intermediate to low elevations and *C. cunninghamii* and *C. coronopifolia* at higher to intermediate elevations. The emergence of *A. denticulata* and *C. cunninghamii* in December suggests delayed germination and a preference for moist rather than water-logged soils. The variable responses of these and other species suggest patchy germination, or a lack of seed and other propagules, including rhizomes. Adult *E. acuta* initially were absent (perhaps due to dry conditions, grazing by kangaroos, or both), but re-sprouted from buried rhizomes. The record of *M. verrucosum* (JE) also arose from a vegetative propagule.

Germination was rarely observed, despite flooding and favourable air temperatures of 21-24°C (Commonwealth Bureau of Meteorology data, Renmark) (Britton and Brock 1994). This suggests an impoverished seed bank or, less likely, the effects of grazing. Wetland seed densities may be as low as 1300 m^{-2} (Brock and Rogers 1998) but typically are > 10,000 m^{-2} (McIntyre 1985; Nicol and Ganf 2000). Unpublished studies (Frears 2001; Stone 2001; Chong 2002) suggest that the soil seed bank in some areas of the Murray floodplain is indeed sparse. The changed flooding regime associated with river regulation may have limited the opportunities for flood-tolerant and responsive species to replenish the seed bank so that, when floods do occur, there is little capacity to respond. Comparable changes are described by Poiani and Johnson (1989) and Brock and Rogers (1998).

Grazing also may have limited plant responses. Flooding produced attractive new growth for kangaroos, and limited their access to some areas; they ate *S. mitchellii* and *A. vesicaria* and the shoots of less common species like *E. acuta*. Where grazing animals like these are abundant, they may counter the benefits of environmental flows for riparian vegetation (cf. Robertson and Rowling 2000).

Terrestrial weeds may compete with re-establishing wetland vegetation (e.g. Baird 1989). In this case, however, only five of 32 recorded plant species were weed species, and only three were recorded at flooded elevations. While exotic species may benefit from flooding (e.g. *Panicum repens*, torpedo grass: David 1999), the low incidence of germination, and the death of most germinants, suggest that in this case the flood did not promote exotics.

As parts of the Murray floodplain are saline, flooding might be expected to increase near-surface soil salinity (e.g. Jolly 2001). In this study, however, no increases were detected in conductivity or pH in the topmost 15 cm of soil at WW (the primary root zone for most plants recorded here); indeed, conductivity declined at WW:E3. The hydrostatic pressure from rising floodwaters may have been insufficient to draw saline water nearer the surface.

5.5.2 Future trials

In this study the quadrats at each elevation were not appropriately replicated, and a revised sampling design is a priority for future trials. It is recommended that the depth and duration of inundation of future trials be increased to promote aquatic and semi-aquatic species. Increased depth would promote flood-tolerant species higher on the elevation gradient and increased duration would promote clonal growth and the production and dispersal of propagules by flood-tolerant and aquatic plants lower on the gradient (cf. Cellot *et al.* 1999). This will increase the time available for plants like *E. acuta* to spread *via* clonal growth. Species like *E. acuta, C. coronopifolia* and *M. drummondii* responded to the enhanced flood and the succeeding flood in December, but died back by February. On the other hand, *S. mitchellii* apparently is able to endure at least 4 years without flooding. If it is desirable to avoid adverse effects on this species, flooding to 20-60 cm should not exceed 2 months (Blanch *et al.* 1999).

The long-term value of an enhanced flood rests upon recruitment of new individuals, and not merely the survival, growth and reproduction of established plants. In this study, although some new vegetative ramets developed, recruitment from new seed was not observed. Seeds produced during one flood might not germinate until later flooding, however, and recruitment properly should be monitored over a longer period. A single flood event in isolation may have very limited effects, and repeat flooding may be necessary to sustain the response. It is possible that plant responses to trial floods will be muted until serial floods are restored, effectively to enrich and maintain the seed bank and thereby ensure greater capacity to respond to flooding. The role of small, isolated events such as the enhanced flood described here may be more in maintenance of existing communities rather than restoration of degraded ones.

Figure 5.1. The lower River Murray showing the three floodplain areas: NN (Ninkle Nook), JE (Jane Eliza) and WW (Wide Waters). Ral Ral Creek is an anabranch of the Murray. Renmark is 568 km from the mouth of the river. Lock 5 is shown as a bar across the river. Locks 4 and 6 are located south (47 river km) and north (58 river km) of Lock 5, respectively.

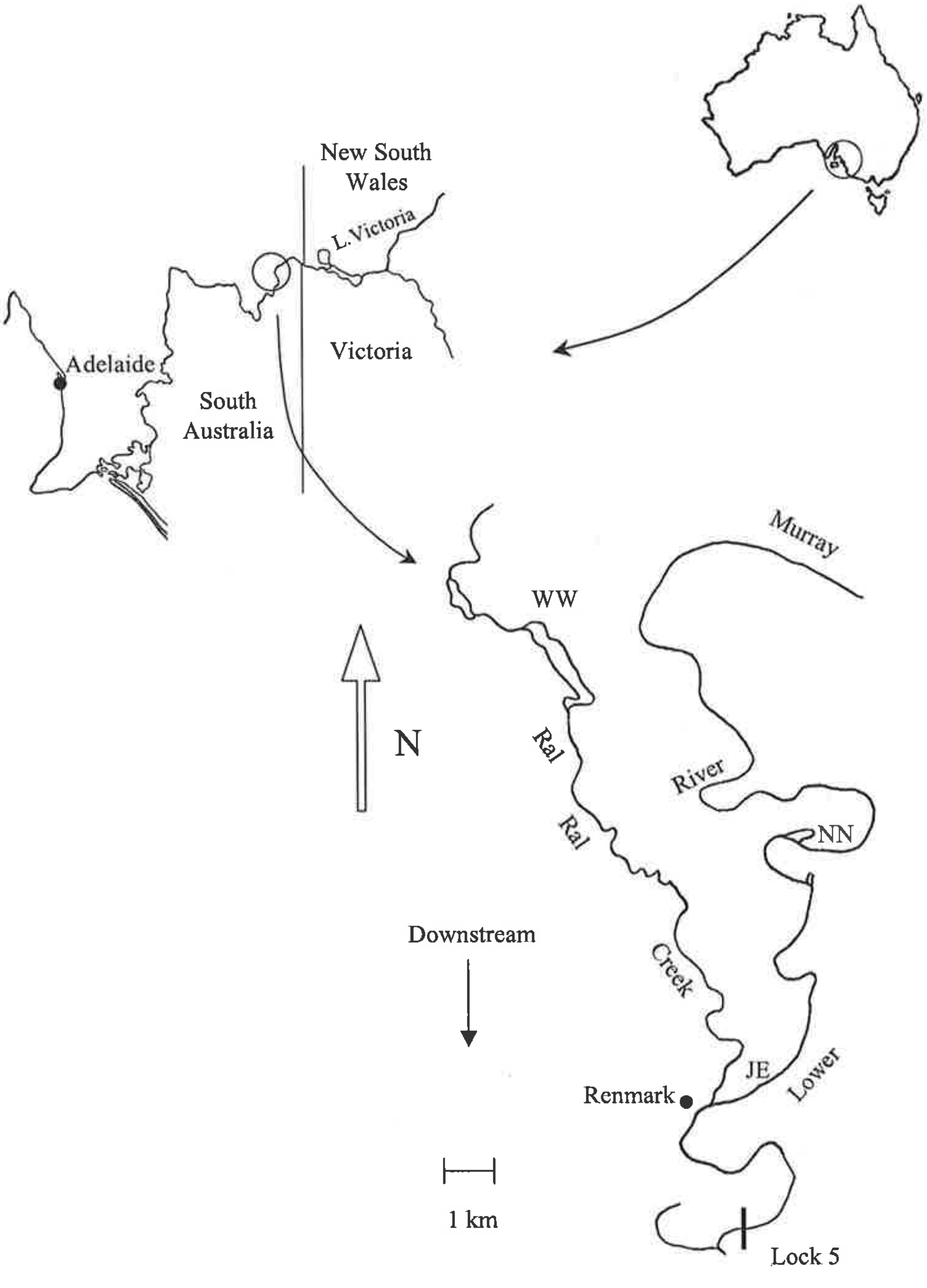
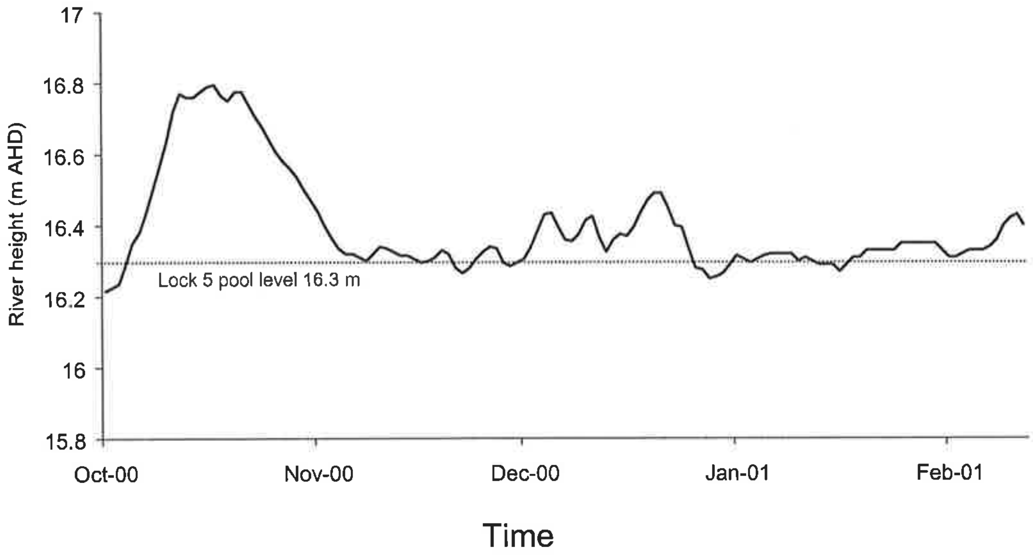

New South Wales
L. Victoria
Victoria
Adelaide
South Australia
Murray
River
Lower
WW
Ral
Ral
Creek
NN
JE
Renmark
N
Downstream
1 km
Lock 5

Figure 5.2. The hydrograph of the River Murray upstream of Lock 5 from 1 October 2000 to 12 February 2001. Water levels peaked on 17 October 2000 and returned to weir pool level on 8 November.


17
16.8
16.6
16.4
16.2
16
15.8
River height (m AHD)
Lock 5 pool level 16.3 m
Oct-00
Nov-00
Dec-00
Jan-01
Feb-01
Time

CHAPTER 6

RESPONSE OF *MUEHLENBECKIA FLORULENTA* AND *SPOROBOLUS MITCHELLII* TO AN ENHANCED FLOOD

6.1 Abstract

The response of two common floodplain plants, *Muehlenbeckia florulenta* (tangled lignum, Polygonaceae) and *Sporobolus mitchellii* (rats tail couch, Graminae), was monitored following inundation of the floodplain above Lock 5 on the Lower Murray during October 2000. The aim of the study was to characterise the response of the species with a view to selecting morphological variables suitable for measuring biological responses to future floods. Of the 12 and nine variables selected to describe *M. florulenta* and *S. mitchellii*, respectively, vegetative growth responses dominated. The number (B) and length (BL) of branches for *M. florulenta* and the number (R) and length (RL) of runners and total plant height (H) for *S. mitchellii* were most responsive. The reproductive response of both species was variable and establishment from seed did not occur. Groups of plants with common responses to flooding were identified but were not strictly aligned to elevation suggesting a non-uniform response to flooding. R, RL, H, B and BL were compared to assessment criteria for flood-response metrics and found to be favourable candidates for future flood trials.

6.2 Introduction

The Lower Murray floodplain is characterised by *Eucalyptus camuldulensis* (river red gum) and *Eucalyptus largiflorens* (black box) woodlands with a shrub layer dominated by *Muehlenbeckia florulenta* (tangled lignum: Margules and Partners *et al.* 1990). *Sporobolus mitchellii* (rats tail couch) and other grasses, dominate the area between *M. florulenta* bushes.

M. florulenta is a long lived perennial shrub (at least 100 years: K.F. Walker pers.

comm.) capable of asexual reproduction through layering. It responds rapidly to flooding with the production of leaves and flowers (Roberts and Marston 2000). *S. mitchellii* is a perennial creeping grass known to form dense mats following rainfall and/or flooding (Cunningham *et al.* 1999) via vegetative growth.

The enhanced flood in October 2000 described in Chapter 5, provided an opportunity to characterise the responses of *M. florulenta* and *S. mitchellii* and to determine the morphological variables most responsive to floodplain inundation. These species were selected to assess a vegetation response to the enhanced flood because they were known to be sensitive to water regime, easily sampled, amenable to repeated measures and were known to have populations spanning the elevations equal to the predicted extent of the flood.

Morphological variables were chosen to provide a measure of growth and reproduction. It was predicted that when flooded:

1) *M. florulenta* would increase branch length and number and produce new flowers and leaves; and

2) *S. mitchellii* would invest in asexual reproduction and increase the length and number of its runners.

Twelve and nine variables were assessed for *M. florulenta* and *S. mitchellii*, respectively. Combined (multivariate) responses for individuals of each species were determined using all variables. Cluster analysis was then used to determine groups of individuals within each species with similar combined responses. The response of groups was investigated to determine whether there was uniformity in each species' response to inundation. It was predicted that groups would be distributed across the floodplain according to elevation and thus water regime. The variables were also scrutinised to determine which were most suitable for monitoring the response of these species during future floods.

6.3 Species descriptions

Species descriptions have been compiled from information presented in Sainty and Jacobs (1981), Jessop and Toelken (1986), Cunningham *et al.* (1999) and Roberts and Marston (2000).

Muehlenbeckia florulenta (Meissn.) F. Muell. Polygonaceae – Tangled lignum

A perennial shrub that grows to a diameter of 1-2 m and height of 3 m. Stems are usually leafless with many slender, tangled branches and branchlets. Leaves are produced after flooding or rainfall and are generally up to 4 cm long and < 1 cm wide. Flowers are yellowish-white and produced throughout the year but prolifically after flooding or heavy rains. Fruits (achenes) are top-shaped and about 5 mm long with an ovoid-conical seed. Bushes can spread by vegetative reproduction through forming roots on branches that contact the sediment.

Sporobolus mitchellii (Trin.) C. E. Hubbard ex S.T. Blake Poaceae – Rats tail couch

A spreading perennial grass, 20-45 cm high, with wiry stems, erect or bent at the nodes, often running for 1-3 m. Leaves are pale to bluish-green, 2.5-10 cm long, broad at the base tapering to a fine but not sharp point. Flower heads are spike-like with panicles 6-13 cm long, 4-6 mm wide, borne 5- 20 cm above leaves. Flowering occurs from late spring to autumn. *S. mitchellii* is capable of clonal growth by forming roots at the nodes of runners.

6.4 Methods

The method of hydrograph and water regime determination is outlined Chapter 5. The water regime depth ranges used in this chapter differ from those in Chapter 5 and are described in Table 6.1.

6.4.1 Site selection and sampling

Sampling was undertaken on the floodplain areas described in Chapter 5: Ninkle Nook, NN; Jane Eliza, JE; Wide Waters, WW. *S. mitchellii* was distributed broadly across all floodplain areas enabling a wide range of elevations to be sampled. In contrast, *M. florulenta* was restricted to lower elevations and hence the plants sampled were representative of a much narrower elevation range.

Six plants were chosen at each of eight sites at NN and WW and 10 at JE. Sites were selected above and below the predicted extent of the enhanced flood to ensure exposure to a range of water regimes. The elevation of plants was determined in m AHD (m Australian Height Datum) using a theodolite and linear interpolation from elevations of known height.

Table 6.1. Water regime indices used to describe the number of days an elevation spent in depth ranges, above and below the sediment surface. A negative sign (–) indicates water levels below the sediment surface.

Water Regime Indices	Depth range	Water Regime Indices	Depth range
A	≥ 0	G	< 0 cm
B	0 to 5 cm	H	0 to -5 cm
C	5 to 10 cm	I	-5 to -10 cm
D	10 to 20 cm	J	-10 to -20 cm
E	20 to 60 cm	K	-20 to –60 cm
F	60 to 100 cm	L	-60 to –100 cm

One survey was conducted before the flood (8-10 October 2000), and three after the flood receded (8-10 November 2000, 3-5 December 2000, 5-7 February 2001).

6.4.2 Vegetation monitoring

Response variables were selected to provide a measure of the growth and reproductive response of plants and take into account the growth form of both species. The description of variables along with their codes is provided in Table 6.2.

The small size of *S. mitchellii* allowed use of variables that described the response of entire plants. The larger size of *M. florulenta* meant that only four whole-of-bush measurements were devised (greenness, general bush flowering, layering and seedling number). Additional variables were measured on one branch with live wood (green, flexible stems) and viable nodes per plant, which was chosen as a sub-sample of a bush.

The only variables not measured on a continuous scale were for *M. florulenta*:

- general bush greenness - scored on a scale from 1-4: 1 = 0-25%, 2 = 25-50%, 3= 50-75% and 4 = 75-100%.
- general bush flowering - scored on a scale from 1-4: 1 = 0-25% of the bush possessing flowering branches, 2 = 25-50%, 3= 50-75% and 4 = 75-100%.

Kangaroo grazing reduced the number of *S. mitchellii* plants at NN to 17, at JE to 39 and at WW to 22 and for *M. florulenta* branches at NN to 41, at JE to 37 and at WW to 35.

Table 6.2. The variables used to describe the response of *S. mitchellii* and *M. florulenta*, their respective codes and variable description.

Code	Code description	Variable description
S. mitchellii		
C	Clump diameter	Diameter of the clump forming the base of the plant
F	Number of flowers	Number of flowers on the plant
H	Height	Height of the plant
IL	Inter-leaf length	Distance between the 2nd and 3rd leaf from the growth apex of the longest runner
LL	Leaf length	The length of the 3rd leaf from the growth apex of the main runner
R	Number of runners	Number of runners on the plant
RE	Rooting established	The number of nodes on runners that have formed roots in the sediment
RL	Runner length	Combined length of all the runners on the plant
S	Seedling number	The number of seedlings within a 1 m radius of the target plant
RL	Length of runners	Combined length of all of the runners on the plant
M. florulenta		
B	Number of branches	Number of branches
BD	Branch diameter	Diameter at the base of the main branch
BL	Length of branches	Total length of all branches combined
F	Number of flowers	Number of flowers on the branch
G	Greenness	Estimate of the general bush greenness
GBF	General bush flowering	Estimate of general bush flowering
IL	Inter-leaf length	Distance between the 2nd and 3rd leaf from the growth apex of the main branch
L	Number of leaves	Number of leaves on the selected branch
LL	Leaf length	The length of the 3rd leaf from the growth apex of the main branch
LW	Leaf width	The width of the 3rd leaf from the growth apex of the main branch
LY	Layering	Number of new ramets produced via layering
S	Seedling number	The number of seedlings within a 1 m radius of the target plant

6.4.3 M. florulenta *germination trial*

M. florulenta germination trials were carried out in the field and in growth cabinets using achenes collected from three locations across the floodplain at JE. A second flood was predicted for late December following the first in October. In early December, 20 seeds were placed 1-2 cm beneath the sediment surface at 5 elevations spanning the predicted extent of inundation at each of 3 locations on the floodplain at JE. To test for the affect of the pericarp on germination, 10 of the 20 seeds had their pericarp removed. All elevations were re-visited in February to determine if establishment had occurred.

Another germination trial took place in two Warren Sherer Controlled Atmosphere Cabinets during December 2000. Seeds with and without their pericarps were placed on filter paper in petri dishes and exposed to treatments of 40°C/30°C (day/night) and 25°C/15°C. For each treatment 4 petri dishes, each with 8 seeds, were used for each of the 3 seed collection areas. The photoperiod for all treatments was 16h/8h day/night with 12×115W fluorescent tubes and 3×100W incandescent bulbs as a light source.

Treatments were monitored daily and kept saturated for the duration of the experiment using de-ionised water. Germination was recorded every seven days. The experiment was terminated when no additional germination was observed from 21-28 days.

6.4.4 Analysis

Combined (multivariate) **responses** for individuals of each species were determined using all morphological variables. **Groups** of individuals with similar multivariate responses were identified using cluster analysis, which determined similarity using the Relative Sorensen distance measure and assigned clusters using the Group Average Linkage method (PC-ORD ver. 4.21, McCune and Mefford 1999). Distance data were further analysed using Non-metric Multidimensional Scaling (PC-ORD ver. 4.21). The relationship between the combined response of individuals, each morphological variable and indices of water regime and elevation was examined using Pearson's r correlation coefficient.

Relative rates of increase in response variables were used for cluster and ordination analyses. *S. mitchellii* grew throughout the study and hence the October to February rate of increase was used. In contrast, most leaves and flowers of *M. florulenta* abscised between December and February and so cluster and ordination analyses were performed on the rate of increase from both October to December and October to February.

Plant height (H), number of runners (R) and total length of runners (RL) for *S. mitchellii* and number (B) and length of branches (BL) for *M. florulenta* were highly correlated with samples in ordination space and were used to further analyse the response of groups. These variables are referred to throughout this chapter as the '**key variables**' for each species. Changes in the key variables through time were analysed using repeated measures ANOVA (JMP IN ver. 3.2.1, SAS Institute Inc. 1994). Comparisons between groups for February were performed using one-way ANOVA and Tukey's HSD test (JMP IN ver. 3.2.1).

The relative rates of increase for variables indicative of a reproductive response were regressed against elevation. Student's *t* was used to assess the significance of the relationship by determining whether the regression coefficient (= slope) was different from zero (JMP IN ver. 3.2.1).

6.5 Results

6.5.1 M. florulenta *group characterisation and their correlation with morphological variables*

Ninkle Nook

Cluster analysis of the October to February data (i.e. relative rate of increase in response variables between October and February) revealed three groups separating at Relative Sorensen distances of 2.4×10^{-5} and 1.1×10^{-5}. Combined responses in ordination space were correlated strongly with the number and length of branches (Table 6.3), both of which increased from Group 1 to Groups 2 and 3 (Figure 6.1 a).

The October to December data (i.e. relative rate of increase in response variables between October and December) showed three response groups separating at Relative Sorensen distances of 1.7×10^{-5} and 1.1×10^{-5}. Most of the members of Groups 2 and 3 from the October to February analysis combined to form Group 3. The distribution of samples in ordination space was influenced by the length of branches and to a lesser extent the number of branches and flowers (Table 6.3; Figure 6.1 b).

Jane Eliza

The October to February data demonstrated three response groups separating at 1×10^{-4} and 3.7×10^{-5}. Group 3 consisted of only one member. The distribution of samples

Table 6.3. Pearson correlations for the variables used to describe the response of *M. florulenta* with axes 1 and 2 of the ordination plots in Figure 6.1. Correlations for the October to February (Oct-Feb) and October to December (Oct-Dec) analysis are presented. See Table 6.1 for code descriptions.

	Ninkle Nook				Jane Eliza				Wide Waters			
	Oct-Feb		Oct-Dec		Oct-Feb		Oct-Dec		Oct-Feb		Oct-Dec	
Axis	1	2	1	2	1	2	1	2	1	2	1	2
B	.656	-.595	.561	.556	-.255	.636	-.194	.580	-.634	-.654	.503	-.339
BD	.539	-.530	.492	.517	0.53	.421	-.322	.267	-.427	-.465	.183	-.141
BL	.970	-.999	.984	.991	-.472	.974	-.942	.972	-.997	-.996	.999	-.861
F	.253	-.168	.502	.291	-.146	.345	.179	.294	.017	.010	.190	-.134
G	.029	.021	.348	.279	-.122	.281	-.196	.340	-.207	-.259	.487	-.407
GBF	.028	.038	.133	.108	-.036	.202	-.119	.237			.293	-.164
IL	.130	-.120	.411	.376	.086	-.266	-.202	.351	.315	.361	-.169	.126
L	.058	-.135	.382	.511	.209	-.333	-.680	.738	.247	.307	.109	.172
LL	.207	-.175	.094	.082	.155	-.453	-.204	.172	.550	.587	-.326	-.008
LW	.073	-.038	-.050	-.057	.183	-.537	.110	-.174	.428	.461	-.190	-0.12
LY					-.351	.227	-.032	.256				

across ordination space was influenced by BL and B (Table 6.3), both increasing toward Groups 2 and 3 (Figure 6.1 c). The October to December data exposed three groups, which formed at distances of 1.5×10^{-4} and 8.1×10^{-5}. The distribution of samples in ordination space was influenced most by BL, with the number of leaves the second most strongly correlated variable (Table 6.3; Figure 6.1 d).

Wide Waters

Three response groups were identified from the October to February data separating at distances of 1.9×10^{-6} and 1.1×10^{-6}. The distribution of groups on the ordination plot was influenced mainly by BL and to a lesser extent B and LL (Table 6.3), which all increased toward Group 3 (Figure 1 e).

Groups for the October to December data separated at a lower distance than for the October to February data (5.0×10^{-6} and 7.2×10^{-6}). Whereas 4/3 and 8/4 had a substantially different response in the October to February analysis, they were joined by an additional six plans to form Group 3. The distribution of groups in ordination space was influenced by BL and to a lesser extent B, G and LL which all increased towards Groups 1 and 3 (Table 6.3; Figure 6.1 f).

6.5.2 Key variable response and water regime for M. florulenta *groups*

Ninkle Nook

The length of branches increased for Groups 2 and 3 from October to February and by the latter survey both were greater than Group 1 (Table 6.4). The number of branches also increased between October and February for Group 2, with B for Group 2 in February over 3 times greater than for Group 1 (Table 6.4).

All plants were inundated during the enhanced flood for a minimum of 10 days and across the entire study to 20-60 cm for at least 16 days. Group 3 plants were only found at elevations that received water during the second flood. Plants from Group 1 occupied all elevations bar the second lowest (Table 6.5).

Jane Eliza

There was a 2.5 and 6-fold increase in branch length and a 6.5 and 6-fold increase in the number of branches for Groups 2 and 3 respectively from October to February. In contrast, there was no change in either variable in Group 3 (Table 6.4). During February, Group 3 had the greatest total branch length, while Group 2 had more branches (Table 6.4).

Group 2 and 3 plants were only found at inundated elevations (Table 6.5). The Group 3 plant was at the lowest elevation on the floodplain and inundated to 20 to 60 cm for 14 consecutive days. Group 2 plants were flooded from 10-63 days, with three inundated to 20 to 60 cm for 2-38 days (Table 6.5). Group 1 was found at all elevations (Table 6.5).

Wide Waters

BL was initially the same for all groups. By February, Group 3 had the longest branches, more than double that for Group 2 and triple that of Group 1 (Table 6.4). Similarly, the number of branches for Group 3 increased from 1 in October to 22 in February, compared to Group 2, which increased from 2 to 10 (Table 6.4).

The two plants that formed Group 3 were at elevations flooded for 21-24 days. Group 2 plants were positioned where water levels rose to within 10 to 20 cm of the sediment surface for 10 days and at elevations flooded for up to23 days. Similarly,

Table 6.4. The mean number (B) and length of branches (BL) for *M. florulenta* response groups on each floodplain (determined from October-February analysis). Superscripts indicate groups with similar means in February (α=0.05). n=1 and n=2 for Group 3 at JE and WW, respectively, and hence changes through time were not subject to statistical analyses.

	B					BL (m)				
		Oct	Nov	Dec	Feb		Oct	Nov	Dec	Feb
NN	*F* (df), *P*					*F* (df), *P*				
Gr 1	0.5 (3,72), 0.68	3	4	4	5^b	2.2 (3,72), 0.1	0.3	0.4	0.3	0.3^b
Gr 2	15.7 (3,33), < 0.0001	3	4	8	12^a	11.0 (3,33), < 0.0001	0.3	0.4	0.6	0.7^a
Gr 3†	3.0 (3,15), 0.06	4	6	7	9^{ab}	19.5 (3,15) < 0.0001	0.2	0.5	0.5	0.9^a
JE										
Gr 1	5.6 (3,81), 0.002	2	3	3	3^b	5.3 (3,81), 0.002	0.3	0.4	0.4	0.4^c
Gr 2	13.1 (3,24), < 0.0001	3	6	10	17^a	38.3 (3,24),< 0.0001	0.5	0.8	1.1	1.1^b
Gr 3		2	3	12	12^{ab}		0.3	1.0	1.3	1.8^a
WW										
Gr 1	8.2 (3,63), 0.0001	3	5	4	6^b	2.3 (3,63), 0.08	0.4	0.4	0.4	0.4^c
Gr 2	12.3 (3,30), < 0.0001	3	7	7	10^b	14.6 (3,40), < 0.0001	0.4	0.6	0.6	0.7^b
Gr 3		1	3	6	22^a		0.5	0.7	0.8	1.4^a

Group 1 plants were distributed broadly across the floodplain occupying the highest and lowest elevations surveyed (Table 6.5).

6.5.3 *Reproductive response for* M. florulenta

Ninkle Nook

The number of flowers for all elevations combined increased from 64 in October (8 plants) to 111 in November (12 plants) and 352 (8 plants) in December before declining to 60 in February (4 plants). Twenty-two plants flowered during the study, however, flowers were recorded consecutively on the same plant on only 11 occasions. Most of the plants flowering in November had abscised flowers beneath the bush in December. This was also observed at JE and WW.

There was a negative relationship between flowering and elevation for the October to December period. Over half the flowering plants occurred at lower elevations (Figure 6.2 a) with the maximum number of flowers (130) recorded at the second lowest elevation.

Jane Eliza

Twenty-one plants flowered, with the total number of flowers increasing from 38 in October to 128 in November and 784 in December. No flowers were recorded in February. Flowering had a negative relationship with elevation with only plants at the lower inundated elevations flowering (Figure 6.2 b). There was no difference in flowering between plants at lower elevations.

Wide Waters

Flowering was recorded on only three plants in October with a combined total of 11. In contrast, 10 and 14 plants were flowering in November and December with 250 and 305 flowers, respectively. No plants were flowering in February. Flowering was greater at lower elevations with only one of flowering plants in December located at an elevation not inundated (Figure 6.2 c).

6.5.4 M. florulenta *germination trials*

Field trial

Only the two lowest elevations of one transect at JE were inundated during the second flood for 9 and 26 days. No seedlings were observed. This was consistent with observations that no seedlings were observed anywhere on NN, JE and WW.

Growth cabinet

Germination was recorded for all treatments. There was no difference in the mean % germination after 21 days between the three source plants used in the 25°C/15°C treatment ($F_{2,8}$=0.60, P=0.56), with an overall germination rate of 73% (Table 6.6). Similarly, there was no difference in the total % germination between source plants used for the 40°C/30°C treatment ($F_{2,8}$=0.001, P=0.99) with an overall germination of 18% (Table 6.6). The % germination under the 25°C/15°C treatment was higher than in the 40°C/30°C treatment (F_{21}=56.9, $P < 0.001$: Table 6.6).

There was no difference in the % germination from different source plants for seeds with the pericarp intact (F_5=0.22, P=0.65). There was also no difference in the % germination between seeds with and without an intact pericarp at 25°C/15°C (F_{21}=0.52, P=0.48).

Table 6.5. The number of days in each water regime indice for *M. florulenta* at Ninkle Nook, Jane Eliza and Wide Waters. Days flooded during the first and second period of floodplain inundation are separated by /. Superscripts indicate to which groups plants belong. * indicates elevations where the floodplain topography prevented the estimation of the depth to ground water. Water regime codes are described in Table 6.1.

Depth range			≥0	0/5	5/10	10/20	20/60	60/100	< 0	0/-5	-5/-10	-10/-20	-20/-60	-60/-100
Ninkle Nook	Site/Plant	Elevation	A	B	C	D	E	F	G	H	I	J	K	L
	1/2-4,6 ^{1}	17.08	10	6	4	0	0	0	125	2	2	9	61	51
	2/1-6 ^{1,2,3}	16.66	27/29	1/5	2/5	5/13	19/6	0	79	13	13	3	50	0
	3/1-6 ^{1}	17.05	11	2	7	2	0	0	124	3	1	11	60	49
	4/1-6 ^{2,3}	16.66	27/29	1/5	2/5	5/13	19/6	0	79	13	13	3	50	0
	5/1-6 ^{1}	17.01	13	3	2	8	0	0	122	2	5	12	55	48
	6/1,4-6 ^{1,2,3}	16.74	24/20	2/6	1/6	5/6	16/2	0	91	7	9	22	53	0
	7/1-6 ^{1,2}	16.64	29/31	3/6	2/5	3/12	21/8	0	75	20	2	4	49	0
	8/1-4 ^{1,2}	17.09	10	7	3	0	0	0	125	1	3	8	60	53
Jane Eliza	Site/Plant	Elevation	A	B	C	D	E	F	G	H	I	J	K	L
	1/1-6 ^{1,2}	16.85	10	8	2	0	0	0	125	3	1	5	115	1
	2/1,3-6 ^{1,2,3}	16.57	24/3	3/3	2/0	5/0	14/0	0	108	4	10	24	70	0
	3/1-6 ^{1,2}	16.58	63	5	7	13	38	0	72	*	*	*	*	*
	4/2-6 ^{1,2}	16.69	50	7	6	35	2	0	85	*	*	*	*	*
	5/1,4,5 ^{1}	17.2	0	0	0	0	0	0	135	*	*	*	*	*
	6/1,3,5 ^{1}	17.15	0	0	0	0	0	0	135	*	*	*	*	*
	7/2,4,6 ^{1}	17.2	0	0	0	0	0	0	135	*	*	*	*	*
	10/1-6 ^{1,2}	16.84	24	19	5	0	0	0	111	*	*	*	*	*

Table 6.5. (continued).

Depth range		≥0	0/5	5/10	10/20	20/60	60/100	< 0	0/-5	-5/-10	-10/-20	-20/-60	-60/-100
Wide Waters	Elevation	A	B	C	D	E	F	G	H	I	J	K	L
1/1,5,6 [1]	17.42	0	0	0	0	0	0	135	0	0	0	30	57
2/3 [1]	17.23	0	0	0	0	0	0	135	0	4	8	52	71
2/6 [1]	17.28	0	0	0	0	0	0	135	0	0	10	45	79
3/1,2,4,6 [1,2]	16.87	19/6	2/3	3/3	4/0	10/0	0	110	5	10	16	78	1
3/3 [2]	16.84	21/8	3/4	2/2	5/2	11/0	0	106	7	8	16	75	0
4/2-6 [1,2,3]	16.74	24/20	2/6	1/6	5/6	16/2	0	91	7	9	22	53	0
5/2 [1]	17.19	0	0	0	0	0	0	135	3	7	4	66	55
5/3 [1]	17.37	0	0	0	0	0	0	135	0	0	0	40	49
5/4,5 [1,2]	17.28	0	0	0	0	0	0	135	0	0	10	45	79
6/1,3 [1]	17.26	0	0	0	0	0	0	135	0	0	10	46	79
6/2 [1]	17.37	0	0	0	0	0	0	135	0	0	0	40	49
6/5 [2]	17.28	0	0	0	0	0	0	135	0	0	10	45	79
6/6 [2]	17.24	0	0	0	0	0	0	135	0	3	8	49	75
7/1 [1]	16.83	21/8	3/3	1/3	4/2	13/0	0	106	10	5	20	71	0
7/2,4,6 [1,2]	16.78	23/16	2/8	3/3	4/5	14/0	0	96	5	11	26	54	0
7/3 [1]	16.8	22/14	2/7	2/3	4/4	14/0	0	99	7	7	26	59	0
8/1 [1]	16.85	20/7	2/3	3/4	4/0	11/0	0	108	8	8	14	78	0
8/2-5 [1,2,3]	16.81	21/12	2/6	2/3	4/3	13/0	0	102	10	7	19	66	0
8/6 [2]	16.84	21/8	3/4	2/2	5/2	11/2	0	106	7	8	16	75	0

Table 6.6. Results of the germination trial for *M. florulenta*. Germination counts were conducted after 14 (a) and 21 days (b) for seeds from the three collection areas. Hence, 1a = germination count after 14 days for seeds from location 1. 'I' indicates germination for seeds with the pericarp removed and 'II' represents seeds with the pericarp intact. All treatments had eight seeds, except * with nine.

	25°C/15°C							40°C/30°C						25°C/15°C				
	I	1a	1b	2a	2b	3a	3b	1a	1b	2a	2b	3a	3b	II	1a	1b	2a	2b
		5*	5*	3	4	5	5	0	2	0	0	0	3		6	7	5	5
		5	7	6	7	5	6	0	2	0	2	0	4		7	8	8	8
		5*	6*	5	5	6	7	0	1	0	1	0	0		5	5	4	4
		5	7	5	6	7	7	0	0	0	2	0	0		6	6	6	6
Mean		5	6.3	4.8	5.5	5.8	6.3	0	1.3	0	1.3	0	1.8		6	6.5	5.8	5.8
% germ		59	74	59	69	72	78	0	16	0	16	0	22		75	81	72	72

6.5.5 S. mitchellii *group characterisation and their correlation with morphological variables*

Ninkle Nook

Three response groups were identified at Relative Sorensen distances of 0.24 and 0.06. The distribution of individuals in ordination space was correlated most strongly with height, internodal length and the number and length of runners, which all increased toward Groups 3 and 2 (Figure 6.3 a; Table 6.7).

Jane Eliza

Plants formed three response groups, with Group 1 separating at 0.25 and Groups 2 and 3 at 0.1. The distribution of individuals in ordination space was correlated with H, R and RL, which all increased from Group 3 to Group 1 (Table 6.7; Figure 6.3 b).

Wide Waters

Plants at WW formed three response groups, separating at a distance of 0.03 and 0.02. The distribution of plants on the ordination plot was correlated with R, RL and H (Table 6.7), which increased from Group 1 through to Groups 3 and 2 (Figure 6.3 c).

Table 6.7. Pearson correlations for the variables used to describe the response of *S. mitchellii* with axis 1 and axis 2 of the 2D ordination plots in Figure 6.3. Code descriptions are presented in Table 6.1.

	NN		JE		WW	
Axis	1	2	1	2	1	2
C	-.446	.636	-.236	.241	-.204	-.298
F	-.664	.542	-.452	.365	-.482	-.338
H	-.855	.881	-.627	.382	-.929	-.719
IL	-.876	.919	-.452	.413	.202	-.119
LL	-.087	.098	.171	-.214	-.116	-.180
R	-.877	.841	-.799	.820	-.641	-.792
RE	-.338	.464	-.499	.592	-.165	-.363
RL	-.801	.699	-.840	.934	-.849	-.992

6.5.6 *Key variable response and water regime for* S. mitchellii *groups*

Ninkle Nook

The number and length of runners increased for individuals in Groups 2 and 3, primarily between December and February. Group 2 and 3 plants had a six and nine fold increase in height, respectively, by February (Table 6.8). In contrast, Group 1 plants had a 45% reduction in height (Table 6.8).

Group 2 and 3 plants were flooded for 24-29 days during the first flood and a further 20-31 days in the second. Inundation was deeper for longer in the first (Table 6.9). Group 1 plants were either shallow flooded or not inundated at all (Table 6.9).

Jane Eliza

The number and length of runners increased for plants in all groups after floodwaters receded, increasing primarily between November and February (Table 6.8). By February, Group 1 had R and RL values two and four times greater than for plants in Group 2 (Table 6.8). The height of plants in all groups increased with the tallest individuals belonging to Group 2 (Table 6.8).

Group 1 was located at elevations flooded for 10-21 days and Group 2 at elevations flooded for 2-27 days (Table 6.9). Group 1 received deeper flooding; from 20 to 60 cm for 11 days (Table 6.9). Group 3 plants were at all bar one of the flooded elevations and were the only plants to occupy non-inundated elevations (Table 6.9).

Wide Waters

The number of runners increased for each group after the flood. By February, Group 2 had the most with an average of seven (Table 6.8). Group 2 also had the greatest increase in H, approximately three-fold (Table 6.8). Only minor increases in RL were recorded for Group 2 and 3 plants (Table 6.8).

Group 2 and 3 plants were flooded for at least 5 days from 10 to 20 cm (Table 6.9). All of the plants not inundated belonged to Group 1. Water levels came to within 5 to 10 cm and 10 to 20 cm of the sediment surface for some plants in Group 1. Group 1 plants were also found at three inundated elevations (Table 6.9).

6.5.7 *Reproductive response for* S. mitchellii

Ninkle Nook

Flower number increased from one on a single plant in December to 45 flowers on five plants in February. An increase in F occurred only for plants at inundated elevations (Figure 6.4 a). Runners rooted in the sediment were only observed in February on 13 occasions on five plants; all were located at lower elevations (Figure 6.4 b). No seedlings were recorded.

Jane Eliza

Seventeen flowers were recorded in December on eight plants. This increased to 37 on 11 plants in February. RE was only recorded for five plants after the flood, predominantly in February. The relationship with elevation was not strong for either variable (Figure 6.4 c,d). No seedlings were recorded.

Wide Waters

Four plants flowered in February at flooded elevations but the relationship with elevation was not significant (Figure 6.4 e). There was also a high number of non-flowering plants at lower elevations. No seedlings were recorded.

Table 6.8. The response of key variables for *S. mitchellii* groups identified on each floodplain. Superscripts indicate groups with similar variable responses in February (α=0.05). *F* and *P* values relate to repeated measures ANOVA across surveys. Superscripts indicate treatments with similar responses during February (α=0.05). Response variable codes are described in Table 6.1.

	R (#)					RL (m)					H (cm)				
	F (df), *P*	Oct	Nov	Dec	Feb	*F* (df), *P*	Oct	Nov	Dec	Feb	*F* (df), *P*	Oct	Nov	Dec	Feb
NN															
Gr 1	2.9 (3,21), 0.06	1	2	2	1^{b}	1.5 (3,21), 0.24	0.1	0.1	0.1	0.1^{b}	19.0 (3,21), < 0.0001	7.1	4.9	4.5	3.9^{b}
Gr 2	16.2 (3,12), 0.0001	0	5	16	35^{a}	7.7 (3,12), 0.004	0	0.4	3.2	7.4^{a}	5.3 (3,12), 0.01	3.2	11.6	16.4	28.0^{a}
Gr 3	5.4 (3,9), 0.02	0	5	8	16^{b}	21.6 (3,9), 0.0001	0	0.3	0.5	1.4^{b}	10.8 (3,9), 0.002	2.0	8.3	7.5	12.0^{b}
JE															
Gr 1	12.8 (3,6), 0.005	0	3	15	22^{a}	19.6 (3,6), 0.002	0	0.4	1.4	3.5^{a}	11.1 (3,6), 0.007	1.3	6.7	8.7	7.3^{ab}
Gr 2	19.2 (3,39), < 0.0001	1	3	7	9^{b}	15.5 (3,39), < 0.0001	0	0.2	0.6	0.7^{b}	10.5 (3,39), < 0.0001	2.1	5.8	6.5	8.9^{a}
Gr 3	19.2 (3,63), < 0.0001	1	1	4	3^{c}	15.5 (3,63), < 0.0001	0.0	0.1	0.2	0.1^{c}	7.2 (3,63), 0.0003	2.0	3.8	5.0	3.7^{b}
WW															
Gr 1	14.9 (3,30), < 0.0001	1	3	3	3^{b}	3.4 (3,30), 0.03	0.1	0.2	0.1	0.1^{c}	1.9 (3,30), 0.15	2.6	3.6	2.3	2.6^{b}
Gr 2	10.4 (3,9), 0.003	1	5	3	7^{a}	9.6 (3,9), 0.004	0.0	0.2	0.2	0.3^{a}	7.6 (3,9), 0.008	2.2	4.2	3.0	7.5^{a}
Gr 3	5.0 (3,18), 0.01	0	4	4	5^{ab}	4.7 (3,18), 0.01	0.0	0.2	0.1	0.2^{b}	2.7 (3,18), 0.08	1.7	6.4	2.1	3.7^{b}

Table 6.9. The number of days in each water regime indice for *S. mitchellii* at Ninkle Nook, Jane Eliza and Wide Waters. Superscripts indicate the response group number. Where values are separated by /, the first value relates to inundation in the enhanced flood and the second value refers to inundation during the second natural flood. * indicates elevations where the floodplain topography prevented the estimation of the depth to ground water. Water regime codes are described in Table 6.1.

Depth range (cm)		≥0	0/5	5/10	10/20	20/60	60/100	< 0	0/-5	-5/-10	-10/-20	-20/-60	-60/-100
Ninkle Nook	Elevation (m AHD)	A	B	C	D	E	F	G	H	I	J	K	L
3/1,2 ^{1}	17.05	11	2	7	2	0	0	124	3	1	11	60	49
4/2-6 ^{1}	17.55	0	0	0	0	0	0	135	0	0	0	15	67
5/4-6 ^{2}	16.73	24/22	1/6	2/8	4/6	17/2	0	89	9	9	18	53	0
7/1,2,4-6 ^{1,2,3}	16.74	24/20	2/6	1/6	5/6	16/2	0	91	7	9	22	53	0
8/2,4,6 ^{2,3}	16.64	29/31	3/6	2/5	3/12	21/8	0	75	20	2	4	49	0
Jane Eliza	Elevation (m AHD)	A	B	C	D	E	F	G	H	I	J	K	L
1/1-3,5,6 ^{1,2}	16.85	10	8	2	0	0	0	125	3	1	5	115	1
2/1-6 ^{1,2,3}	16.63	21	3	3	4	11	0	114	3	6	21	84	0
4/2-4 ^{3}	17.12	0	0	0	0	0	0	135	*	*	*	*	*
5/3-5 ^{3}	17.1	0	0	0	0	0	0	135	*	*	*	*	*
6/2,5 ^{3}	17.08	0	0	0	0	0	0	135	*	*	*	*	*
7/3-5 ^{3}	17.04	0	0	0	0	0	0	135	*	*	*	*	*
8/1,3-6 ^{2,3}	16.89	2	2	0	0	0	0	133	*	*	*	*	*
9/1-6 ^{2,3}	16.82	27	14	13	0	0	0	108	*	*	*	*	*

Table 6.9. (continued).

Depth range (cm)		≥0	0/5	5/10	10/20	20/60	60/100	< 0	0/-5	-5/-10	-10/-20	-20/-60	-60/-100
Wide Waters	Elevation (m AHD)	A	B	C	D	E	F	G	H	I	J	K	L
10/1-6 2,3	16.88	5	5	0	0	0	0	130	*	*	*	*	*
1/2-4 1	17.48	0	0	0	0	0	0	135	0	0	0	23	61
3/1,2,5,6 [1,2,3]	16.9	18/4	3/4	1/0	5/0	9/0	0	113	4	9	15	83	2
4/2,3,5,6 [1,2,3]	16.96	15	2	3	10	0	0	120	5	5	18	48	44
5/3,4,6 [1]	17.28	0	0	0	0	0	0	135	0	0	10	45	79
6/4 [1]	17.18	0	0	0	0	0	0	135	4	6	4	67	54
7/1-3,5 [1,3]	16.94	16/2	2/2	3/0	8/0	3/0	0	117	4	7	15	62	29
8/1-3,4,5 [2,3]	16.92	17/3	3/3	1/0	8/0	5/0	0	115	5	5	19	75	11

6.6 Discussion

6.6.1 Vegetative growth response to flooding

For *M. florulenta*, rates of increase in morphological variables between October and February and October and December were both analysed because it was thought that leaf and flower abscission after December may affect the group composition calculated using each data set. However, the October-February and October-December analyses both yielded three groups, of which the differences in composition between analyses were minor. This suggests that it was approximately the same suite of plants detected responding in both analyses.

M. florulenta was inundated for 27 to 60 days to a range of depths. Many plants responded to flooding by increasing the length and number of branches. Leaf number also increased, but was only evident in the October to December analysis because most leaves had abscised by February.

The increase in branch length and number appeared greatest for flooded plants, however, the response was statistically independent of the depth and duration of inundation. The duration of inundation was within the known tolerance limits of *M. florulenta*, which has been recorded at sites flooded from 2-3 months (Sharley and Huggan 1995) to 6-12 months (Goodrick 1984). Blanch *et al.* (1999) found *M. florulenta* restricted to elevations flooded from 20 to 60 cm for less than 71 days and hence deeper flooding for longer during this study may have had a negative impact on vegetative growth.

S. mitchellii was exposed to a range of flooding depths and durations across the three floodplain areas: NN ≥ 0 cm for 11-60 days, JE 2-27 days and WW 5-22 days. As predicted, plants grew taller and the length and number of runners increased. Lateral extension via runners, tillers or stolons is a common response for perennial floodplain grasses following inundation (e.g. *Echinochloa pyramidalis* and *Oryza longistaminata*: van der Valk 1992). The increase in the number and length of runners was greatest between December and February suggesting that warmer temperatures coupled with moist sediment led to maximum growth. This is supported by observations that vigorous growth follows summer rainfall (Cunningham *et al.* 1999).

The increase in the length and number of runners enabled *S. mitchellii* to increase the area of the floodplain occupied. The increase in height followed the recession of floodwaters was presumably part of general plant growth rather than a strategy for flood-tolerance.

Groups with the greatest key variable response were always composed of individuals from flooded elevations, however, there was no apparent impact of flood depth or duration. The non-negative effect of depth supports Blanch *et al.*'s (1999) observations that *S. mitchellii* tolerates 73 days flooding from 20 to 60 cm. This compares to the maximum recorded duration of flooding for this study of 38 days from 20 to 60 cm at WW.

For both species, cluster analysis identified response groups at low Relative Sorensen distances. This was a result of the redundancy of a number of the variables such as leaf length (LL) and clump diameter (C) that differed little between flooded and non-flooded plants. The integrity of groups is supported by the difference in the response of key variables.

Contrary to prediction, the response of groups was not strictly aligned with elevation and inundation did not necessarily promote a growth response. For both species it was common for plants at the same elevation to be present in all groups. This may reflect natural variability in plant responses or be attributable to minor variations in floodplain relief causing small differences in the water regime.

Rising sub-surface water only initiated a response by *M. florulenta*. This suggests that *M. florulenta,* which has roots that extend to > 3 m (Craig *et al.* 1991), may be able to draw on rising groundwater to support growth. The absence of a response by *S. mitchellii*, which was found at elevations where groundwater was predicted to have come within 20 cm of the sediment surface, was possibly a function of its shallow rooting depth (< 20 cm: MAS pers. obs.) or a lack of water movement through the soil profile. If the latter is true this suggests that *S. mitchellii* may rely on floodwaters moving across the surface of the floodplain to provide moisture to support growth.

Both species demonstrated variability in response across all floodplain areas. For example, the *S. mitchellii* group had the greatest response at NN with an average of 35 runners and a total length of 7.4 m, while at WW there was on average seven runners with a total length of 0.29 m. Analysis of floodplain water regimes suggest that this was not a result of differential flooding. Soil conductivity is, however, a candidate and undoubtedly differed between floodplains given that the halophyte *Sarcocornia quinqueflora* was absent at NN, but present at JE and abundant at WW.

6.6.2 Sexual and asexual reproduction in response to flooding

In comparison with the key variables, both modes of reproduction only had a minimal influence on the distribution of groups in ordination space. For *M. florulenta*, layering was recorded only once. For *S. mitchellii*, runners taking root was only recorded for about half the flooded plants at NN, a quarter at JE and none at WW. This was despite the large investment in runners that increased seven-fold in length at some sites.

Flowering was more common for both species than investment in asexual reproduction. *M. florulenta* commenced flowering at inundated elevations during the first flood. The transition from flowering to achene abscission was 4-6 weeks. In contrast, *S. mitchellii* did not flower until at least 2 months after floodwaters receded.

For all bar one *S. mitchellii*, flowering only occurred at flooded elevations. In contrast, *M. florulenta* flowered at elevations above and below the height of flood levels. *M. florulenta* flowering in the absence of flooding is common and occurs throughout most of the year (Cunningham *et al.* 1999). It is not known whether this is a stress response or in anticipation of flooding. None of these flowers formed fruits.

No germination or seedling establishment was observed for either species. This suggests that seed was not present or that germination cues were not triggered. Given that *S. mitchellii* germinates readily on moist sediment at ~25°C (J. Nicol, University of Adelaide, pers. comm.) and *M. florulenta* had a high germination rate at fluctuating 25°C/15°C, it is unlikely that the mean daily temperature for October 2000 (21-24°C; Bureau of Meteorology) were insufficient to trigger germination.

The timing of flowering for *S. mitchellii* meant that any germination directly after the flood would have relied on a pre-existing seed bank. Opportunities for *S. mitchellii* to replenish its seed bank may have declined in the wake of river regulation because of the reduction in the frequency of medium sized floods that would have periodically flooded these sites (Walker and Thoms 1993). This favours a depauperate seed bank as a possible reason for no germination.

M. florulenta does not have a persistent seed bank and primarily relies on newly produced seed for establishment (Chong 2002). Achene abscission meant that seeds were on the sediment soon after the first flood. However, none of these germinated following the December 2000 flood. The germination trial in growth cabinets suggested that germination was reduced at elevated temperatures. Given that the mean daily temperature in December was 32.5°C, with the maximum exceeding 39°C on five occasions, high temperatures may have inhibited germination. Hence, the timing of a second flood to stimulate germination may be important.

The completion of the cycle from flower production to seed germination within a single flood depends on the duration of inundation. The reduced duration of floods under current regulated conditions in the Lower Murray may mean that two floods within close temporal proximity of one another are required for *M. florulenta* establishment: an initial flood to promote flowering and seed production and a second to enable germination of newly produced seeds. The second flood would have to occur outside the extremes of winter or summer so as to not inhibit germination. The resultant opportunities for establishment may thus lie between late winter and late spring or late summer and late autumn.

6.6.3 Selection of variables for use as flood response indicators

Measuring a biological response to environmental flows requires careful selection of response variables. Selection of variables should consider a) the sensitivity of the variable to flooding, b) the ease of measurement, c) the time taken for a response to occur, d) whether the variable is amenable to repeated measures, e) whether the variable responds uniformly to flooding and f) what the variable measures (e.g. growth, reproduction, recruitment).

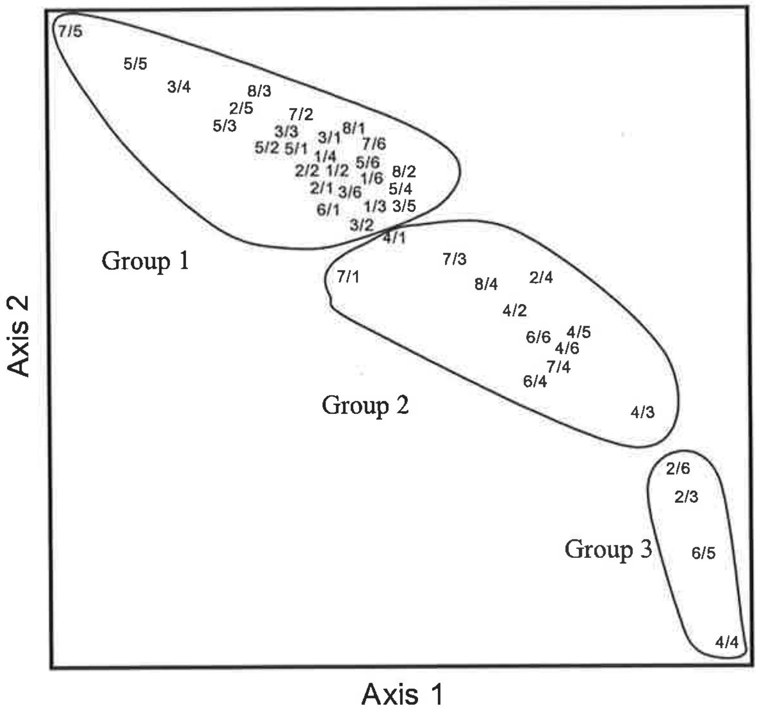
Cluster and ordination analyses proved useful techniques for identifying the variables that most influenced the combined response of individual plants. The key variables for both species were responsive to flooding, but were representative only of vegetative growth. Despite the contrasting size and growth forms of the species, measurements were simple and rapid assessment was possible. Although plants were amenable to repeated measures, kangaroo grazing reduced the number of plants for which repeated measures could be taken. Fenced plots could be used in future studies to protect plants from grazing.

The response time differed between variables for both species. Measures such as flower number and length and branch number and length started to respond between the first and second survey for *M. florulenta* whereas no flowers were observed until December and February for *S. mitchellii*. This implies that different survey frequency and timing may be necessary to capture information on specific responses for different species.

The frequency and timing of surveys required is also influenced by whether a variable demonstrates a cumulative response. A cumulative response occurs if new growth accumulates rather than abscises over the monitoring period. For example, *S. mitchellii's* new runners remained on the parent plant for at least the duration of the study. This compares with the leaves and flowers of *M. florulenta* that abscised soon after floodwater recession. The advantage of a cumulative response variable is that if plants cannot be monitored regularly during and after the flood a response can still be recorded 2-3 months after the event.

Figure 6.1. Ordination plots for the rates of increase in the response variables for *M. florulenta* for the periods October-December and October-February at a) Ninkle Nook, October-February (r^2= 0.96, stress = 3.6%), b) Ninkle Nook, October-December (r^2= 0.99, stress = 2.0%), c) Jane Eliza, October-February, (r^2= 0.99, stress = 2.1%), d) Jane Eliza, October-December, (r^2= 0.95, stress = 2.95), e) Wide Waters, October-February (r^2= 0.99, stress = 6.1%) and f) Wide Waters, October-December (r^2= 0.96, stress = 2.4%). Each plant on the ordination plot is labelled according to site and plant number e.g. 4/6, site 4, plant 6.

a)


7/5
5/5
3/4
8/3
2/5
7/2
5/3
3/3
3/1
8/1
5/2
5/1
7/6
1/4
2/2
1/2
5/6
8/2
2/1
3/6
1/6
5/4
6/1
1/3
3/5
3/2
4/1
Group 1
7/3
7/1
8/4
2/4
4/2
6/6
4/5
4/6
7/4
6/4
Group 2
4/3
2/6
2/3
Group 3
6/5
4/4
Axis 2
Axis 1

b)

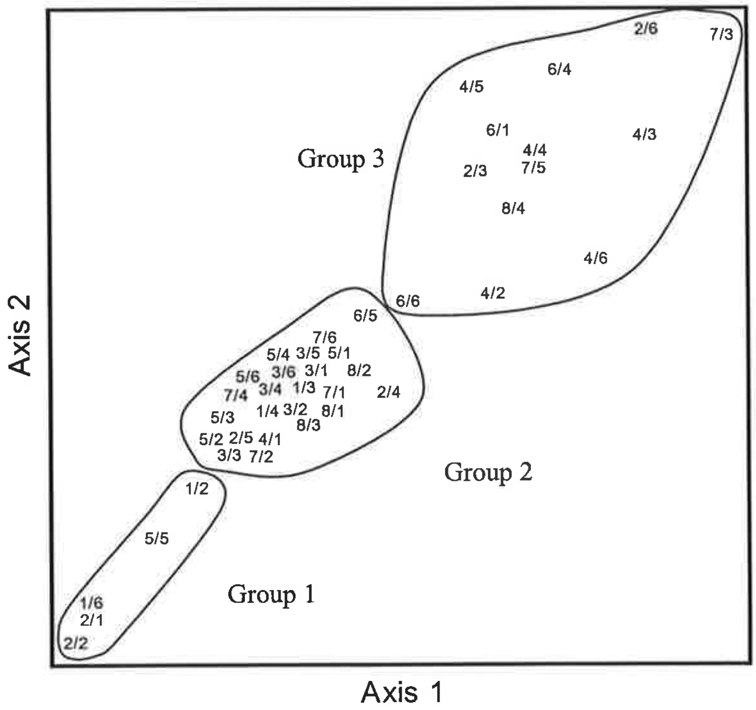
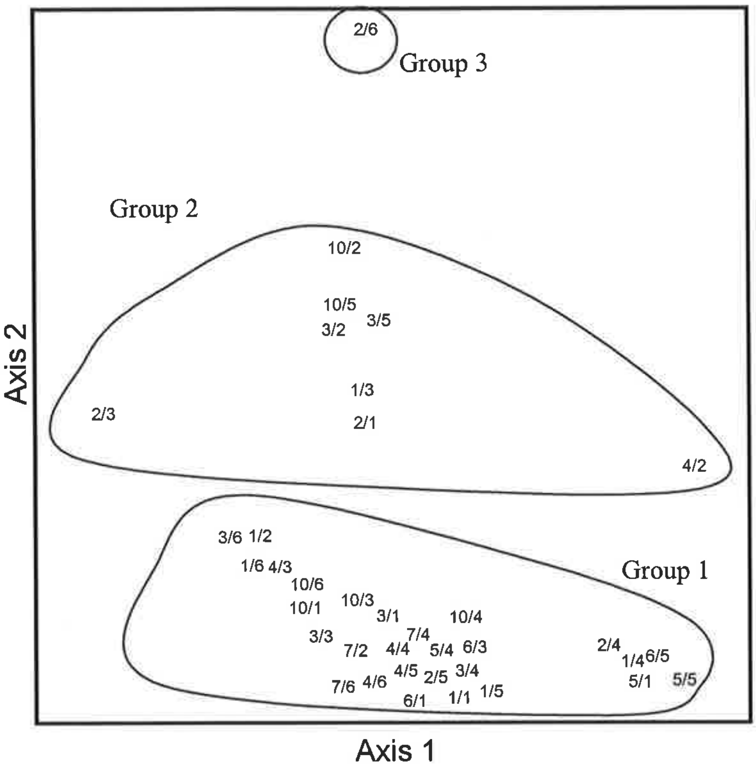

2/6
7/3
6/4
4/5
6/1
4/3
Group 3
4/4
2/3
7/5
8/4
4/6
6/6
4/2
6/5
7/6
5/4
3/5
5/1
5/6
3/6
3/1
8/2
7/4
3/4
1/3
7/1
2/4
5/3
1/4
3/2
8/1
8/3
5/2
2/5
4/1
3/3
7/2
Group 2
1/2
5/5
Group 1
1/6
2/1
2/2
Axis 2
Axis 1

Figure 6.1. (continued).

c)


2/6
Group 3
Group 2
10/2
10/5
3/2
3/5
1/3
2/3
2/1
4/2
3/6
1/2
1/6
4/3
10/6
10/1
10/3
3/1
10/4
Group 1
3/3
7/2
4/4
7/4
5/4
6/3
2/4
1/4
6/5
7/6
4/6
4/5
2/5
3/4
5/1
5/5
6/1
1/1
1/5
Axis 2
Axis 1

d)

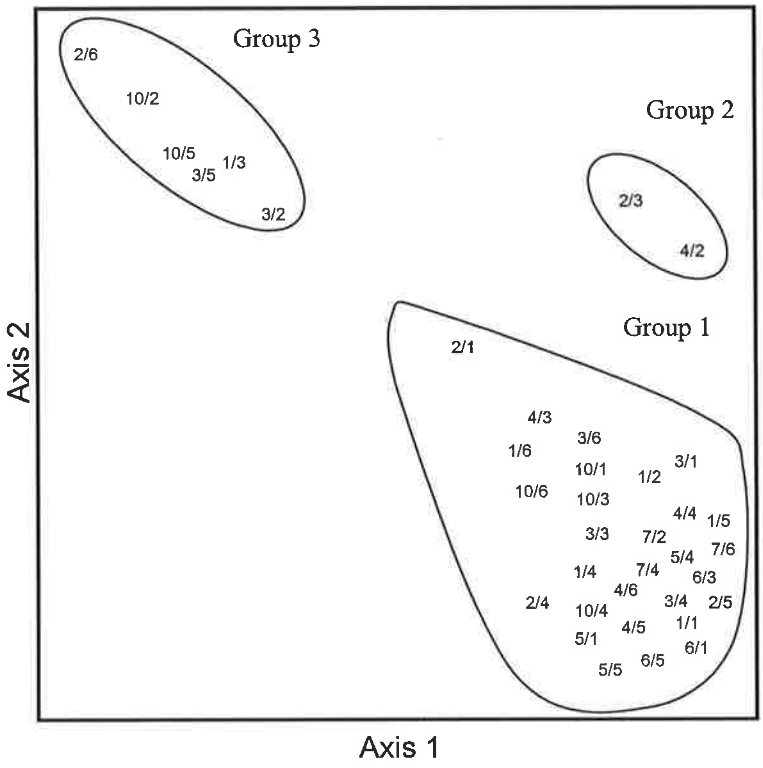
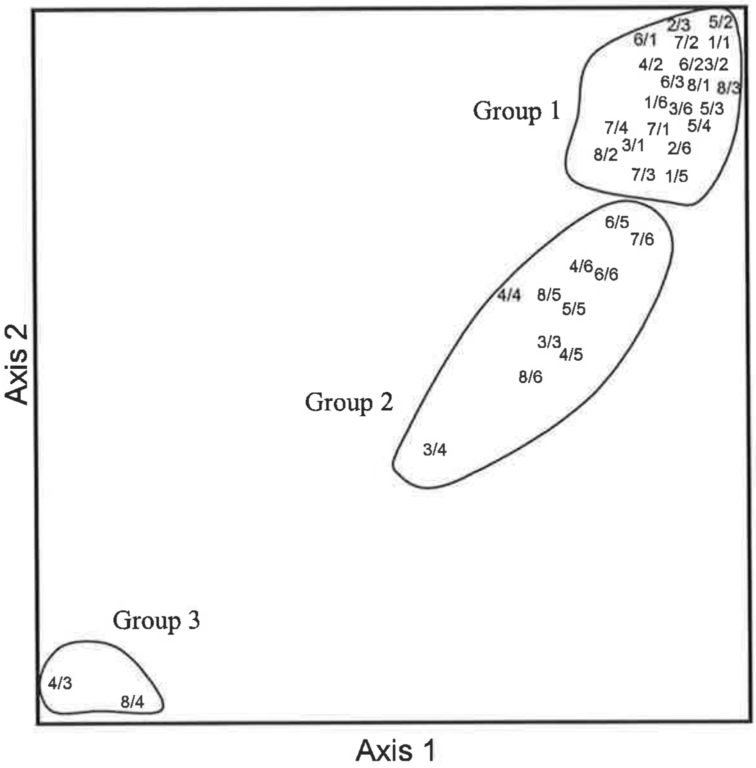

2/6
Group 3
10/2
10/5
1/3
3/5
3/2
Group 2
2/3
4/2
Group 1
2/1
4/3
3/6
1/6
10/1
1/2
3/1
10/6
10/3
4/4
1/5
3/3
7/2
7/6
5/4
1/4
7/4
6/3
4/6
2/4
10/4
3/4
2/5
1/1
4/5
5/1
6/1
5/5
6/5
Axis 2
Axis 1

Figure 6.1. (continued).

e)


Group 1
2/3
5/2
6/1
7/2
1/1
4/2
6/2
3/2
6/3
8/1
8/3
1/6
3/6
5/3
7/4
7/1
5/4
8/2
3/1
2/6
7/3
1/5
Group 2
6/5
7/6
4/6
6/6
4/4
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5/5
3/3
4/5
8/6
3/4
Group 3
4/3
8/4
Axis 2
Axis 1

f)

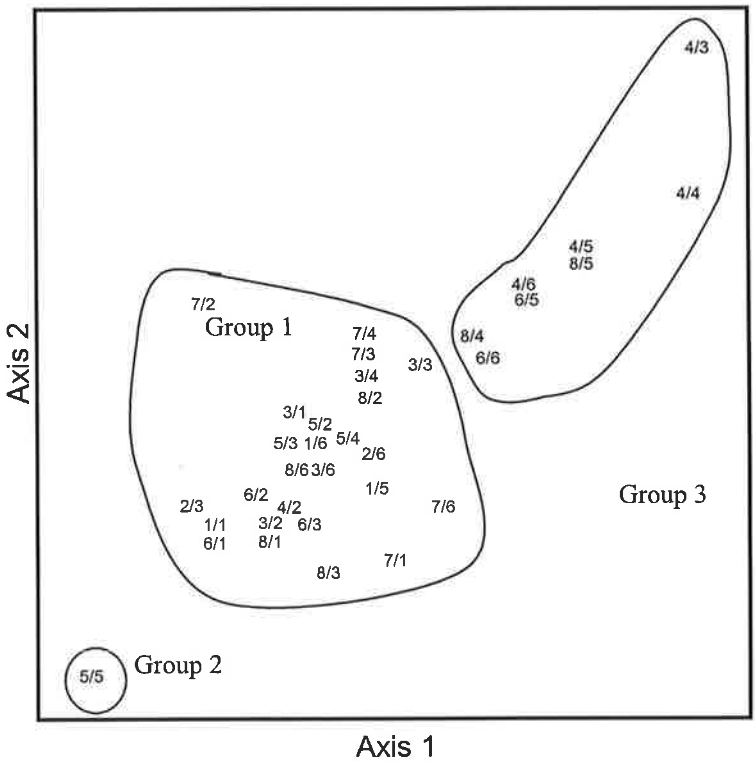
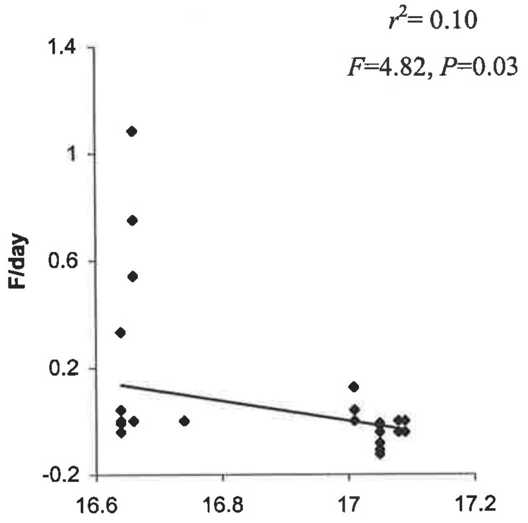
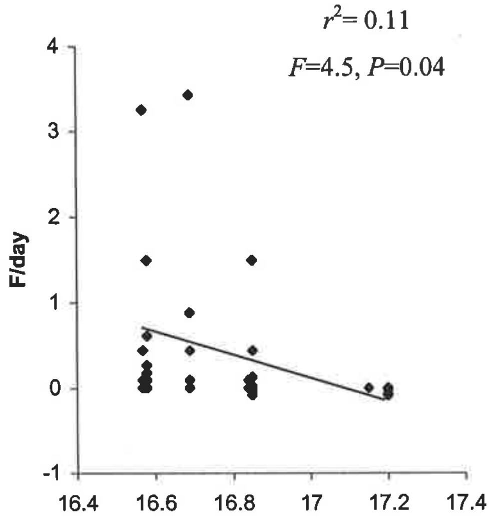

4/3
4/4
4/5
8/5
4/6
6/5
8/4
6/6
Group 3
7/2
Group 1
7/4
7/3
3/4
3/3
8/2
3/1
5/2
5/3
1/6
5/4
2/6
8/6
3/6
1/5
2/3
6/2
4/2
7/6
1/1
3/2
6/3
6/1
8/1
7/1
8/3
5/5
Group 2
Axis 2
Axis 1

Figure 6.2. The rates of increase for *M. florulenta* flowers at a) Ninkle Nook, b) Jane Eliza and c) Wide Waters. A trend line is included to show the slope of the linear regression where $P < 0.05$.

a)


r^2= 0.10
F=4.82, P=0.03
F/day
1.4
1
0.6
0.2
-0.2
16.6
16.8
17
17.2

b)


r^2= 0.11
F=4.5, P=0.04
F/day
4
3
2
1
0
-1
16.4
16.6
16.8
17
17.2
17.4

c)

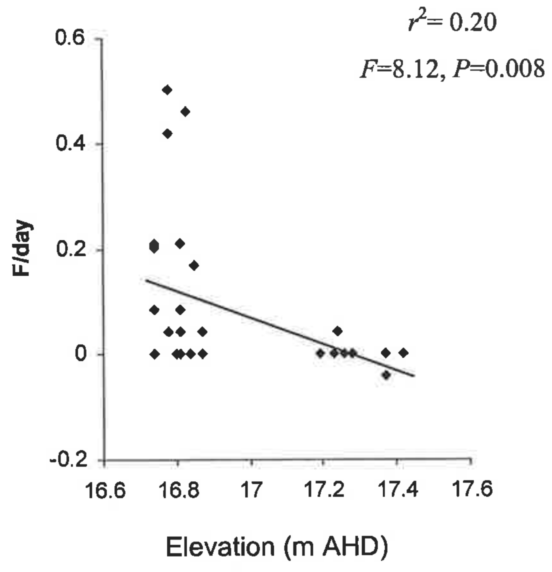
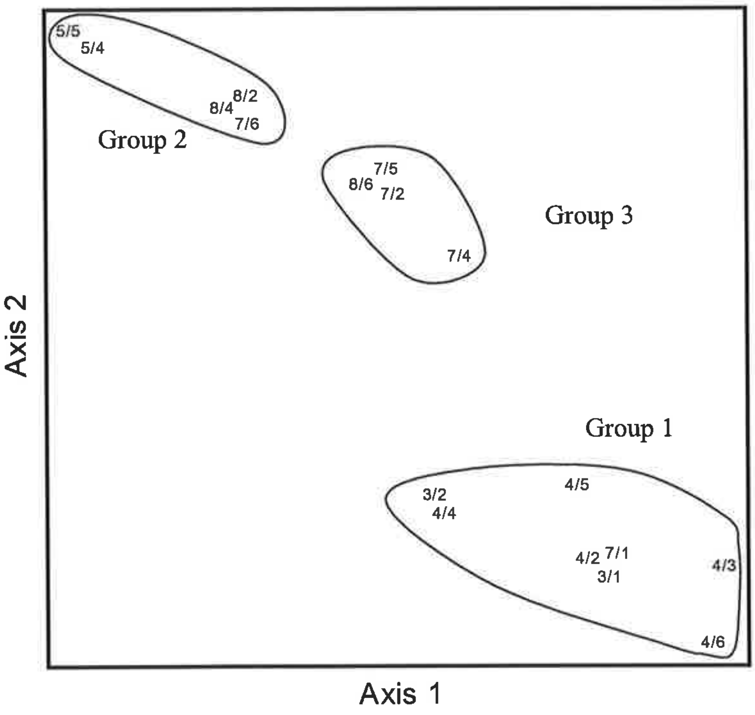

r^2= 0.20
F=8.12, P=0.008
F/day
0.6
0.4
0.2
0
-0.2
16.6
16.8
17
17.2
17.4
17.6
Elevation (m AHD)

Figure 6.3. Ordination plots for the rates of increase in the response variables for *S. mitchellii* from October to February at a) Ninkle Nook (r^2= 0.92, stress = 0.3%), b) Jane Eliza (r^2= 0.99, stress=1.1%) and c) Wide Waters (r^2= 0.96, stress = 3.6%). Each plant on the ordination plot is labelled according to site and plant number e.g. 4/6, site 4, plant 6.

a)


5/5
5/4
8/2
8/4
7/6
Group 2
7/5
8/6
7/2
7/4
Group 3
Group 1
3/2
4/4
4/5
4/2
7/1
3/1
4/3
4/6
Axis 2
Axis 1

b)

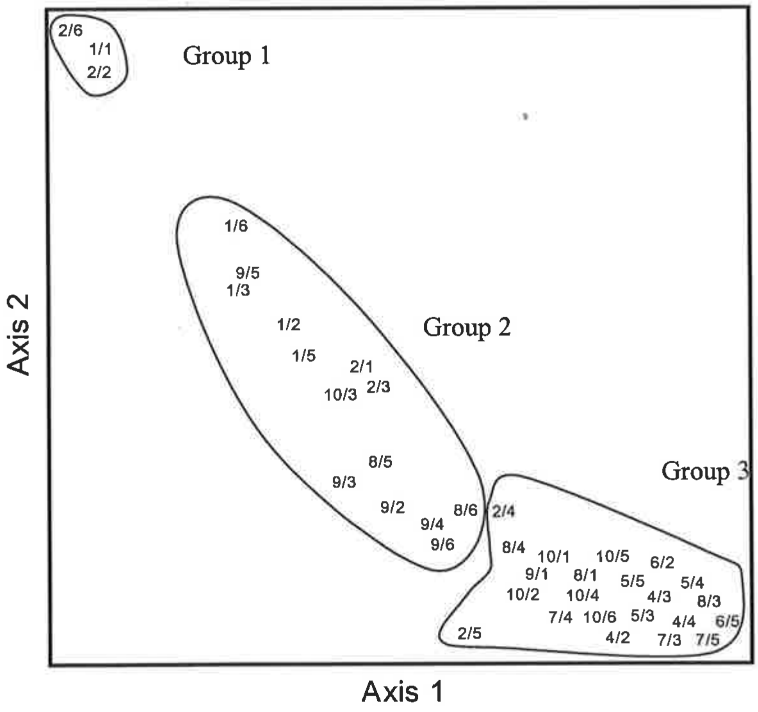

2/6
1/1
2/2
Group 1
1/6
9/5
1/3
1/2
1/5
2/1
10/3
2/3
Group 2
8/5
9/3
9/2
8/6
9/4
9/6
2/4
Group 3
8/4
10/1
10/5
6/2
9/1
8/1
5/5
5/4
10/2
10/4
4/3
8/3
7/4
10/6
5/3
4/4
6/5
2/5
4/2
7/3
7/5
Axis 2
Axis 1

Figure 6.3. (continued).

c)

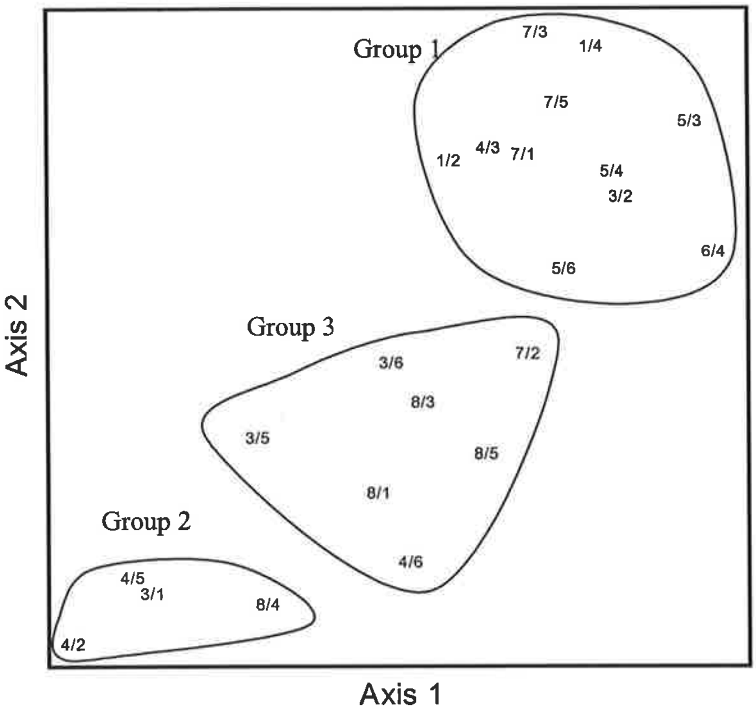
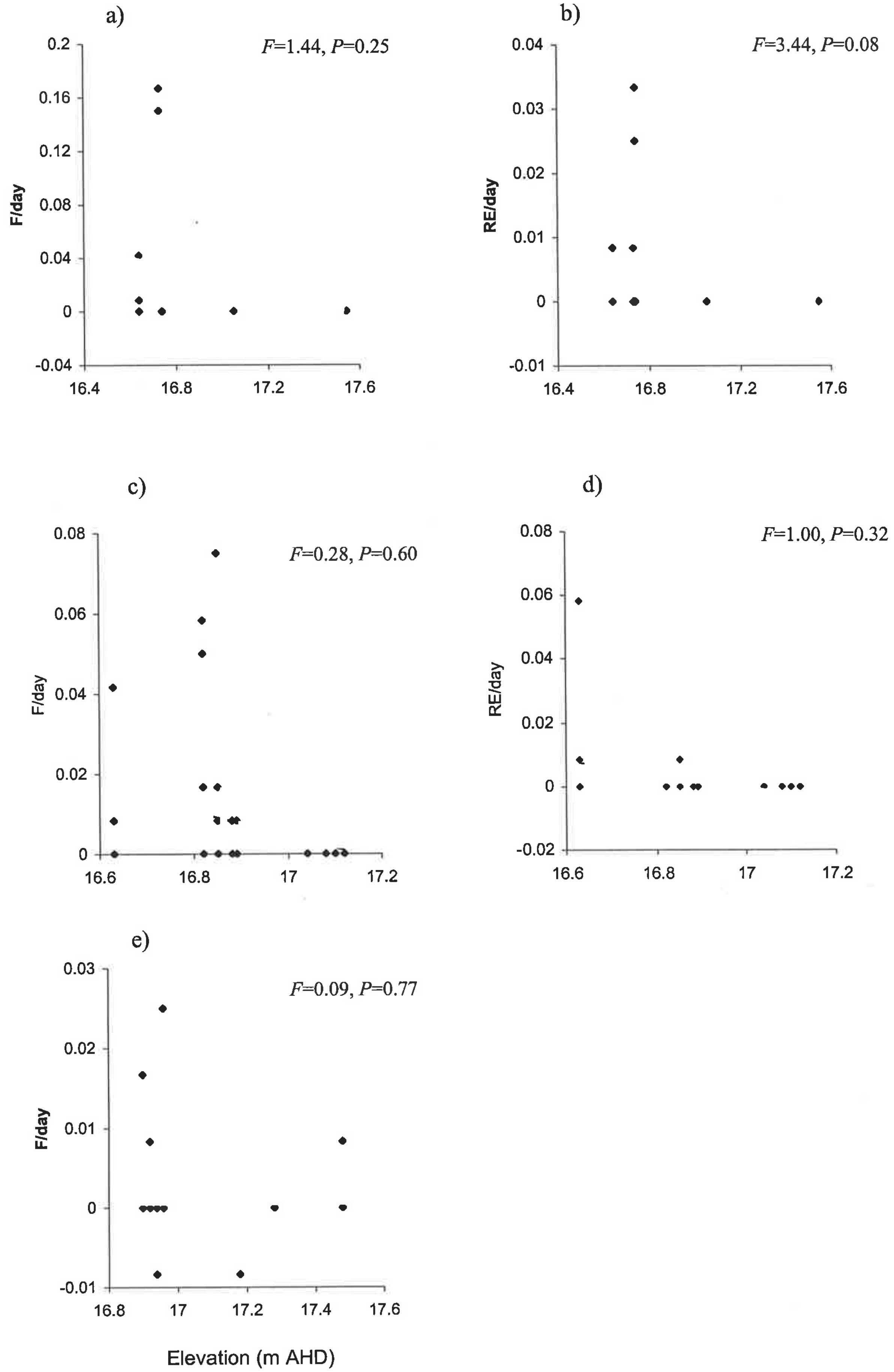

Group 1
7/3
1/4
7/5
5/3
1/2
4/3
7/1
5/4
3/2
6/4
5/6
Group 3
3/6
7/2
8/3
3/5
8/5
8/1
4/6
Group 2
4/5
3/1
8/4
4/2
Axis 2
Axis 1

Figure 6.4. The rates of increase for *S. mitchellii* a) flowers at Ninkle Nook, b) rooting established at Ninkle Nook, c) flowers at Jane Eliza, d) rooting established at Jane Eliza and e) flowers at Wide Waters. Trend lines are not shown because the slope of the linear regression for all data had $P > 0.05$.


a)
F=1.44, P=0.25
F/day
0.2
0.16
0.12
0.08
0.04
0
-0.04
16.4
16.8
17.2
17.6
b)
F=3.44, P=0.08
RE/day
0.04
0.03
0.02
0.01
0
-0.01
16.4
16.8
17.2
17.6
c)
F=0.28, P=0.60
F/day
0.08
0.06
0.04
0.02
0
16.6
16.8
17
17.2
d)
F=1.00, P=0.32
RE/day
0.08
0.06
0.04
0.02
0
-0.02
16.6
16.8
17
17.2
e)
F=0.09, P=0.77
F/day
0.03
0.02
0.01
0
-0.01
16.8
17
17.2
17.4
17.6
Elevation (m AHD)

CHAPTER 7

MORPHOLOGICAL AND PHYSIOLOGICAL RESPONSES OF EMERGENT MACROPHYTES TO CONTRASTING WATER REGIMES

7.1 Abstract

This study examined the morphological and physiological responses of four emergent macrophytes from the Lower Murray to slow (1 cm d^{-1}) and rapid (5 cm d^{-1}), shallow (20 cm) and deep (60 cm) flood and drawdown. *Bolboschoenus caldwellii*, which had the highest relative growth rate (RGR), and *Schoenoplectus validus* maintained growth across the widest range of water regimes followed by *Juncus aridicola* and *Cyperus gymnocaulos*. RGR was correlated with emergent photosynthetic area and root mass for all species. *B. caldwellii* extended culms when flooded and roots when exposed to drawdown. *S. validus* similarly increased culm height when flooded but failed to extend roots when subject to deep drawdown. In contrast, *C. gymnocaulos* and *J. aridicola* were unable to extend culms to maintain emergent tissue when flooded but were able to distribute roots throughout the soil profile when exposed to drawdown. The timing and magnitude of stomatal conductance changes suggest that *C. gymnocaulos* and *J. aridicola* may be better suited to drawdown induced low soil moisture stress. These results suggest that tolerance of drawdown requires a suite of specialised strategies in the same way that flood tolerance does and that it is equally as legitimate a factor in influencing the distribution of emergent macrophytes in wetlands subject to fluctuating water levels.

7.2 Introduction

When resources are limiting plants respond by allocating biomass to organs capable of harvesting the limiting resource (Chapin *et al.* 1987). Emergent macrophytes frequently increase shoot height when flooded to maintain contact with gaseous carbon dioxide (Stevenson and Lee 1987; Grace 1989; Squires and van der Valk

1992; Rea and Ganf 1994b). However, the response of emergent macrophytes to drawdown is less well documented.

Root extension, regulation of stomatal conductance, leaf abscission and reduced leaf area all contribute to drought tolerance (Taiz and Zeiger 1991; Fukai and Cooper 1995). Root extension is a common response to soil drought, e.g. sunflowers (Angadi and Entz 2002) and wheat (Shepherd et al. 2002), but has rarely been examined for emergent macrophytes. Root extension may be especially important where it enables plants to maintain contact with falling groundwater.

Intuitively, the rate and extent of flood or drawdown may determine whether shoots maintain access to the atmosphere and roots to water. The emergent macrophytes *Bolboschoenus caldwellii*, *Cyperus gymnocaulos*, *Juncus aridicola* and *Schoenoplectus validus* occupy a range of positions across the littoral zone of the Lower Murray (Blanch et al. 1999b; Blanch et al. 2000). *Cyperus gymnocaulos* occurs high on the elevation gradient at locations subject to infrequent flooding; *Juncus aridicola* and *Bolboschoenus caldwellii* occur near the water's edge; *Schoenoplectus validus* occupies sites low on the gradient that are generally permanently inundated. The differential species distribution suggests they possess different strategies for tolerating flood and drawdown.

This study examines the strategies used by *B. caldwellii*, *C. gymnocaulos*, *J. aridicola* and *S. validus* to tolerate contrasting regimes of flood and drawdown. Relative growth rate (RGR) enabled comparison of species performance and the net assimilation rate (NAR) and leaf area ratio (LAR) were used to analyse how the growth response was achieved. The ability to maintain access to photosynthetic resources (carbon dioxide and water) was assessed by culm and root extension and stomatal conductance was used as a measure of drought tolerance.

Based on their distribution across the littoral zone of the Lower Murray, it was predicted that:

1) *C. gymnocaulos* would prefer habitats liable to drawdown, a function of stomatal control and root extension, but would not tolerate inundation due to limited culm extension;
2) *B. caldwellii* and *J. aridicola* would maximise growth rates when subjected to shallow flood and drawdown but would have limited capacity to extend culms or

roots when exposed to deep flood and drawdown;

3) optimal growth rates for *S. validus* would be limited to flooded environments and plants would tolerate inundation by extending culms, but, would have a limited capacity to extend roots in the advent of drawdown.

7.3 Species description

Species descriptions have been compiled from information presented in Sainty and Jacobs (1981), Jessop and Toelken (1986), Sainty and Jacobs (1994), Cunningham *et al.* (1999) and Roberts and Marston (2000).

Bolboschoenus caldwellii (V.Cook) Soják Cyperaceae – Three-cornered rush

A native perennial sedge to 1-1.5m tall with creeping rhizomes that bears hard ovoid or bulbous tubers (15-25 mm diameter) giving rise to triquetrous culms with leaves up to 30-70 cm long and 2.5-10mm wide. Flowers occur in terminal ovoid clusters, 1-2 cm long, with several clusters in an inflorescence. Seeds are straw coloured to deep golden brown, 3-4 × 2-2.5 mm. Culms relate to a combination of leaves and culms whereas ramets refer to both above and below ground tissues for one asexual unit. Plants grow in fresh and brackish water and forms dense stands along the littoral zone of creeks and channels and may dieback during winter in temperate areas. Flowering occurs throughout the year, but most intensely from October to April.

Cyperus gymnocaulos Steudel Cyperaceae - Spiny sedge

A densely tufted native perennial with short, woody, horizontal rhizomes. Culms are cylindrical and spreading as they grow longer (50-100 cm). Leaves are reduced to thin membranous sheaths except in juvenile plants. Inflorescences have 1-6 stalked globular heads and are often proliferous (viviparous). Viviparous propagules are called bulbils. Seeds are dark brown and ovoid to ellipsoid. Plants may be common in localised areas forming dense stands on river and creek banks, lake shores, around swamps and near bores. Flowering occurs throughout the year.

Juncus aridicola L.Johnson in J.Black Juncaceae - Tussock rush

A shortly rhizomatous native perennial with cylindrical to conical culms from 60-150 cm tall and a diameter of 1-6 mm. True leaves are absent. Inflorescences are lateral, open and spreading with numerous regularly spaced flowers, subtended by a terminal bract. Seeds are 2-3 mm long. Plants are found in permanently to periodically flooded areas in climatically dry regions, especially in the semi-arid and arid zones. Growth and flowering is generally dependent on standing water and usually occurs in late autumn to spring.

Schoenoplectus validus (Vahl) Á.Löve & D.Löve Cyperaceae – River club-rush

A native perennial with creeping rhizomes up to 1-3 cm in diameter. Culms erect and cylindrical to 3 m tall, diameter to 10-20 mm. Leaves reduced to sheathing bases. Inflorescences are 2-7 cm long, subtended by a solitary bract, terminal but appearing lateral with numerous spikelets. Seed dark brown and ovoid 2-3 × 1-2 mm. *S. validus* is cosmopolitan and found in other climatically similar areas across the world e.g. California, United States of America. It occurs along the margins of slow moving water bodies, in deep water in natural wetlands, winter wet depressions and the upper reaches of estuaries. Flowering occurs from summer to autumn with the main growth period from October to April.

7.4 Methods

7.4.1 Experimental design

Plants were grown in ponds (4.5 × 3.5 × 1.2 m deep) located at the Department of Environmental Biology, University of Adelaide, South Australia. Material was collected from Banrock Station wetland, near Kingston-on-Murray, South Australia.

B. caldwellii was established from tubers, *C. gymnocaulos* and *S. validus* from rhizomes and *J. aridicola* from two culms with a small root mass. Ramets of each species were placed into 10 L black plastic bags (diameter 30 cm, depth 20 cm) filled with sandy loam and topped with grey cracking clay. Nutrients were supplied via a slow release fertiliser (8-9 month Osmocote®) at a rate equivalent to 100 g N $m^{-2}yr^{-1}$. For a justification of this rate of application see Morris and Ganf (2001).

Sixty plants of each species were established over a 50-day period with water levels kept at the sediment surface (8 August 2000 to 26 September 2000). Six plants of each species (one plant per pot = six pots) were allocated to each treatment and care was taken to ensure that there were no significant differences in mean weights between groups.

Table 7.1. Codes for the nine water regime treatments. Water levels at STAT remained at 0 cm throughout the study. 'Days' indicates the time taken for a treatment to reach its final depth. S – slow, R – rapid, F – flood, D - drawdown.

Code	Rate	Depth	Days	Code	Rate	Depth	Days
RD60	-5 cm d^{-1}	-60 cm	12	RF60	5 cm d^{-1}	60 cm	12
SD60	-1 cm d^{-1}	-60 cm	60	SF60	1 cm d^{-1}	60 cm	60
RD20	-5 cm d^{-1}	-20 cm	4	RF20	5 cm d^{-1}	20 cm	4
SD20	-1 cm d^{-1}	-20 cm	20	SF20	1 cm d^{-1}	20 cm	20
STAT	N/A	0 cm	N/A				

Nine water regimes (Table 7.1) were imposed through lowering (-20 and –60 cm, D) or raising (+20 and +60 cm, F) water levels above the sediment at slow (S - 1 cm d^{-1}) and rapid (R - 5 cm d^{-1}) rates. For one treatment water levels remained at the sediment surface (STAT). Plants subjected to a drawdown of 60 cm were placed into re-enforced plastic cylinders (30 cm diameter, 100 cm high) filled with sandy-loam. These provided plants with an opportunity to maintain contact with falling water levels via root extension. The ponds were fitted with solenoids and depth sensors that enabled automated water level fluctuations.

The experimental period coincided with the species growing season and lasted 100 days (27 September 2000 to 5 January 2001). The large number of pots (total = 208) meant that the experiment had to harvested over 19 days (5 January to 24 January 2001).

7.4.2 Data collection

The initial dry weight of propagules was estimated from the fresh to dry weight ratio of propagules. The fresh weights spanned a range equivalent to that of the experimental material. This yielded the following relationships:

B. caldwellii	dw = -0.43 + 0.54×fw	(r^2=0.96, n=20, F=464.0, P <0.0001)
C. gymnocaulos	dw = -0.101+0.36×fw	(r^2=0.99, n=20, F=2277.8, P <0.0001)
J. aridicola	dw = -0.086+0.33×fw	(r^2=0.88, n=20, F=137.4, P <0.0001)

S. validus dw = 1.45+0.15×fw (r^2=0.60, n=20, F=27.4, P <0.0001)

where dw represents the dry weight of propagules (g) and fw the fresh weight (g).

Six plants of each species were randomly harvested from the plants present at the completion of the establishment phase. Dry weights were used to determine the growth rate for each species during the establishment phase, which was used to estimate the weight of plants at the start of the experimental period. The initial leaf area of plants was determined using the relationship between culm height and photosynthetic area for plants harvested at the end of the establishment phase.

All species possessed stems, but leaves were highly reduced for *C. gymnocaulos*, *J. aridicola* and *S. validus*. For consistency, stems, with or without leaves, were collectively referred to as 'culms'.

The height and density of culms was recorded at the start of the establishment period and the start and end of the experimental period. Measurements were also taken on 7 October, 23 October and 29 November to coincide with the plants reaching different depths within their respective water regimes.

Prior to harvest, stomatal conductance was measured with a Null-balance Porometer (LI-2600, Li-Cor). For plants at STAT and RD60, measurements were made along the upper third of the culm or leaf. Six leaves were randomly measured on each of eight runs from 7:00h to 19:00h. Recordings were taken over two consecutive days to ensure that stomatal conductance was measured at approximately the same time for all species.

At the completion of the experiment the emergent photosynthetic tissue from one pot per species per treatment was harvested and used to determine the relationship between emergent area and dry weight. All remaining plants were separated into their constituent parts.

Above ground tissue was divided into culms and flowers (bulbils for *C. gymnocaulos*). For flooded plants the emergent (above the water surface) and submerged (below the water surface) portion of the culm were separated. For plants exposed to drawdown and STAT, the entire culm was considered to be emergent. Below ground tissue was separated into rhizomes, roots and tubers for *B. caldwellii*; *C. gymnocaulos* - rhizomes and roots; *S. validus* - emergent rhizomes, roots. Although

J. aridicola has rhizomes, these are small and difficult to isolate and plants were divided into the emergent and submerged portion of culms, flowers and rhizomes + roots.

The weight of roots in the soil sections 0-25 cm, 25- 40 cm and 40 – 60 cm were determined for SD60 and RD60 by excavating soil from the cylinders. Soil moisture content in the top 10 cm of soil for STAT and all drawdown treatments was measured using a Delta T Theta Probe. The probe measured volumetric soil moisture content (m^3 m^{-3}).

All tissue was dried at 80°C to constant weight.

7.4.3 Analyses

Relative Growth Rate, Net Assimilation Rate and Leaf Area Ratio (RGR, NAR, LAR), were calculated after Harper (1977):

$$RGR = \frac{\ln W_f - \ln W_i}{\Delta t} \qquad \text{mg g}^{-1}\text{ d}^{-1} \qquad (1)$$

$$NAR = \frac{W_f - W_i}{\Delta t} \times \frac{\ln L_f - \ln L_i}{L_f - L_i} \qquad \text{g m}^{-2}\text{ d}^{-1} \qquad (2)$$

$$LAR = \frac{L_f - L_i}{W_f - W_i} \times \frac{\ln W_f - \ln W_i}{\ln L_f - \ln L_i} \qquad \text{m}^{2}\text{ kg}^{-1} \qquad (3)$$

Δt days represents the length of the experimental period. W_f and W_i are the final and initial dry weights and L_f and L_i are the final and initial photosynthetic areas.

Blanch *et al.* (1999a) demonstrated that submerged leaves of *B. medianus* do not photosynthesise. It was assumed that this applied to *B. caldwellii* and the other species and L_f was equivalent to the emergent leaf area. The emergent area for each species was estimated from the relationship between emergent area and the dry weight of emergent tissue. The relationship differed across water regime treatments and a separate relationship was calculated for each (Appendix 5).

The emergent area of the culms and leaves (one side) of *B. caldwellii* was measured using a Delta T leaf area meter. The other species have leafless culms with an approximately circular base. When culms ended in a point, the formula for the area of a cone was applied, whereas for culms with a blunt end the formula for the surface area of a frustum was used. Final weights of above and below ground tissue were used to determine the ratio of above to below ground biomass (AG:BG).

Responses across treatments were compared using analysis of variance (ANOVA) after testing for normality with the Shapiro-Wilk test and for equality of variances using the O'Brien and the Brown-Forsythe test (JMP IN ver. 3.2.1, SAS Institute Inc. 1994). Where data were not normally distributed, a non-parametric Kruskal-Wallis test was applied. Proportional data were analysed with ANOVA after applying an arcsine square root transformation followed by a normality check with the Shapiro-Wilk test.

Means for parametric data were compared using Tukey's Honestly Significant Difference (HSD) test (JMP IN ver. 3.2.1). The Nemenyi test was applied to determine differences for non-parametric data (Zar 1984). Statistical significance for all tests was determined with $\alpha = 0.05$.

Stomatal conductance was analysed using a repeated measures ANOVA after checking for the significance of the sphericity test and an adjusted or unadjusted univariate test (JMP IN ver. 3.2.1).

7.5 Results

7.5.1 Survival and relative growth rate and its components

B. caldwellii

Relative growth rates were similar for plants subjected to shallow drawdown, STAT and slow deep flooding (Table 7.2). RGR declined for plants subject to deep drawdown and rapid deep flooding. Only three plants survived at RF60 with RGR varying from 1.1 mg g^{-1} d^{-1} to 55.2 and 57.1 mg g^{-1} d^{-1}.

The lowest net assimilation rates were recorded for the treatments STAT and SF20 but these were accompanied by increased leaf area ratios that enabled these plants to maintain RGR. Plants exposed by 60 cm had the highest NAR but this was offset by lower LAR. The other treatments had similar NAR's and LAR's that enabled them to maintain optimal growth rates (Table 7.2).

Growth was asymptotically related to the logarithm of emergent leaf area and root

Table 7.2. The mean relative growth rate (RGR), net assimilation rate (NAR) and leaf area ratio (LAR) (± SD) for *B. caldwellii* across the treatment water regimes. *n*=6 for all treatments except RF60 where *n*=3 for all variables. Superscripts indicate treatments with similar responses (α=0.05). Treatment codes are in Table 7.1.

Treatment	RGR (mg g^{-1} d^{-1})		NAR (g m^{-2} d^{-1})		LAR (m^2 kg^{-1})	
F (df), *P*	8.2 (8,42), <0.0001		2.8 (8,42), 0.01		9.7 (8,42), <0.0001	
SD60	45.3^{bcd}	2.7	28.4^{a}	10.6	1.8^{de}	0.6
RD60	39.5^{cd}	2.5	25.7^{ab}	4.1	1.6^{e}	0.3
SD20	53.6^{ab}	1.9	21.8^{ab}	1.3	2.5^{abcd}	0.2
RD20	51.5^{ab}	2.0	20.0^{ab}	2.3	2.6^{abc}	0.3
STAT	52.3^{ab}	1.9	18.3^{b}	2.7	2.9^{ab}	0.4
SF20	57.4^{a}	2.8	18.2^{b}	1.3	3.2^{a}	0.1
RF20	56.7^{a}	4.2	20.7^{ab}	4.1	2.8^{abc}	0.4
SF60	49.5^{abc}	5.7	23.0^{ab}	4.0	2.2^{bcde}	0.2
RF60	33.9^{d}	23.0	17.7^{ab}	10.3	1.9^{cde}	1.2

Table 7.3. The mean relative growth rate (RGR), net assimilation rate (NAR) and leaf area ratio (LAR) (± SD) for *C. gymnocaulos* across the treatment water regimes. *n*=6 for all treatments except for RD20 (*n*=5), SF60 and RF60. For RGR, *n*=6 at SF60, but *n*=2 for NAR and LAR. For RGR, *n*=5 at RF60. Superscripts indicate treatments with similar responses (α=0.05). Treatment codes are described in Table 7.1.

Treatment	RGR (mg g^{-1} d^{-1})		NAR (g m^{-2} d^{-1})		LAR (m^2 kg^{-1})	
F (df), *P*	47.9 (8,43), <0.0001		15.8 (7,35), <0.0001		18.1 (7,35), <0.0001	
SD60	34.4^{a}	2.6	14.4^{a}	2.5	2.4^{b}	0.3
RD60	31.5^{a}	1.3	13.0^{a}	2.1	2.5^{b}	0.4
SD20	28.1^{a}	2.1	6.2^{cd}	0.6	4.6^{a}	0.5
RD20	29.9^{a}	6.6	8.1^{bc}	1.7	3.7^{a}	0.3
STAT	31.0^{a}	4.5	7.6^{c}	1.0	4.1^{a}	0.7
SF20	8.7^{b}	2.1	4.3^{cd}	1.9	2.3^{b}	0.8
RF20	1.5^{b}	12.4	1.9^{d}	5.5	1.7^{b}	1.0
SF60	0.8^{b}	2.6	2.9^{cd}	1.6	1.2^{b}	0.3
RF60	-0.4^{b}	2.6	N/A		N/A	

mass (Figures 7.1 and 7.2).

C. gymnocaulos

Plants subjected to drawdown and static water regimes had similar growth rates, which were markedly higher, compared with plants subjected to flood. Most plants flooded to 60 cm had negative RGRs (Table 7.3).

The strategies for maintaining RGR differed among plants exposed to shallow versus deep drawdown; plants exposed to shallow drawdown maintained high leaf area ratios but lower NARs, whereas under deep drawn down plants responded to a decline in LAR by increasing NAR (Table 7.3). Reduced growth for flooded plants was due primarily to declining LAR and to a lesser extent declining assimilation rates (Table 7.3).

Growth was asymptotically related to the logarithm of emergent leaf area and root mass (Figures 7.3 and 7.4).

J. aridicola

One plant from each of SF20, RD20, SD20 and RD60 did not survive. The distribution of these plants between treatments and the response of other plants within the same treatment suggests that death was not a function of water regime.

Relative growth rate was greatest for plants exposed to drawdown and static conditions (Table 7.4). Rapid shallow flooding led to a decline in growth compared to plants at SD20, but deep flooding resulted in rates of biomass accumulation significantly less than for all other treatments (Table 7.4). Three plants at RF60 had negative growth rates. The low RGR was a result of the inability of plants to maintain emergent photosynthetic tissue when flooded. Although there was no emergent tissue at the end of the experiment growth did occur for two plants (RGRs of 8.7 and 3.4 mg g^{-1} d^{-1}: Table 7.4).

The lower RGR at SF60 was a result of a combination of decreasing NAR and LAR. The assimilation rate and leaf area ratio for plants at SF60, were 57% and 52 % lower than the maximum recorded values (Table 7.4).

Growth was asymptotically related to the logarithm of emergent leaf area and root mass (Figures 7.5 and 7.6).

Table 7.4. The mean relative growth rate (RGR), net assimilation rate (NAR) and leaf area ratio (LAR) (± SD) for *J. aridicola* across the treatment water regimes. *n*=6 for all except RD20, RD60, SD20, SF20 where *n*=5. Superscripts indicate treatments with similar responses (α=0.05). Treatment codes are described in Table 7.1.

Treatment	RGR (mg g^{-1} d^{-1})		NAR (g m^{-2} d^{-1})		LAR (m^2 kg^{-1})	
F (df), *P*	18.9 (8,41), <0.0001		4.7 (7,35), 0.0008		7.0 (7,35), <0.0001	
SD60	29.8^{ab}	3.2	8.1^{a}	1.1	3.7^{ab}	0.3
RD60	22.3^{ab}	5.4	6.8^{abc}	1.4	3.3^{bc}	0.5
SD20	32.1^{a}	1.7	7.1^{abc}	0.8	4.6^{a}	0.4
RD20	29.0^{ab}	5.6	7.1^{abc}	1.6	4.1^{ab}	0.7
STAT	29.4^{ab}	4.0	7.7^{ab}	1.6	3.9^{ab}	0.8
SF20	22.5^{ab}	2.8	5.3^{bc}	0.9	4.3^{ab}	0.4
RF20	21.7^{b}	5.3	5.5^{abc}	0.9	3.9^{ab}	0.6
SF60	11.3^{c}	7.0	4.6^{c}	2.1	2.4^{c}	0.9
RF60	5.6^{c}	6.5	N/A		N/A	

Table 7.5. The mean relative growth rate (RGR), net assimilation rate (NAR) and leaf area ratio (LAR) (± SD) for *S. validus* across the treatment water regimes. Three plants did not survive the experimental period and hence *n*=4 for RD60 and *n*=5 for RF60. *n*=6 for all other treatments. Superscripts indicate treatments with similar responses (α=0.05). Treatment codes are described in Table 7.1.

Treatment	RGR (mg g^{-1} d^{-1})		NAR (g m^{-2} d^{-1})		LAR (m^2 kg^{-1})	
F (df), *P*	11.7 (8,42), <0.0001		7.5 (8,42), <0.0001		14.3 (8,42), <0.0001	
SD60	15.6^{b}	2.0	8.1^{bcd}	1.0	2.0^{cd}	0.4
RD60	8.1^{c}	2.5	5.1^{d}	1.5	1.6^{d}	0.2
SD20	20.2^{ab}	2.7	7.2^{bcd}	0.6	2.8^{b}	0.2
RD20	18.8^{ab}	4.0	9.1^{abc}	1.6	2.1^{cd}	0.4
STAT	22.9^{a}	2.4	6.5^{cd}	1.1	3.6^{a}	0.5
SF20	19.4^{ab}	3.4	7.8^{bcd}	1.0	2.5^{bc}	0.3
RF20	22.4^{a}	1.4	10.9^{a}	1.1	2.1^{cd}	0.3
SF60	19.3^{ab}	1.7	9.9^{a}	2.8	2.1^{bcd}	0.5
RF60	17.6^{ab}	3.8	7.6^{bcd}	1.6	2.3^{bcd}	0.3

S. validus

Plants at STAT and RF20 had the highest RGRs that were similar to those for all other treatments except the slow and rapid drawdowns to 60 cm. Exposure by 60 cm resulted in significantly depressed RGRs and (Table 7.5) two plants did not survive this treatment.

The rank order of the RGRs was not reflected by the rank order of NAR or LAR. Instead, different combinations of NAR and LAR maintained RGR. In four treatments plant leafiness was crucial and in another four net assimilation was paramount. For plants rapidly exposed by 60 cm the lowest RGR was a reflection of low NAR and LAR.

Relative growth rate had a logarithmic relationship with emergent area and root mass (Figures 7.7 and 7.8).

7.5.2 Species comparison of relative growth rate and its components

Under the static treatment, RGRs ranked the species *B. caldwellii* > *C. gymnocaulos* = *J. aridicola* > *S. validus*. A similar ranking occurred for all drawdown treatments. *B. caldwellii* maintained its ranking under flood treatments, whereas *C. gymnocaulos* performed poorly and was generally relegated to fourth position. *J. aridicola* and *S. validus* occupied intermediate rankings under shallow flooding with the latter performing better under RD60 (Table 7.6.).

The high growth rate of *B. caldwellii* was a function of an assimilation rate at least double that recorded for the other species for most treatments (Table 7.6). In contrast, the leaf area ratio for *B. caldwellii* was less than for other species for drawdown treatments and equivalent for flooded treatments.

Among the remaining species the assimilation rate varied little and the difference in growth rate for plants exposed to drawdown was mainly a function of leafiness. In contrast, the difference in growth for plants subject to flooding was due to a combination of assimilation rate and leaf area ratio (Table 7.6).

Table 7.6. Comparison of the mean relative growth rate (RGR), net assimilation rate (NAR) and leaf area ratio (LAR) (± SD) between species. Superscripts indicate species with similar responses for respective treatments (α=0.05). Treatment codes are described in Table 7.1.

	Species	RGR (mg g^{-1} d^{-1})		NAR (g m^{-2} d^{-1})		LAR (m^{2} kg^{-1})	
F (df), *P*		84.9 (3,17), <0.0001		65.1 (3,17), <0.0001		24.4 (3,17), <0.0001	
RD60	*B. caldwellii*	39.5^{a}	2.5	25.7^{a}	4.1	1.6^{c}	0.3
	C. gymnocaulos	31.5^{b}	1.3	13.0^{b}	2.1	2.5^{b}	0.4
	J. aridicola	22.3^{c}	5.4	6.8^{c}	1.4	3.3^{a}	0.5
	S. validus	8.1^{d}	2.5	5.1^{c}	1.5	1.6^{c}	0.2
F (df), *P*		127.9 (3,20), <0.0001		18.1 (3,20), <0.0001		27.8 (3,20), <0.0001	
SD60	*B. caldwellii*	45.3^{a}	2.7	28.4^{a}	10.6	1.8^{b}	0.6
	C. gymnocaulos	34.4^{b}	2.6	14.4^{b}	2.5	2.4^{b}	0.3
	J. aridicola	29.8^{c}	3.2	8.1^{b}	1.1	3.7^{a}	0.3
	S. validus	15.6^{d}	2.0	8.1^{b}	1.0	2.0^{a}	0.4
F (df), *P*		50.6 (3,18), <0.0001		61.6 (3,18), <0.0001		25.4 (3,18), <0.0001	
RD20	*B. caldwellii*	51.5^{a}	2.0	20.0^{a}	2.3	2.6^{b}	0.3
	C. gymnocaulos	29.9^{b}	6.6	8.1^{b}	1.7	3.7^{a}	0.3
	J. aridicola	29.0^{b}	5.6	7.1^{b}	1.6	4.1^{a}	0.7
	S. validus	18.8^{c}	4.0	9.1^{b}	1.6	2.1^{b}	0.4
F (df), *P*		259.3 (3,19), <0.0001		414.5 (3,19), <0.0001		61.4 (3,19), <0.0001	
SD20	*B. caldwellii*	53.6^{a}	1.9	21.8^{a}	1.3	2.5^{b}	0.2
	C. gymnocaulos	28.1^{c}	2.1	6.2^{b}	0.6	4.6^{a}	0.5
	J. aridicola	32.1^{b}	1.7	7.1^{b}	0.8	4.6^{a}	0.4
	S. validus	20.2^{d}	2.7	7.2^{b}	0.6	2.8^{b}	0.2
F (df), *P*		87.2 (3,20), <0.0001		62.4 (3,20), <0.0001		4.5 (3,20), 0.01	
STAT	*B. caldwellii*	52.3^{a}	1.9	18.3^{a}	2.7	2.9^{b}	0.4
	C. gymnocaulos	31.0^{b}	4.5	7.6^{b}	1.0	4.1^{a}	0.7
	J. aridicola	29.4^{b}	4.0	7.7^{b}	1.6	3.9^{a}	0.8
	S. validus	22.9^{c}	2.4	6.5^{b}	1.1	3.6^{ab}	0.5
F (df), *P*		62.8 (3,20), <0.0001		33.0 (3,20), <0.0001		15.3 (3,20), <0.0001	
RF20	*B. caldwellii*	56.7^{a}	4.2	20.7^{a}	4.1	2.8^{b}	0.4
	C. gymnocaulos	1.5^{c}	12.4	1.9^{c}	5.5	1.7^{c}	1.0
	J. aridicola	21.7^{b}	5.3	5.5^{bc}	0.9	3.9^{a}	0.6
	S. validus	22.4^{b}	1.4	10.9^{b}	1.1	2.1^{bc}	0.3

Table 7.6. (continued).

	Species	RGR (mg g^{-1} d^{-1})		NAR (g m^{-2} d^{-1})		LAR (m^{2} kg^{-1})	
F (df), *P*		335.6 (3,19), <0.0001		131.2 (3,19), <0.0001		19.4 (3,19), <0.0001	
SF20	*B. caldwellii*	57.4^{a}	2.8	18.2^{a}	1.3	3.2^{b}	0.1
	C. gymnocaulos	8.7^{c}	2.1	4.3^{c}	1.9	2.3^{c}	0.8
	J. aridicola	22.5^{b}	2.8	5.3^{c}	0.9	4.3^{a}	0.4
	S. validus	19.4^{b}	3.4	7.8^{b}	1.0	2.5^{bc}	0.3
F (df), *P*		8.5 (3,15), 0.001		5.1 (1,6) 0.07		0.006 (1,6), 0.94	
RF60	*B. caldwellii*	33.9^{a}	23.0	17.7^{a}	10.3	1.9^{a}	1.2
	C. gymnocaulos	-5.9^{c}	13.8	N/A		N/A	
	J. aridicola	5.6^{bc}	6.5	N/A		N/A	
	S. validus	17.6^{ab}	3.8	7.6^{a}	1.6	2.3^{a}	0.3
F (df), *P*		115.0 (3,20), <0.0001		45.5 (3,16), <0.0001		2.0 (3,16), 0.15	
SF60	*B. caldwellii*	49.5^{a}	5.7	23.0^{a}	4.0	2.2^{a}	0.2
	C. gymnocaulos	0.8^{d}	2.6	2.9^{bc}	1.6	1.2^{a}	0.3
	J. aridicola	11.3^{c}	7.0	4.6^{c}	2.1	2.4^{a}	0.9
	S. validus	19.3^{b}	1.7	9.9^{b}	2.8	2.1^{a}	0.5

7.5.3 *Morphological responses and biomass allocation*

B. caldwellii

Deep flooded plants increased the proportional allocation to above ground tissue by five to six times compared to plants at STAT (Table 7.7). This was paralleled by an increase in the height of flooded plants, especially those subject to deep flooding that were about 30 cm taller than at STAT ($F_{8,42}$=62.6, P<0.0001; Figure 7.9). Although the proportion of submerged tissue increased under flooding, increased height enabled plants to maintain emergent tissue (Table 7.7). The proportion of weight allocated to emergent tissue was also the same across drawdown treatments, but culms declined in height from STAT and shallow drawdown treatments to slow deep drawdown and again to rapid deep drawdown (Table 7.7).

All plants exposed to drawdown and STAT allocated more biomass to below ground tissue (Table 7.7). However, the allocation of biomass to roots differed across drawdown treatments and declined from RD20 to deep drawdown (Table 7.7).

Plants slowly and rapidly drawndown to –60 cm allocated approximately the same

Table 7.7. The mean above to below ground biomass ratio (AG:BG) and the proportion of total weight allocated to culms and roots for *B. caldwellii* (±SD). For flooded plants, allocation to culms is divided between the emergent and submerged portion of the culm. Superscripts indicate treatments with similar responses ($\alpha=0.05$).

	AG:BG		Emergent		Submerged		Roots	
F (df), *P*	7.1 (8,42), <0.0001		2.2 (8,42), 0.05		26.7 (3,17), <0.0001		4.5 (8,42), 0.0005	
SD60	0.98^{c}	0.75	0.37^{a}	0.19	N/A		0.06^{b}	0.01
RD60	0.51^{c}	0.09	0.33^{a}	0.04	N/A		0.09^{ab}	0.03
SD20	0.90^{c}	0.11	0.44^{a}	0.03	N/A		0.10^{ab}	0.03
RD20	0.91^{c}	0.26	0.46^{a}	0.07	N/A		0.14^{a}	0.05
STAT	0.83^{bc}	0.11	0.44^{a}	0.04	N/A		0.08^{ab}	0.03
SF20	1.42^{bc}	0.24	0.43^{a}	0.03	0.15^{b}	0.02	0.11^{ab}	0.03
RF20	1.76^{bc}	0.67	0.40^{a}	0.08	0.20^{b}	0.09	0.14^{a}	0.07
SF60	4.04^{a}	2.43	0.36^{a}	0.06	0.40^{a}	0.04	0.06^{b}	0.02
RF60	3.99^{ab}	2.83	0.27^{a}	0.11	0.49^{a}	0.12	0.06^{ab}	0.03

root weight to each soil section (0.15 – 0.40 g/cm). There was also an equal distribution of root weight to different soil sections within treatments.

C. gymnocaulos

The AG:BG of *C. gymnocaulos* declined from 4.82 at STAT to < 1 for deep flooded plants as a result of the dieback of above ground tissue rather than increased allocation to below ground tissue (Table 7.8). This conclusion is supported by the significant reduction in the proportion of weight allocated to emergent tissue for flooded versus drawndown plants (Table 7.8).

Culm height declined for flooded plants with none of the deep flooded plants possessing emergent tissue ($F_{8,41}=22.5$, $P < 0.0001$: Figure 7.8). Culms on deep flooded plants remained alive until the end of the experiment. The longest culms were for plants at STAT (131 cm) and those subject to slow, shallow drawdown (133 cm). The allocation of biomass to below ground tissue increased for plants exposed to rapid shallow drawdown and deep drawdown relative to STAT (Table 7.8). This trend was also evident for the proportion of weight allocated to roots, with plants at RD60

Table 7.8. The mean above to below ground biomass ratio (AG:BG) and the proportion of total weight allocated to culms and roots for *C. gymnocaulos* (±SD). For flooded plants, allocation to culms is divided between the emergent and submerged portion of the culm. Superscripts indicate treatments with similar responses (α=0.05).

	AG:BG		Emergent		Submerged		Roots	
F (df), *P*	24.8 (8,43), <0.0001		153.5 (8,43), <0.0001		0.2 (3,19), 0.9		10.5 (8,43), <0.0001	
SD60	2.34^{cd}	0.40	0.45^{c}	0.07	N/A		0.16^{ab}	0.03
RD60	1.53^{cde}	0.72	0.50^{bc}	0.07	N/A		0.22^{a}	0.10
SD20	4.18^{ab}	1.05	0.74^{a}	0.03	N/A		0.07^{bcd}	0.02
RD20	2.32^{bc}	1.21	0.56^{ab}	0.28	N/A		0.10^{abc}	0.06
STAT	4.82^{a}	1.02	0.66^{ab}	0.05	N/A		0.06^{bcd}	0.01
SF20	1.74^{cde}	0.78	0.26^{d}	0.09	0.30^{a}	0.01	0.05^{cd}	0.01
RF20	1.04^{de}	0.89	0.04^{e}	0.06	0.29^{a}	0.07	0.04^{d}	0.05
SF60	0.61^{e}	0.39	0.01^{e}	0.01	0.28^{a}	0.16	0.04^{cd}	0.03
RF60	0.47^{e}	0.13	-		0.41^{a}	0.29	0.02^{d}	0.02

allocating nearly one-quarter of its weight to roots (Table 7.8). The allocation to roots for flooded plants was comparatively low (< 5%).

The weight of roots per cm within the soil sections 0-25 cm, 25-40 cm and 40-60 cm was the same for plants subject to slow and rapid drawdown to –60 cm (0.15 – 0.30 g cm^{-1}). There was no difference in the allocation of biomass between soil sections within treatments.

J. aridicola

When shallow flooded rapidly, biomass allocated to above ground tissue increased by 37% compared to plants at STAT. Further increases in depth decreased the allocation to above ground biomass to levels equivalent to those at STAT (Table 7.9). This coincided with a significant decline in culm height ($F_{8,41}$=2.6, P=0.02; Figure 7.11). Combined with an increase in the proportion of submerged tissue (Table 7.9), this led to a decline in the proportion of emergent tissue to 5% for slow deep flooded plants. Even though the average height of culms at RF60 was > 60 cm, all were 'folded' in the upper third portion of the culm and no plants had emergent tissue.

Table 7.9. The mean above to below ground biomass ratio (AG:BG) and the proportion of total weight allocated to culms and roots for *J. aridicola* (± SD). For flooded plants, allocation to culms is divided between the emergent and submerged portion of the culm. Superscripts indicate treatments with similar responses (α=0.05).

	AG:BG		Emergent		Submerged		Roots	
F (df), *P*	3.2 (8,41), 0.006		81.6 (8,41), <0.0001		84.4 (3,19), <0.0001		2.4 (8,41), 0.03	
SD60	2.68^{c}	1.28	0.53^{a}	0.09	N/A		0.32^{a}	0.16
RD60	3.28^{bc}	0.77	0.57^{a}	0.03	N/A		0.24^{ab}	0.04
SD20	3.09^{c}	0.79	0.58^{a}	0.03	N/A		0.25^{ab}	0.06
RD20	2.89^{c}	0.81	0.56^{a}	0.12	N/A		0.27^{ab}	0.07
STAT	3.83^{bc}	0.88	0.61^{a}	0.07	N/A		0.21^{ab}	0.04
SF20	4.57^{ab}	0.91	0.32^{b}	0.09	0.36^{b}	0.04	0.18^{ab}	0.03
RF20	5.26^{a}	0.91	0.37^{b}	0.12	0.32^{b}	0.08	0.16^{b}	0.02
SF60	3.82^{bc}	1.80	0.05^{c}	0.04	0.71^{a}	0.03	0.23^{ab}	0.07
RF60	2.95^{c}	1.35	-		0.75^{a}	0.06	0.39^{ab}	0.37

When exposed to drawdown, *J. aridicola* allocated two to three times more biomass to above than below ground tissue (Table 7.9). The proportion allocated to roots was similar among drawdown treatments, although the greatest allocation was for plants at SD60, nearly one third of total plant weight (Table 7.9).

Root weight was greater for plants exposed to slow rather than rapid deep drawdown for each of the soil sections (0-25 cm, $F_{1,10}$=62.4, $P < 0.0001$; 25-40 cm, $F_{1,10}$=33.1, P=0.0003; 40-60 cm, $F_{1,10}$=16.8, P=0.003: Figure 7.12). Within each treatment there was also more root mass in the uppermost section, compared to the two lower sections (SD60, $F_{2,16}$=13.0, P=0.0003; RD60, $F_{2,12}$=23.1, $P < 0.0001$: Figure 7.12).

S. validus

Flooded plants allocated at least four times as much biomass to above ground tissue (Table 7.10) and had greater culm heights than at STAT and drawdown treatments ($F_{8,42}$=18.0, $P < 0.0001$: Figure 7.17). Rapid deep flooding resulted in at least a 29% greater allocation to above ground biomass compared to shallow flooded plants. Despite these responses, there was still a significant increase in submerged tissue and a concomitant decline in emergent tissue (Table 7.10).

Table 7.10. The mean above to below ground biomass ratio (AG:BG) and the proportion of total weight allocated to culms and roots for *S. validus* (± SD). For flooded plants, allocation to culms is divided between the emergent and submerged portion of the culm. Superscripts indicate treatments with similar responses (α=0.05).

	AG:BG		Emergent		Submerged		Roots	
F (df), *P*	12.5 (8,42), <0.0001		5.6 (8,42), <0.0001		29.1 (3,19), <0.0001		4.7 (8,42), 0.0003	
SD60	1.29^{d}	0.18	0.51^{abc}	0.03	N/A		0.07^{ab}	0.02
RD60	0.79^{d}	0.31	0.41^{bc}	0.10	N/A		0.09^{a}	0.03
SD20	5.01^{bc}	0.75	0.67^{a}	0.03	N/A		0.05^{bc}	0.01
RD20	3.49^{c}	1.09	0.63^{ab}	0.09	N/A		0.06^{abc}	0.02
STAT	4.27^{bc}	0.27	0.63^{ab}	0.05	N/A		0.04^{abc}	0.01
SF20	4.50^{bc}	0.36	0.47^{abc}	0.04	0.23^{c}	0.03	0.05^{bc}	0.01
RF20	4.45^{bc}	0.31	0.45^{abc}	0.04	0.20^{c}	0.02	0.06^{abc}	0.01
SF60	5.48^{ab}	1.49	0.37^{c}	0.06	0.40^{a}	0.05	0.04^{bc}	0.01
RF60	5.82^{a}	3.00	0.41^{c}	0.21	0.32^{b}	0.06	0.04^{c}	0.04

S. validus maintained a high AG:BG for plants exposed to shallow drawdown. Deep drawdown was met by an increase in the allocation to below ground tissue with plants at RD60 allocating more biomass below than above ground (Table 7.10). This led to a decline in culm height but an increase in the allocation of biomass to roots that was greatest at RD60.

Plants exposed to slow deep drawdown had more root mass in the soil sections 0-25 cm ($F_{1,10}$=7.7, P=0.02) and 25-40 cm ($F_{1,10}$=10.3, P=0.009) than for plants at RD60 (Figure 7.14). Plants subject to slow and rapid deep drawdown treatments also had a decrease in root weight from the uppermost to the lowest soil section (SD60, $F_{2,15}$=8.0, P=0.004; RD60, $F_{2,15}$=5.3, P=0.02; Figure 7.14). While all plants exposed to slow deep drawdown had roots to –60 cm, only two subject to rapid deep drawdown had roots at > 25 cm.

7.5.4 Initial response to slow and rapid deep flooding

<u>*B. caldwellii*</u>

Before flooding, each plant in the RF60 treatment had 1-2 culms with neither taller than > 60 cm. Upon the depth reaching 60 cm (12 days), three plants had emergent tissue indicating rates of extension of 2-3 cm d^{-1} (Figure 7.15). Two of the plants that produced emergent tissue after the filling period also recorded the greatest height after a further 48 days and recorded the highest growth rate at the end of the experiment (Figure 7.15). Despite three of the remaining four plants also possessing emergent tissue after 60 days, only one survived.

Before flooding, the height of the tallest culm for plants allocated to SF60 was 30-59 cm and density was 1-2. Upon reaching 60 cm (60 days), five plants had 32-49 culms each, of which, 71-98% had emergent tissue. The proportion of culms > 100 cm tall per plant ranged from 50-100%.

C. gymnocaulos

Rapid, deep flooded plants had low rates of culm extension (0.35 cm d^{-1}), which when combined with short culms (initial heights of 18-24 cm), meant that no plants had emergent tissue after 12 days, with maximum heights ranging from 21-29 cm (Figure 7.16). No extension occurred between 12 and 60 days and there was no change in density.

After 60 days of slow flooding to 60 cm, the two tallest plants (initial heights of 20 and 23 cm), had emergent tissue with heights of 63 and 65 cm. None of the remaining plants (initial heights of 12-23 cm) produced emergent tissue after 60 days.

J. aridicola

Plants in the RF60 treatment had culms at least 60 cm tall before flooding, with densities of 1-4. Although the average rate of extension was 1 cm d^{-1} during the filling phase, this was variable and some plants remained at the same height. The number of emergent culms per plant after 60 days varied from 1-5 with at least 1 culm per plant > 70 cm tall (Figure 7.17).

For slow deep flooded plants, less than one-third of culms were > 60 cm before flooding, but at the completion of filling, 40-61 % of culms on each plant were emergent. In addition, the number of culms rose from 3-6 per plant to 5-20 after 60 days.

S. validus

Before flooding, only one plant in the RF60 treatment had culms > 60 cm. Most extended at 2-3 cm d^{-1} during filling and upon depth reaching 60 cm, plants had

Table 7.11. The soil moisture content ($m^3\ m^{-3}$) in the top 10 cm of sediment for plants exposed to drawdown treatments and STAT. The values for STAT represent those of saturated sediment. Superscripts indicate species with sediment of similar soil moisture content for respective treatments (α=0.05). *n*=6.

	F (df), *P*	SD60	RD60	SD20	RD20	STAT
B. caldwellii	1254.3 (4,25), <0.0001	0.06^{b} (0.01)	0.07^{b} (0.02)	0.42^{a} (0.02)	0.42^{a} (0.01)	0.43^{a} (0.01)
C. gymnocaulos	138.3 (4,25), <0.0001	0.06^{c} (0.01)	0.06^{c} (0.01)	0.41^{a} (0.03)	0.33^{b} (0.08)	0.40^{a} (0.01)
J. aridicola	264.0 (4,25), <0.0001	0.06^{c} (0.02)	0.06^{c} (0.01)	0.37^{b} (0.05)	0.39^{ab} (0.01)	0.43^{a} (0.01)
S. validus	356.9 (4,25), <0.0001	0.07^{c} (0.04)	0.06^{c} (0.01)	0.41^{ab} (0.01)	0.38^{b} (0.02)	0.43^{a} (0.01)

emergent tissue. Culm extension continued and after 60 days five plants had 5-9 emergent culms each (Figure 7.18). Plants subject to SF60 had maximum heights of 30-60 cm prior to flooding, with densities of 1-4. After slow flooding to 60 cm (60 days), 62-93% of culms were emergent with densities of 7-20 per plant.

7.5.5 *Soil moisture content*

STAT sediments were saturated at the end of the treatment period (soil moisture: 0.40-0.43 $m^3\ m^{-3}$). There was a species dependent decrease in soil moisture for the drawdown to 20 cm but this was negligible compared with the soil moistures recorded for drawdowns to 60 cm (Table 7.11). There was no difference in the affect of rate for drawdowns to 60 cm across species within the top 15 cm of soil (Table 7.11).

7.5.6 *Stomatal conductance*

Changes in stomatal conductance occurred for all species during the day but increased the most for *C. gymnocaulos* (STAT, $F_{7,35}$= 33.6, $P < 0.0001$; RD60, $F_{7,35}$= 9.7, $P <$ 0.0001: Figure 7.19). Conductance rose early in the day and declined in the late afternoon, with a greater increase at STAT compared to RD60 from late morning ($F_{1,10}$=7.3, P=0.02) to early afternoon ($F_{1,10}$=33.4, P=0.0002; Figure 7.19).

The magnitude of change in conductance was approximately the same for *J. aridicola* (STAT, $F_{7,35}$= 10.6, $P < 0.0001$; RD60, $F_{7,35}$= 3.6, P= 0.007: Figure 7.20) and *B. caldwellii* (STAT, $F_{7,35}$=4.1, P=0.003; RD60, $F_{7,35}$=2.4, P=0.04; Figure 7.21), although conductance rose early in the day for the latter compared to mid-afternoon for the former. For *J. aridicola*, plants at STAT had greater conductance than at RD60 from mid-morning through to early afternoon (9:30 h, F_{10}=5.8, P=0.04; 11:00 h, F_{10}=19.8, P=0.001; 13:00 h, F_{10}=27.7, P=0.0004; Figure 7.20) whereas for *B. caldwellii* this only occurred at 15:00 h (F_{10}=17.9, P=0.002, Figure 7.21).

Conductance remained the same throughout the day for *S. validus* at STAT and only varied minimally for plants at RD60 ($F_{7,35}$=5.1, P=0.0004; Figure 7.22). The only difference in conductance between treatments was at 11:00 h (F_{10}=16.3, P=0.002; Figure 7.22).

7.6 Discussion

7.6.1 Influence of water regime on RGR, NAR and LAR

The growth of all species under the experimental water regimes reflected their distribution across the elevation gradient of Lower Murray wetlands. *C. gymnocaulos* is characteristic of positions higher on the elevation gradient and performed best when exposed to drawdown regimes. *S. validus*, typical of permanently inundated elevations, maintained optimal growth rates across flooded treatments but reduced growth when subject to deep drawdown. *B. caldwellii* and *J. aridicola*, both characteristic of locations close to the water's edge, maintained growth for shallow flood and drawdown treatments. However, *B. caldwellii* was more tolerant of deeper flooding and *J. aridicola* was better able to maintain RGR when exposed to deep drawdown.

Relative growth rate was consistently greatest for *B. caldwellii*. The RGR for all species was similar to the submerged macrophytes *Vallisneria americana*, (17.5 mg g^{-1} d^{-1}: Blanch *et al.* 1998), *Potamogeton tricarinatus* (70 mg g^{-1} d^{-1}) and *Potamogeton ochreatus* (57 mg g^{-1} d^{-1}: Cenzato and Ganf 2001) and the emergent macrophyte *Bolboschoenus medianus* (40-45 mg g^{-1} d^{-1}: Blanch *et al.* 1999a; Morris and Ganf 2001). However, the response of all compared poorly to selected European species such as *Juncus effusus* (147.1 mg g^{-1} d^{-1}), *Juncus squarrosus* (231.4 mg g^{-1} d^{-1}: Grime and Hunt 1975) and *Carex* spp. (90-120 mg g^{-1} d^{-1}: Konings *et al.* 1989).

The growth response of each species was a result of different contributions of NAR and LAR. *B. caldwellii* maintained the assimilation rate of emergent tissue across most treatments and growth only declined when leafiness decreased under deep drawdown and rapid deep flooding. In contrast, both lower NAR and LAR contributed to the reduced growth of *S. validus*, especially for plants exposed to deep drawdown. The decline in the growth rate of *C. gymnocaulos* and *J. aridicola* under flooded conditions was due to both declining assimilation rates and emergent leafiness. *C. gymnocaulos* demonstrated a plastic response to drawdown and maintained growth by increasing NAR as the leafiness of plants declined. In contrast, *J. aridicola* maintained NAR and LAR across all drawdown treatments. The rate and extent of water level change was important for all species. Rapid rates impacted on NAR and/or LAR more than slow rates.

The net assimilations rates of *B. caldwellii* were high compared with the other three species which had NARs similar to published values e.g. 6.8-13.3 g m^{-2} d^{-1} for *Carex* spp. (Konings *et al.* 1989). However, plant leafiness was low in comparison to values recorded by Poorter and Remkes (1990; 24 species, 14-36 m^2 kg^{-1}), Mason and van der Valk (1992; *Nymphoides indica*, 4-11 m^2 kg^{-1}) and Konings *et al.* (1989; *Carex* spp., 5.4-9.0 m^2 $kg^{-}1$). The low LAR of *C. gymnocaulos*, *J. aridicola* and *S. validus* may be a function of their growth form, since the weight invested in photosynthetic culms is comparatively more than needed for leaves.

Beyond LAR and NAR, RGR had a relationship with emergent area and root mass for all species. This implies that biomass accumulation is restricted by the need to maintain tissue capable of harvesting resources for photosynthesis. The asymptotic nature of these relationships suggest that ultimately further increases in either emergent area or root mass do not greatly increase growth rate.

7.6.2 Responses to flooding

Greater culm height for flooded *B. caldwellii* and *S. validus* compared to those under the static treatment enabled maintenance of emergent photosynthetic tissue. This response is consistent with a number of other emergent macrophytes where culm extension provides a mechanism to maintain contact with atmospheric carbon dioxide when depth increases (e.g. Rea and Ganf 1994; Coops *et al.* 1996; Middleboe and Markager 1997; Blanch *et al.* 1999a; Cooling *et al.* 2001). In contrast, flooded *J. aridicola* and *C. gymnocaulos* did not increase culm height with depth, with rapid deep flooded plants failing to produce any emergent tissue.

The key to survival under deep flooding is the production of emergent tissue. For most plants culm height was < 60 cm when flooding commenced. This was overcome for *B. caldwellii* and *S. validus* through culm extension at rates of up to 2-3 cm d^{-1} and was achieved even if plants were submerged a the end of filling. In contrast, *C. gymnocaulos* and *J. aridicola* extended at 0.35 and 1 cm d^{-1} respectively and neither extended culms once submerged. As a result, only two deep flooded *C. gymnocaulos* had culm heights > 60 cm at the end of the filling phase.

Culm extension when submerged may occur through cell expansion or biomass re-allocation (Cooling *et al.* 2001). Evidence of biomass re-allocation comes from the increase in AG:BG for deep flooded compared to STAT plants. Re-allocation of biomass from below ground organs (e.g. tubers, rhizomes and corms) has been reported for a number of emergent macrophytes (Rea and Ganf 1994b; Blanch *et al.* 1999a; Lenssen *et al.* 2000). The larger tuber and rhizome of *B. caldwellii* and *S. validus* suggests that their capacity to fuel extension from biomass re-allocation is high, whereas the smaller rhizomes of *C. gymnocaulos* and *J. aridicola* places them at a comparative disadvantage (Clevering *et al.* 1995).

Apart from culm extension, reduced emergent photosynthetic tissue can be avoided by possessing tall culms. Culm height is species dependent and influenced by plant age and preceding environmental conditions. For example, the height of *B. caldwellii* and *S. validus* in the RF60 treatment after the establishment phase (50 days) was 21-49 cm and 34-68 cm respectively, whereas plants at STAT for 150 days (establishment phase + experimental period) had heights of 135-162 cm and 133-164 cm. Hence, a longer establishment phase at 0 cm may better equip plants to tolerate inundation.

7.6.3 Responses to drawdown

All species had a positive relationship between root mass and relative growth rate suggesting that plants allocate biomass to tissue capable of acquiring resources in the sediment e.g. nutrients and water. However, root distribution was as important as root weight under deep drawdown treatments, which significantly reduced moisture levels below saturation in near surface sediment. *B. caldwellii* and *C. gymnocaulos* both allocated the same biomass to roots in each section of the soil profile, regardless of the drawdown rate. While this allowed *C. gymnocaulos* to maintain high RGRs, the reduced growth of *B. caldwellii* at RD60 suggests that its water demand was not met.

J. aridicola and *S. validus* concentrated roots in the uppermost soil section, with

J. aridicola recording the greatest of any species across 0-25 cm at SF60. This may represent a strategy aimed at maximising the water harvested from upper soil layers, or, may relate to oxygen supply to the roots. For example, Pantuwan *et al.* (1997) found that rainfed lowland rice concentrate 69-94% of total root length in the top 10 cm of soil in response to growing on hardpans where oxygen supplies decline with increasing soil in anaerobic lowland conditions (Wade *et al.* 1998).

The importance of the rate of drawdown was highlighted by *S. validus* at RD60 with only two plants extending roots beyond 25 cm, compared to all plants at SF60. Under field conditions, rates of drawdown exceed 5 cm d^{-1}. For example, *B. medianus* in the Lower Murray was exposed to drawdown at 10-12 cm d^{-1}, a rate that it was unable to tolerate. Blanch *et al.* (1996) concluded that more gradual rates (2.5 cm d^{-1}) allow allocation strategies to be altered, a result supported by this study.

Assuming that water was the most limiting factor, Chapin *et al.'s* (1987) theory of resource allocation predicts an increase in biomass allocation to roots under drawdown. However, root extension was paralleled by an increase in the weight allocated to roots for only *C. gymnocaulos* and *S. validus*. For both species the greatest increase was at RD60. *B. caldwellii* in comparison redistributed existing root biomass.

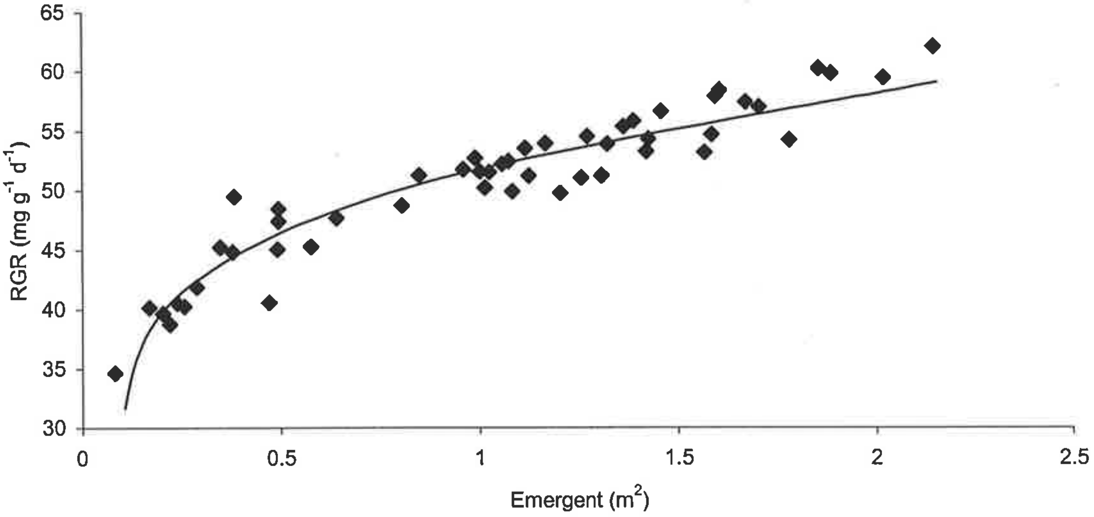
Another form of drought tolerance is regulation of stomatal conductance. Stomatal control was demonstrated by all species with the conductance at RD60, where soil moisture levels were significantly less than saturated, lower than for the static treatment on at least one occasion. The differential response between species suggests that *C. gymnocaulos* has the greatest control, followed equally by *J. aridicola* and *B. caldwellii* with *S. validus* the least flexible. This ranking reflects their distribution across the littoral zone from less to more frequently flooded elevations (Blanch *et al.* 1999b).

Stomatal conductance for *C. gymnocaulos* and *J. aridicola* peaked prior to midday before declining or plateauing during the afternoon and thus they avoid the hottest part of the day when opening stomata. In contrast, conductance remained low for *B. caldwellii* during the morning and peaked in mid-afternoon when temperatures are higher subjecting it to potentially higher transpiration losses. This correlates with the observation that *C. gymnocaulos* and *J. aridicola* were able to maintain optimal growth rates at RD60 while *B. caldwellii* was not.

The distribution of emergent macrophytes across the bank of a wetland is usually explained by their ability to respond to flooding. The results of this study suggest that tolerance of drawdown requires a suite of specialised strategies in the same way that flood tolerance does and that it is equally as legitimate a factor in influencing the distribution of emergent macrophytes in wetlands subject to fluctuating water levels.

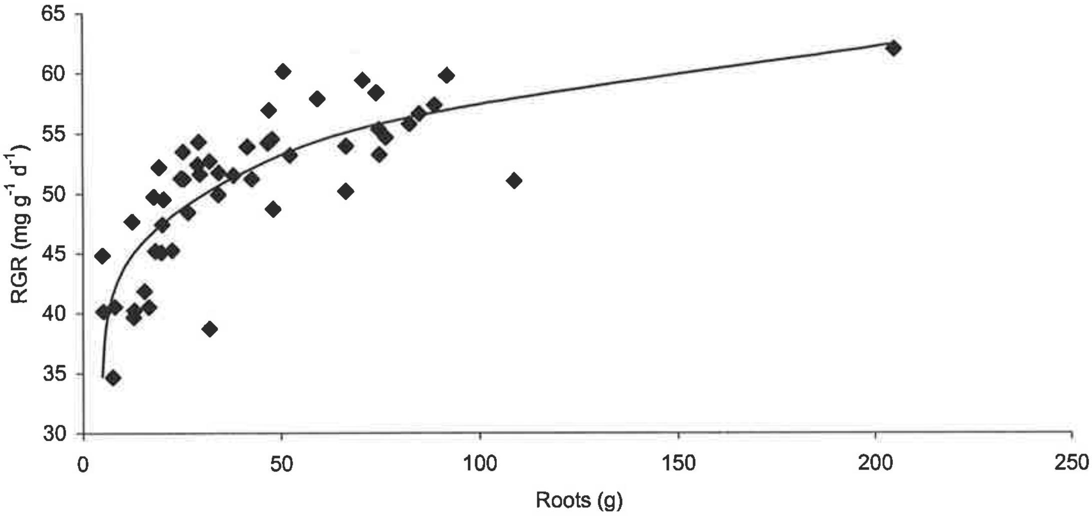
Figure 7.1. The relationship between emergent photosynthetic area (m^2) for *B. caldwellii* and relative growth rate (RGR). Data points are from all treatments combined. *n*=50.

Figure 7.2. The relationship between root mass (g) for *B. caldwellii* and relative growth rate (RGR). Data points are from all treatments combined. *n*=50.



$\mathrm{RGR} = 52.0 + 7.8 \times \ln \mathrm{Area}$

$r^2=0.89$, $F=407.0$, $P<0.0001$



$\mathrm{RGR} = 28.2 + 6.4 \times \ln \mathrm{Root}$

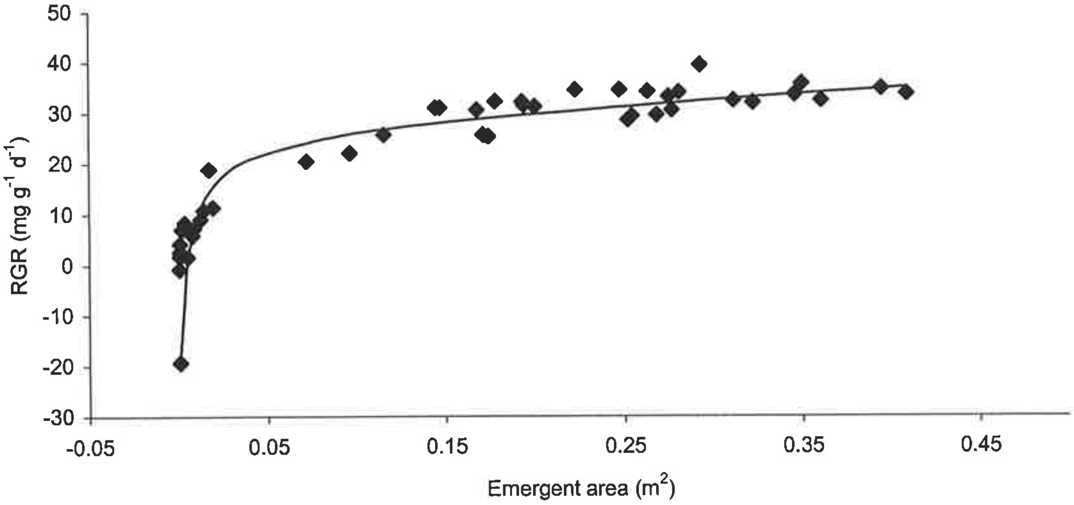
$r^2=0.66$, $F=93.1$, $P<0.0001$

Figure 7.3. The relationship between emergent photosynthetic area (m^2) for *C. gymnocaulos* and relative growth rate (RGR). Data points are from all treatments combined. *n*=43.

Figure 7.4. The relationship between root mass (g) for *C. gymnocaulos* and relative growth rate (RGR). Data points are from all treatments combined. *n*=43.

RGR = 19.1 + 6.3×ln Roots

r^2=0.91, *F*=412.9, *P*<0.0001



RGR = 40.0 + 6.1×ln Area

r^2=0.90, *F*=385.1, *P*<0.0001

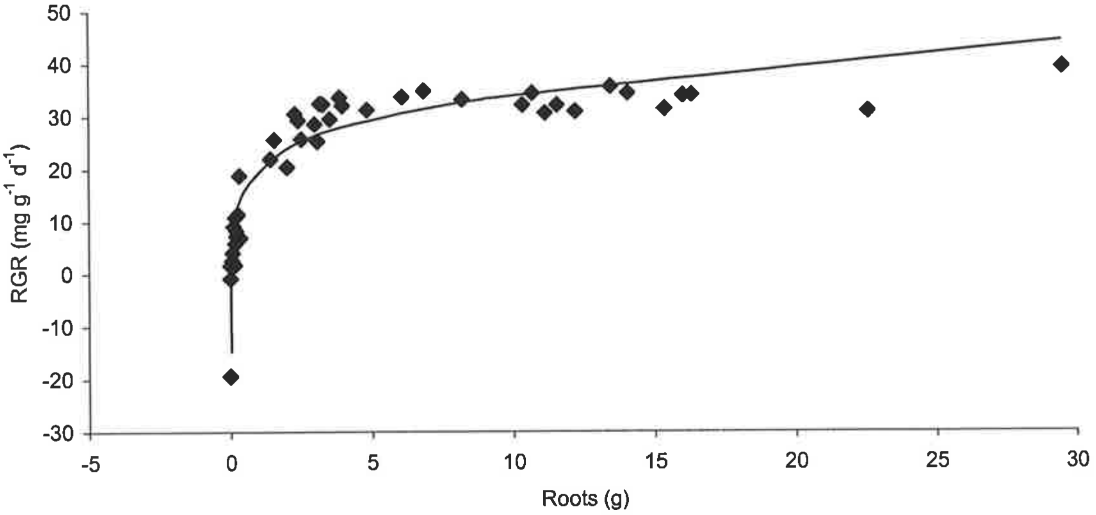
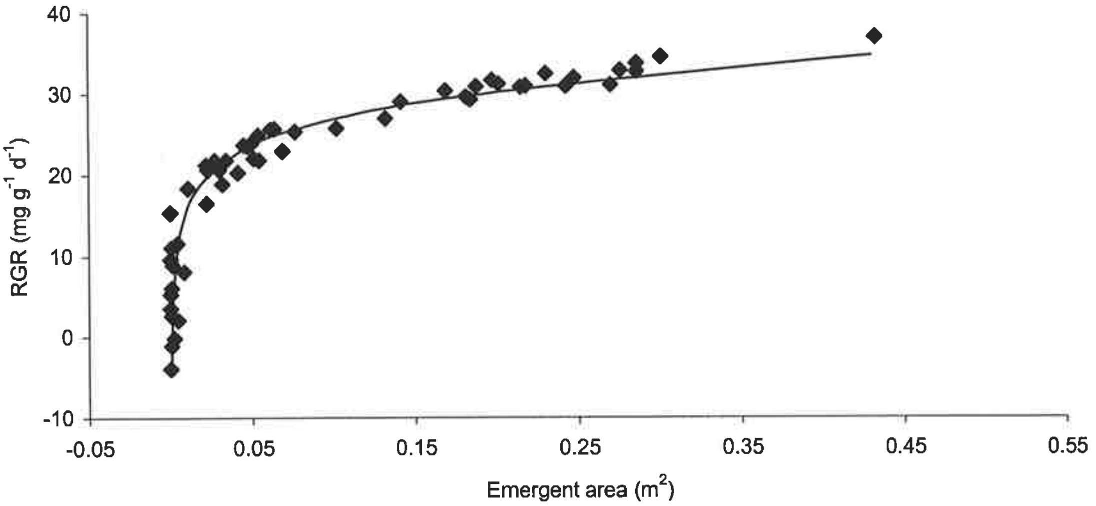


Figure 7.5. The relationship between emergent photosynthetic area (m^2) for *J. aridicola* and relative growth rate (RGR). Data points are from all treatments combined. *n*=44.

Figure 7.6. The relationship between root mass (g) for *J. aridicola* and relative growth rate (RGR). Data points are from all treatments combined. *n*=50.

RGR = 37.4 + 4.4×ln Area

r^2=0.95, *F*=752.3, *P*<0.0001



RGR = 13.0 + 6.8×ln Roots

r^2=0.91, *F*=506.5, *P*<0.0001

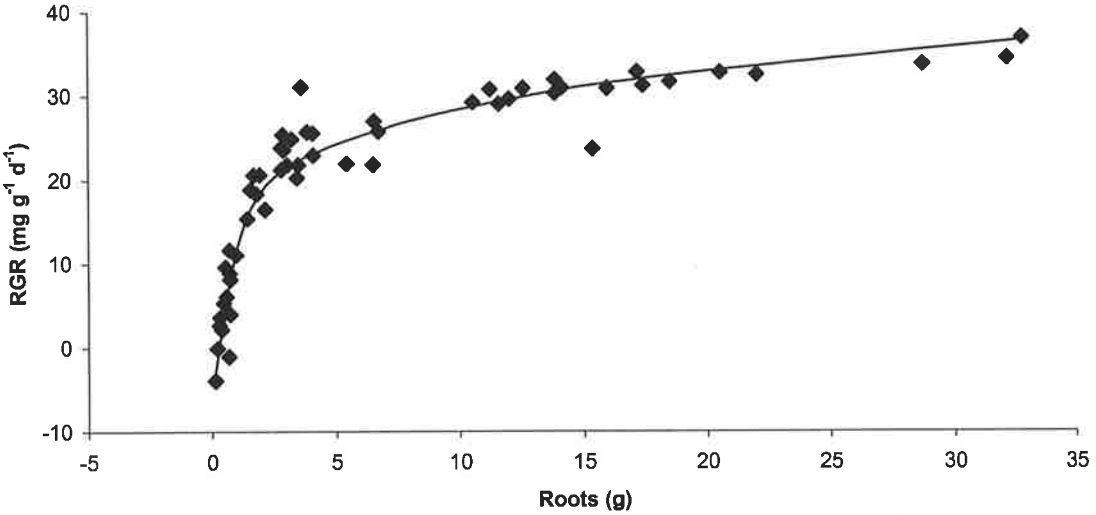
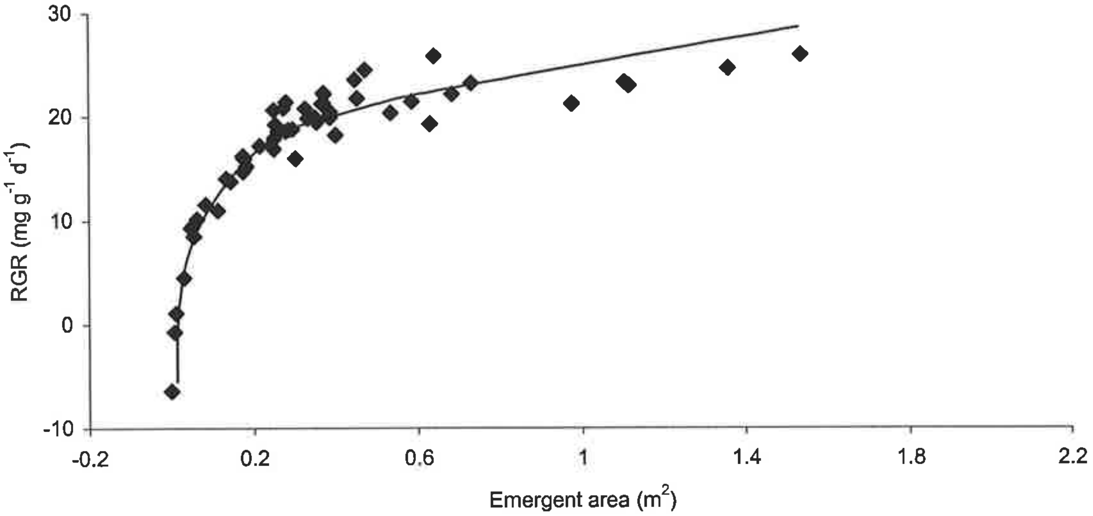


Figure 7.7. The relationship between emergent photosynthetic area (m^2) for *S. validus* and relative growth rate (RGR). Data points are from all treatments combined. *n*=51.

Figure 7.8. The relationship between root mass (g) for *S. validus* and relative growth rate (RGR). Data points are from all treatments combined. *n*=51.

RGR = 24.9 + 5.2×ln Area

r^2=0.85, *F*=285.6, *P*<0.0001



RGR = 10.8 + 5.2×ln Roots

r^2=0.60, *F*=74.1, *P*<0.0001

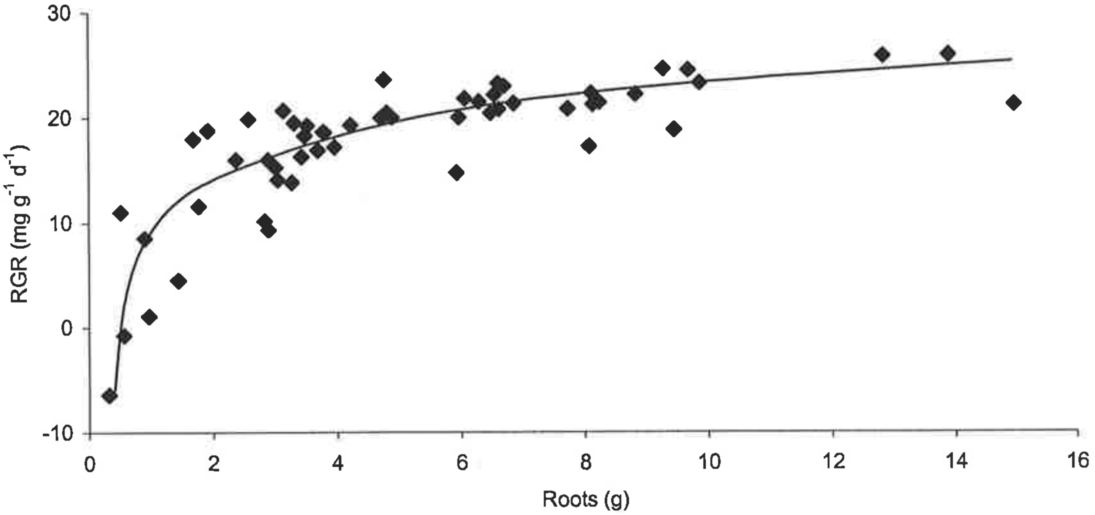
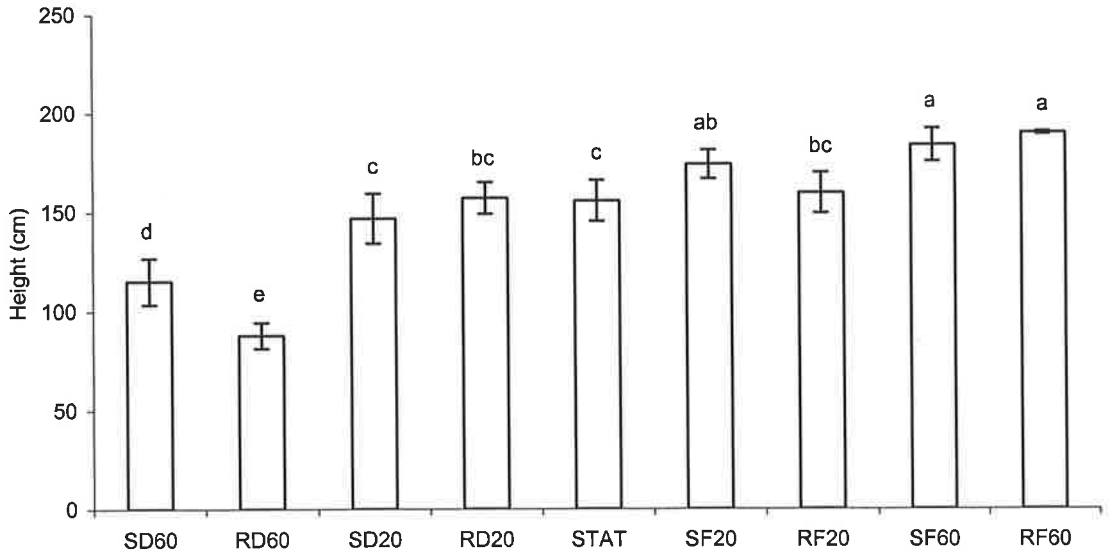


Figure 7.9. The height of the tallest culm for *B. caldwellii* across the water regimes. Culm height was measured to the height of the leaf tip. n=6 for all except RF60 where n=3. Superscripts indicate treatments with similar responses (α=0.05).

Figure 7.10. Height of the tallest culm for *C. gymnocaulos* across the water regime treatments. n=6 for all except RD20 and RF60 where n=5. Superscripts indicate treatments with similar responses (α=0.05).


250
200
150
100
50
0
Height (cm)
d
e
c
bc
c
ab
bc
a
a
SD60
RD60
SD20
RD20
STAT
SF20
RF20
SF60
RF60

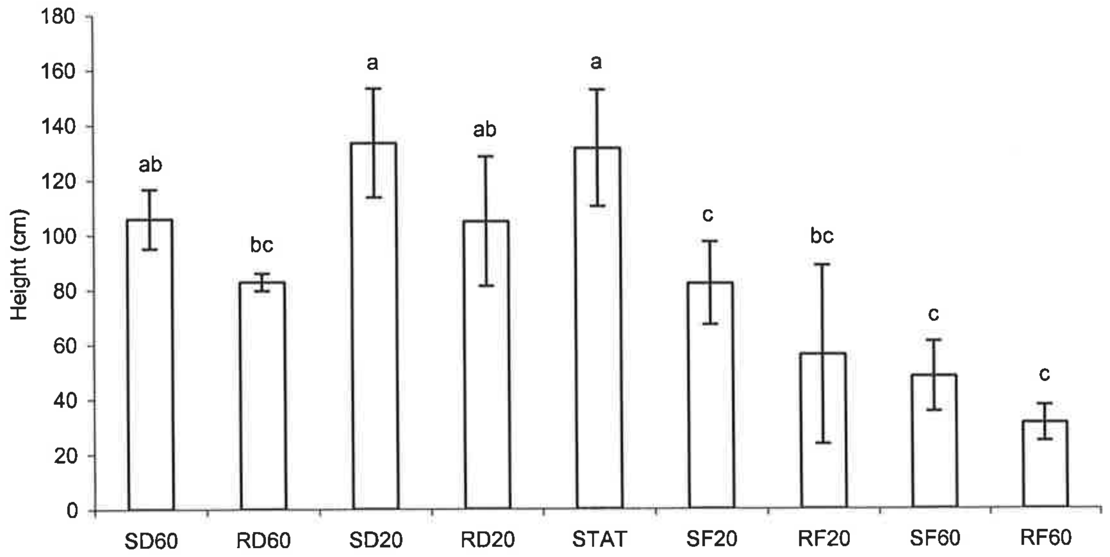
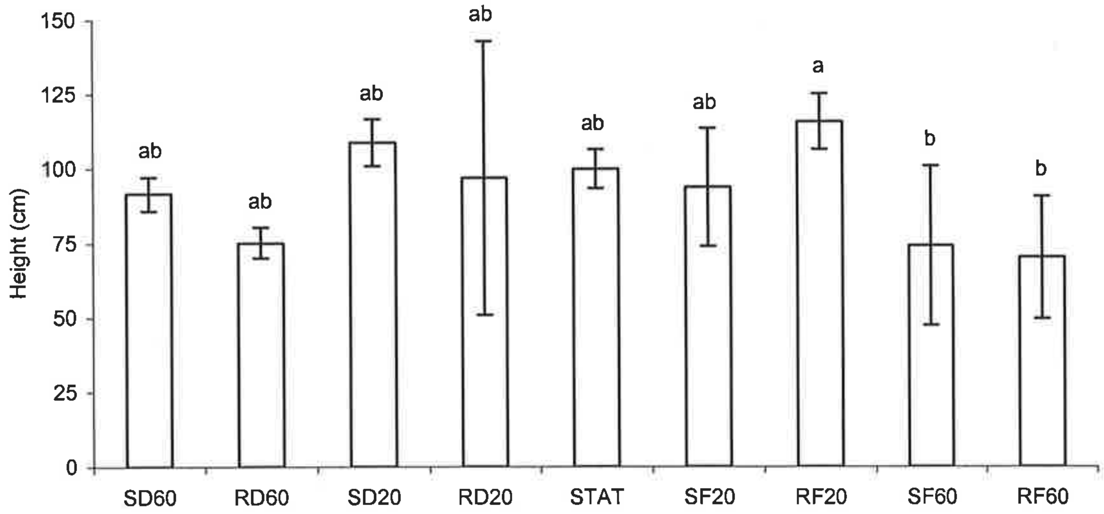

180
160
140
120
100
80
60
40
20
0
Height (cm)
ab
bc
a
ab
a
c
bc
c
c
SD60
RD60
SD20
RD20
STAT
SF20
RF20
SF60
RF60

Figure 7.11. Height of the tallest culm (cm) for *J. aridicola* across the water regime treatments. n=6 for all except RD20, RD60, SF20 and STAT where n=5. Superscripts indicate treatments with similar responses (α=0.05).

Figure 7.12. The root mass for *J. aridicola* in the three soil sections for plants exposed to slow and rapid deep drawdown. Superscripts indicate treatments with similar responses (α=0.05). Upper case relate to differences within soil sections between treatments and lower case superscripts to differences across a soil profile within a treatment.


Height (cm)
150
125
100
75
50
25
0
SD60
RD60
SD20
RD20
STAT
SF20
RF20
SF60
RF60
ab
ab
ab
ab
ab
ab
a
b
b

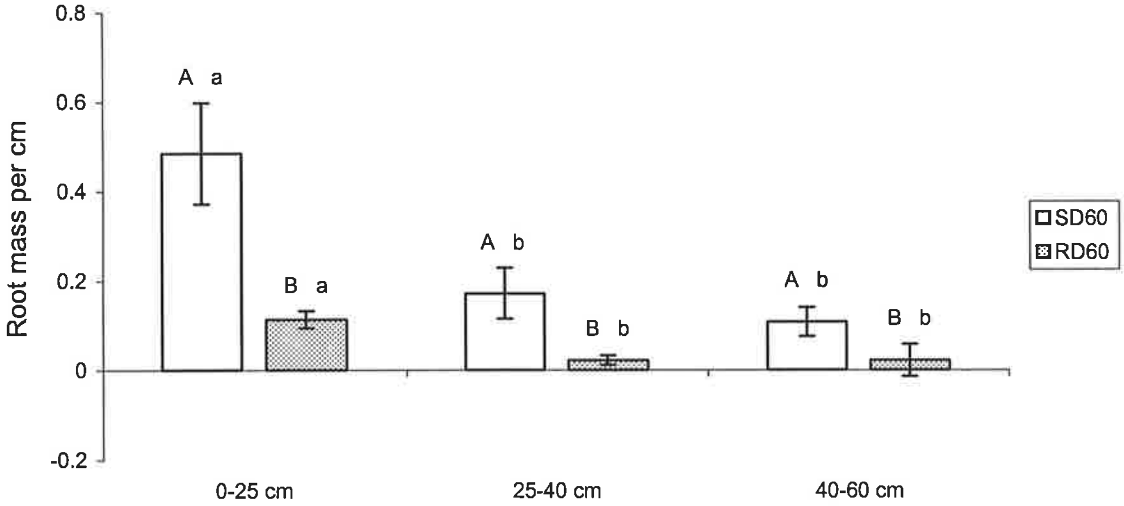
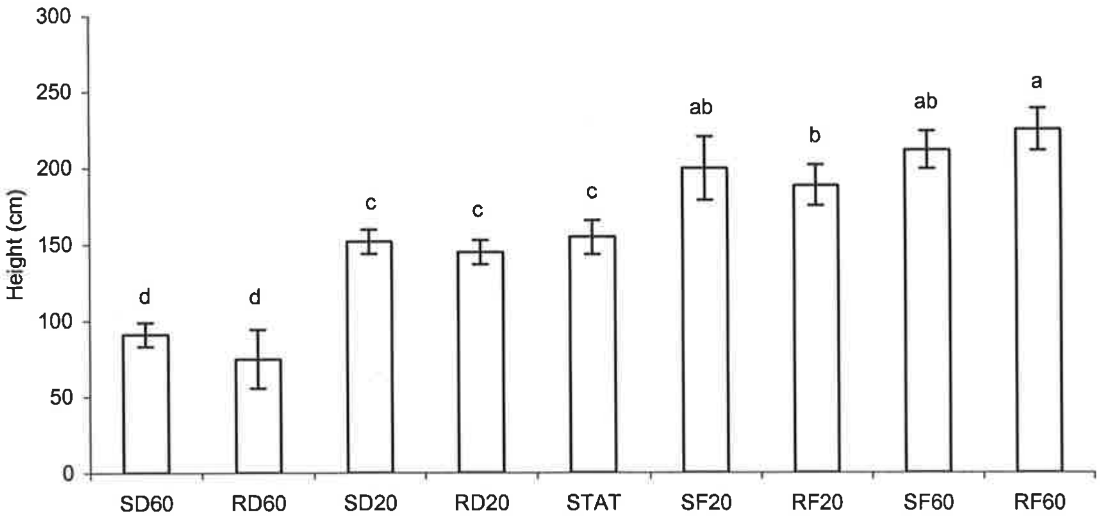

Root mass per cm
0.8
0.6
0.4
0.2
0
-0.2
0-25 cm
25-40 cm
40-60 cm
A a
B a
A b
B b
A b
B b
SD60
RD60

Figure 7.13. The height of the tallest culm for *S. validus* across the water regime treatments. *n*=6 for all except RF60 where *n*=5 and RD60 where *n*=4. Superscripts indicate treatments with similar responses (α=0.05).

Figure 7.14. The root mass for *S. validus* in the three soil sections for plants exposed to slow and rapid deep drawdown. Superscripts indicate treatments with similar responses (α=0.05). Upper case superscripts relate to differences within soil sections between treatments and lower case superscripts relate to differences across a soil profile within a treatment.


Height (cm)
300
250
200
150
100
50
0
d
d
c
c
c
ab
b
ab
a
SD60
RD60
SD20
RD20
STAT
SF20
RF20
SF60
RF60

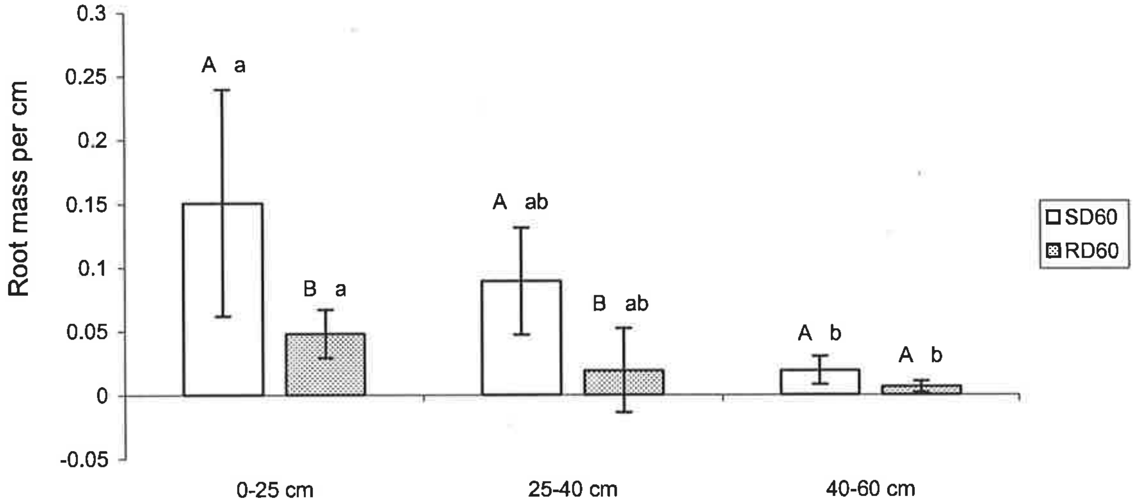
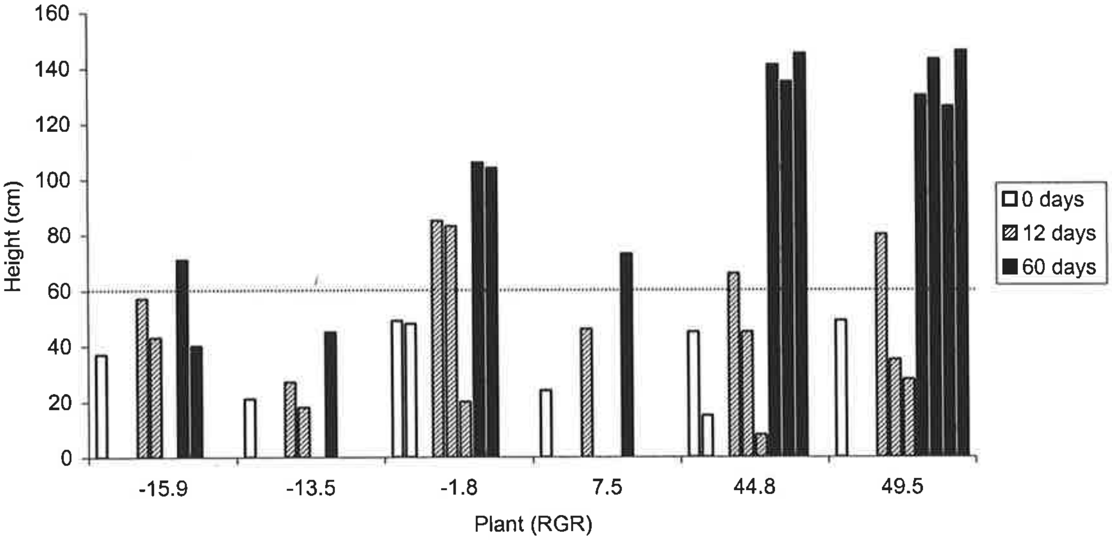

Root mass per cm
0.3
0.25
0.2
0.15
0.1
0.05
0
-0.05
A a
B a
A ab
B ab
A b
A b
0-25 cm
25-40 cm
40-60 cm
□SD60
▨RD60

Figure 7.15. The height of *B. caldwellii* culms for each of the 6 plants at RF60 before flooding (0 days), at the end of the filling phase (12 days) and after 48 days at 60 cm (60 days). The values on the x-axis represent the RGRs (mg g^{-1} d^{-1}) of the plants at RF60. The three plants with negative growth rates had died by the end of the experiment. The dashed line indicates a depth of 60 cm.

Figure 7.16. The height of *C. gymnocaulos* culms for each of the 6 plants at RF60 before flooding (0 days) and at the end of the filling phase (12 days). There was no further increase in height after 12 days. The values on the x-axis represent the RGRs (mg g^{-1} d^{-1}) of the plants at RF60. Water depth is not indicated as no plants grew taller than 30 cm.


160
140
120
100
80
60
40
20
0
Height (cm)
-15.9
-13.5
-1.8
7.5
44.8
49.5
Plant (RGR)
☐ 0 days
▨ 12 days
■ 60 days

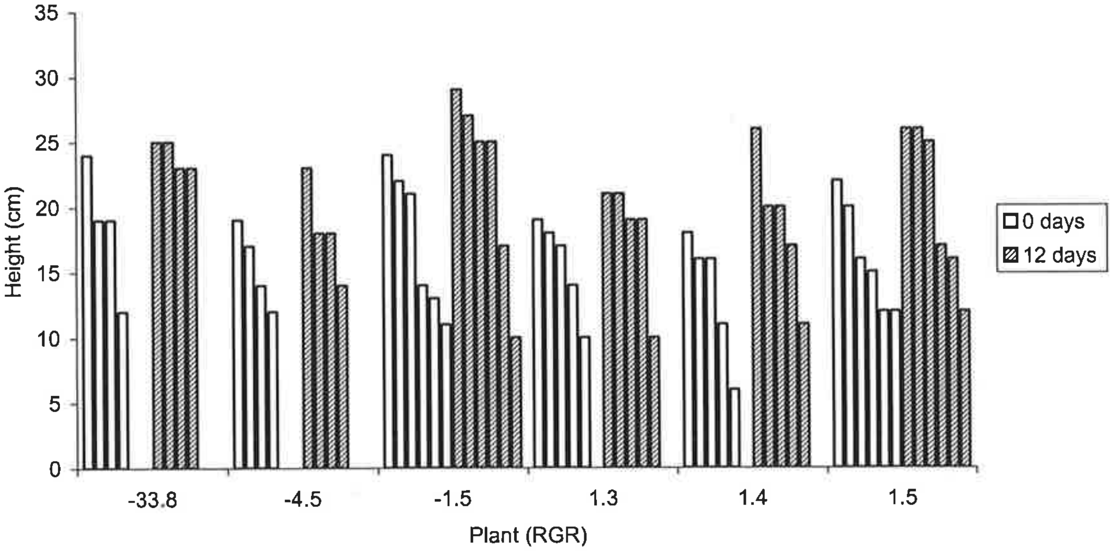
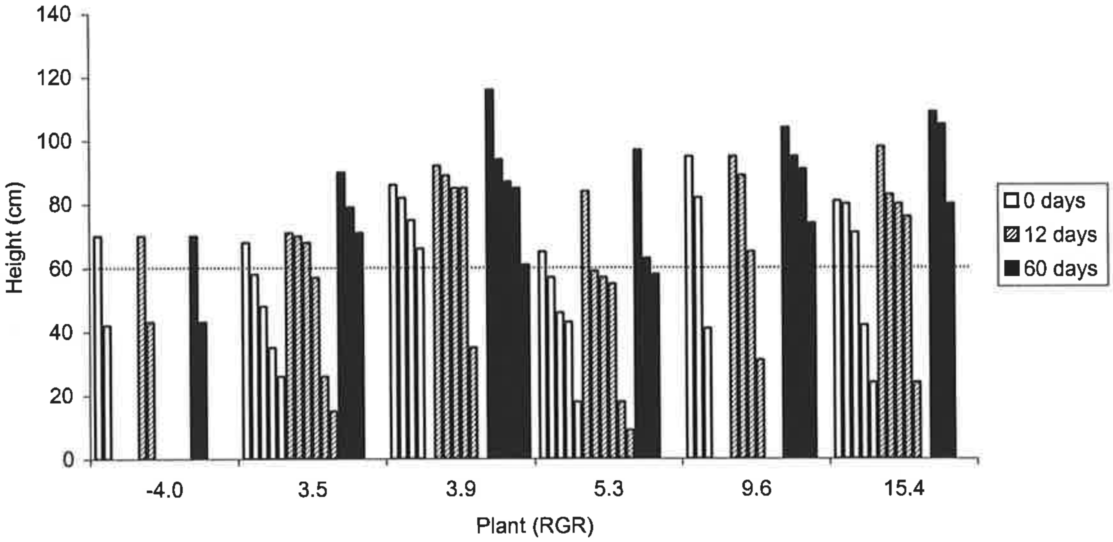

35
30
25
20
15
10
5
0
Height (cm)
-33.8
-4.5
-1.5
1.3
1.4
1.5
Plant (RGR)
☐ 0 days
▨ 12 days

Figure 7.17. The height of *J. aridicola* culms for each of the 6 plants at RF60 before flooding (0 days), at the end of the filling phase (12 days) and after 48 days at 60 cm (60 days). The values on the x-axis represent the RGRs (mg g^{-1} d^{-1}) of the plants at RF60. The dashed line indicates a depth of 60 cm.

Figure 7.18. The height of *S. validus* culms for each of the 6 plants at RF60 before flooding (0 days), at the end of the filling phase (12 days) and after 48 days at 60 cm (60 days). The values on the x-axis represent the RGRs (mg g^{-1} d^{-1}) of the plants at RF60. The culms of the plant with a negative growth rate had died back after 48 days and the plant did not survive the experimental period. The dashed line indicates a depth of 60 cm.


140
120
100
80
60
40
20
0
Height (cm)
-4.0
3.5
3.9
5.3
9.6
15.4
Plant (RGR)
□ 0 days
▨ 12 days
■ 60 days

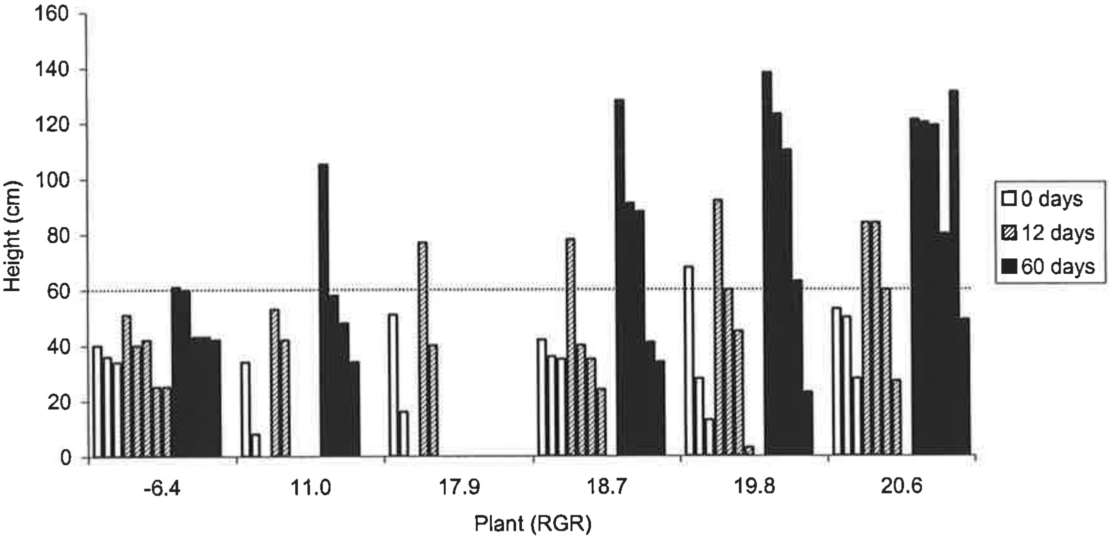
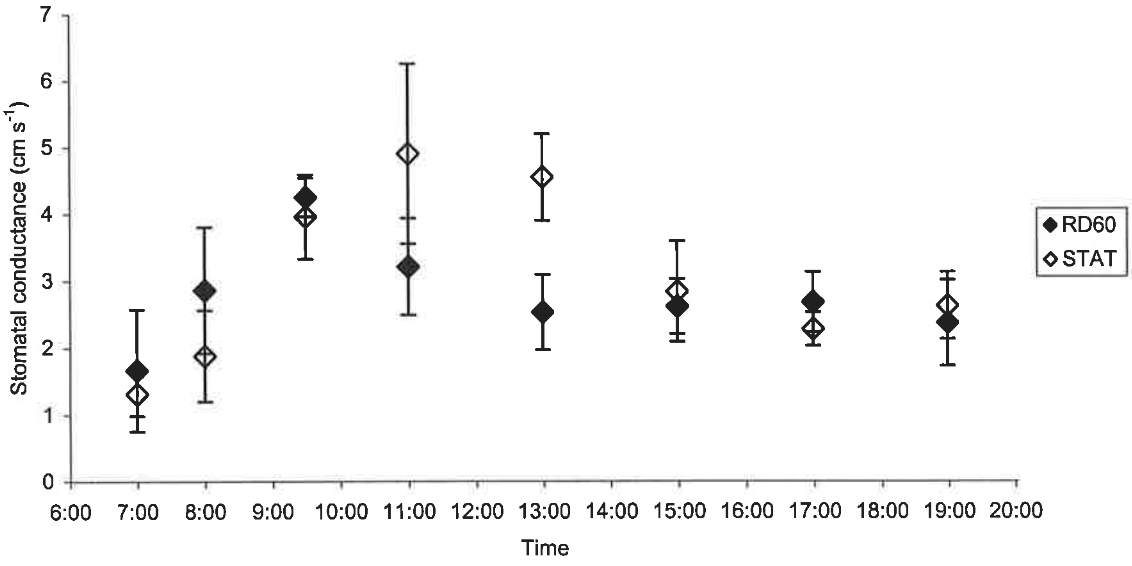

160
140
120
100
80
60
40
20
0
Height (cm)
-6.4
11.0
17.9
18.7
19.8
20.6
Plant (RGR)
□ 0 days
▨ 12 days
■ 60 days

Figure 7.19. The stomatal conductance for *C. gymnocaulos* plants exposed to rapid, deep drawdown and STAT during a 12-hour period on 13 January 2001.

Figure 7.20. The stomatal conductance for *J. aridicola* plants exposed to rapid, deep drawdown and STAT during a 12-hour period on 13 January 2001.


Stomatal conductance (cm s-1)
0
1
2
3
4
5
6
7
6:00
7:00
8:00
9:00
10:00
11:00
12:00
13:00
14:00
15:00
16:00
17:00
18:00
19:00
20:00
Time
◆ RD60
◇ STAT

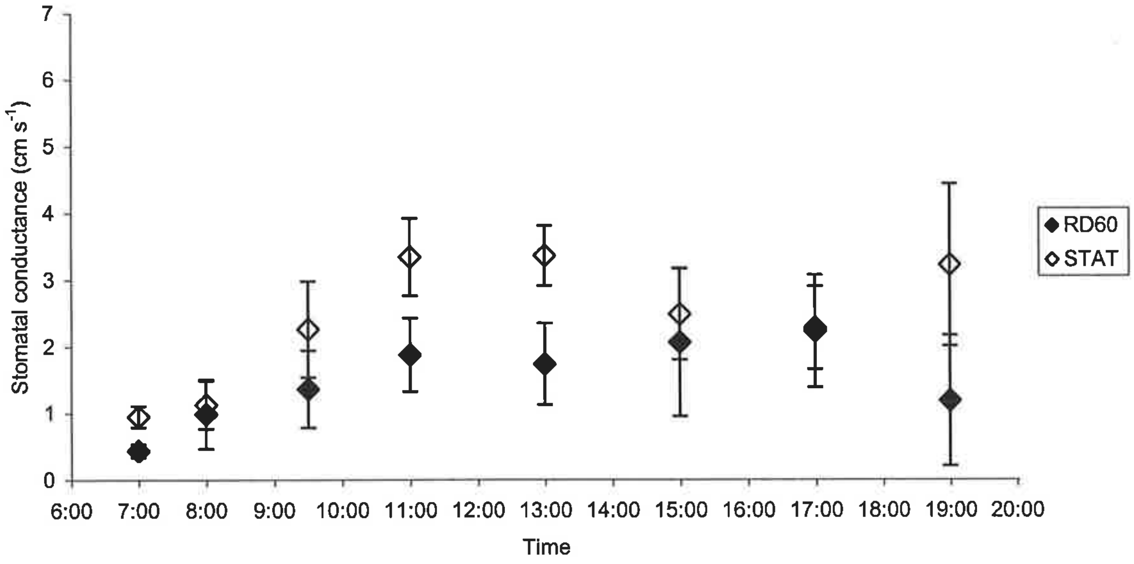
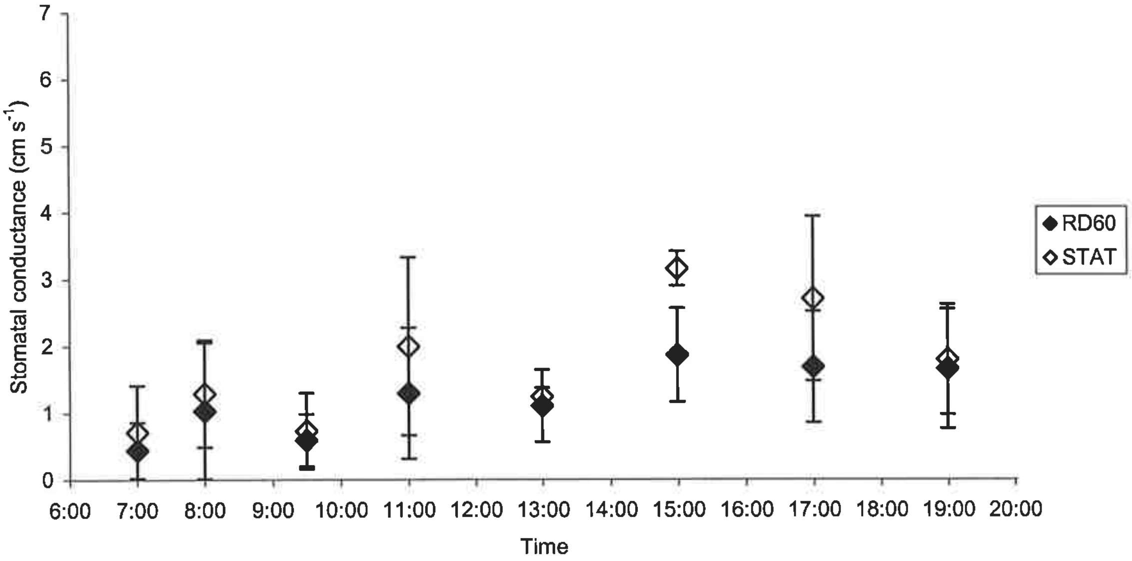
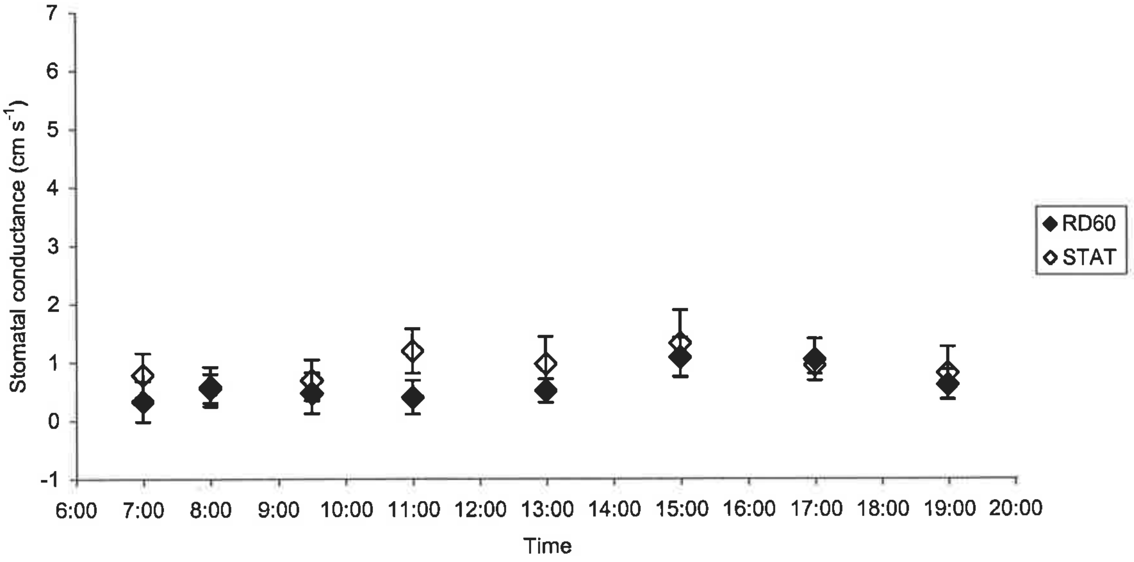

Stomatal conductance (cm s-1)
0
1
2
3
4
5
6
7
6:00
7:00
8:00
9:00
10:00
11:00
12:00
13:00
14:00
15:00
16:00
17:00
18:00
19:00
20:00
Time
◆ RD60
◇ STAT

Figure 7.21. The stomatal conductance for *B. caldwellii* plants exposed to rapid, deep drawdown and STAT during a 12-hour period on 12 January 2001.

Figure 7.22. The stomatal conductance for *S.* validus plants exposed to rapid, deep drawdown and STAT during a 12-hour period on 12 January 2001.


Stomatal conductance (cm s^{-1})
7
6
5
4
3
2
1
0
6:00
7:00
8:00
9:00
10:00
11:00
12:00
13:00
14:00
15:00
16:00
17:00
18:00
19:00
20:00
Time
◆ RD60
◇ STAT


Stomatal conductance (cm s^{-1})
7
6
5
4
3
2
1
0
-1
6:00
7:00
8:00
9:00
10:00
11:00
12:00
13:00
14:00
15:00
16:00
17:00
18:00
19:00
20:00
Time
◆ RD60
◇ STAT

CHAPTER 8

THE EFFECTS OF WATER REGIME ON THE GROWTH AND REPRODUCTION OF FOUR EMERGENT MACROPHYTES

8.1 Abstract

Growth and investment in asexual and sexual reproduction for plants exposed to shallow (20 cm) and deep (60 cm), slow (1 cm d^{-1}) and rapid (5 cm d^{-1}) flood and drawdown was examined for four emergent macrophytes from the littoral zone of Lower Murray wetlands. Optimal growth led to optimal investment in asexual reproduction for *Bolboschoenus caldwellii*, *Cyperus gymnocaulos* and *Juncus aridicola*, whereas *Schoenoplectus validus* decreased culm production despite maintenance of growth. *B. caldwellii* maintained numerical increase when deep flooded slowly by reducing the allocation of biomass to tubers, whereas *S. validus* sacrificed numerical increase to retain investment in rhizomes. The latter response was observed for both species when exposed to deep drawdown. No trade-off was evident between asexual and sexual reproduction. The importance of sexual reproduction for *J. aridicola* was demonstrated by its culms being 2-4 times more likely to possess flowers than *B. caldwellii* and *S. validus*. In place of flowers, *C. gymnocaulos* produced bulbils, providing a method of asexual reproduction. This study suggests that species from different parts of the littoral zone have different patterns of investment in reproduction when subject to contrasting water regimes.

8.2 Introduction

For clonal plants, resources are distributed between vegetative growth, maintenance and asexual and sexual reproduction (Sun *et al.* 2001). Among emergent macrophytes, flowering diverts resources away from clonal expansion (Waters and Shay 1991) and thus asexual and sexual reproduction are often viewed as competing functions (Bazazz *et al.* 1987).

A trade-off between reproductive modes has been hypothesised for clonal species (Bazazz *et al.* 1987). Newell and Tramer (1978) suggested that seed production should decline with increasing plant density and Loehle (1987) proposed that flowering in clonal plants should be favoured by low density or favourable environmental conditions. This investment trend has been observed for a number of emergent macrophytes across a water depth gradient, including *Scirpus maritimus* var. *paludosus* (Lieffers and Shay 1981) and *Scirpus marqueter* (Sun *et al.* 2001).

In contrast to investment in asexual and sexual reproduction, optimal biomass accumulation and investment in asexual reproduction often coincide. For example, total plant biomass accumulation and investment in asexual reproduction was optimal for *Typha domingensis* and *Typha latifolia* in shallow water but declined for both with increasing depth (Grace 1989).

Investment in either mode of reproduction influences opportunities for spatial and temporal dispersal. Asexual reproduction produces genetically similar individuals suited to local population growth that contribute to the survival and reproductive success of the parent plant (Worley and Harder 1996). Asexual reproduction also performs functions such as resource acquisition, protection, storage and anchorage (Grace 1993). Trade-offs between these functions are theoretically possible. For example, rates of numerical increase could be maintained by reducing biomass allocation to the other functions performed by clonal propagules such as storage.

This chapter, which provides a further analysis of the pond experiment described in Chapter 7, examines the impact of contrasting water regimes on the reproductive response of *Cyperus gymnocaulos, Juncus aridicola, Bolboschoenus caldwellii* and *Schoenoplectus validus* which occupy infrequently flooded to more permanently inundated elevations in Lower Murray wetlands.

The pond experiment only allowed for analysis of the investment in reproduction given that flowering was not followed through to subsequent germination of new individuals, nor was ramet production followed through to abscission and establishment of new plants.

It was predicted that all species would:

1) maximise investment in asexual reproduction under optimal growth conditions.
2) maintain rates of numerical increase by altering the biomass allocated to the other

functions performed by clonal propagules; and

3) have an inverse relationship between investment in sexual and asexual reproduction.

The impact of water regime on growth and reproduction was subsequently used to predict the floristic composition that might develop for elevations subject to the experimental water regimes.

Species descriptions are provided in Section 7.3.

8.3 Methods

General experimental design, data collection and analysis of the pond experiment are described in Section 7.4.

Investment in asexual reproduction was measured by recording changes in culm density and analysing biomass allocation to below ground perennating organs. To account for differences in initial density, relative rates of culm increase were calculated. Investment in asexual reproduction for *C. gymnocaulos* was also measured by recording the number of bulbils (viviparous propagules).

Investment in sexual reproduction was determined by recording the total number and weight of flowers and calculating the average weight per flower and number of flowers per culm. The term ‘flower’ is used here as a surrogate for ‘inflorescence’.

The term ‘culm’, as used in this chapter, does not account for inflorescences and bulbils. Ramets describe a culm with its attached below ground tissue. For all species, the average ramet weight was calculated by dividing total weight by culm density.

8.4 Results

8.4.1 Relative growth rate

B. caldwellii

Growth rate peaked for shallow flooded plants and was approximately the same at shallow drawdown, STAT and slow deep flooded treatments (Table 8.1). Growth at

Table 8.1. The relative growth rate (RGR) for the experimental species across the nine treatment water regimes. Superscripts indicate treatments with similar responses within species (α=0.05). Treatment codes are described in Table 7.1.

Treatment	*B. caldwellii*		*C. gymnocaulos*		*J. aridicola*		*S. validus*	
F (df), *P*	8.2 (8,42), <0.0001		47.9 (8,43), <0.0001		18.9 (8,41), <0.0001		11.7 (8,42), <0.0001	
SD60	45.3^{bcd}	2.7	34.4^{a}	2.6	29.8^{ab}	3.2	15.6^{b}	2.0
RD60	39.5^{cd}	2.5	31.5^{a}	1.3	22.3^{ab}	5.4	8.1^{c}	2.5
SD20	53.6^{ab}	1.9	28.1^{a}	2.1	32.1^{a}	1.7	20.2^{ab}	2.7
RD20	51.5^{ab}	2.0	29.9^{a}	6.6	29.0^{ab}	5.6	18.8^{ab}	4.0
STAT	52.3^{ab}	1.9	31.0^{a}	4.5	29.4^{ab}	4.0	22.9^{a}	2.4
SF20	57.4^{a}	2.8	8.7^{b}	2.1	22.5^{ab}	2.8	19.4^{ab}	3.4
RF20	56.7^{a}	4.2	1.5^{b}	12.4	21.7^{b}	5.3	22.4^{a}	1.4
SF60	49.5^{abc}	5.7	0.8^{b}	2.6	11.3^{c}	7.0	19.3^{ab}	1.7
RF60	33.9^{d}	23.0	-0.4^{b}	2.6	5.6^{c}	6.5	17.6^{ab}	3.8

SD60 declined marginally relative to shallow flooded plants, but was significantly less than all of these treatments at RF60 and RD60 (Table 8.1). The variation in response at RF60 was high, a function of one plant with an RGR of 7.5 mg g^{-1} d^{-1} compared to the other two plants with 44.8 and 49.5 mg g^{-1} d^{-1}.

<u>*C. gymnocaulos*</u>

The growth of *C. gymnocaulos* was highest across all drawdown treatments, ranging from 28.1-34.4 mg g^{-1} d^{-1}. In contrast, all flooded plants had growth rates < 9 mg g^{-1} d^{-1}, significantly less than those of plants exposed to drawdown and STAT (Table 8.1). The lowest growth rate was for rapid deep flooded plants, with only three achieving a positive growth rate.

<u>*J. aridicola*</u>

The growth rate remained constant for plants exposed to drawdown as well as STAT and slow, shallow flooding (22.5-32.1 mg g^{-1} d^{-1}: Table 8.1). In contrast, rapid, shallow flooding and deep flooding lead to a decline in growth rate (Table 8.1). The lowest average RGR was recorded at RF60 and was variable, ranging from –4.0 to 15.4 mg g^{-1} d^{-1} (Table 8.1).

S. validus

Growth did not differ for plants exposed to shallow drawdown through to slow, deep flooding (Table 8.1). Significant declines occurred from STAT to RF60 and SD60 (Table 8.1). However, the average growth of the four surviving plants at RD60 was lower than for all other treatments, with individual RGRs ranging from 8.4-9.7 mg g^{-1} d^{-1}.

8.4.2 Impact of flood and drawdown on asexual reproduction

B. caldwellii

B. caldwellii increased the number of culms at approximately the same rate from STAT through to slow deep flooded treatments (Figure 8.1). The rate of increase was significantly lower for plants at RF60 and varied from 0.03 culms d^{-1} in comparison to 0.4-0.5 culms d^{-1} (Figure 8.1).

The biomass allocated to tubers declined for rapid shallow flooded and deep flooded plants ($F_{8,40}$=21.0, $P < 0.0001$: Figure 8.2). This coincided with a decline in the weight per ramet from 9.9 g at RF20 to 4.0 and 1.7 g at SF60 and RF60, respectively ($F_{8,42}$=2.6, P=0.02: Figure 8.3).

Rates of culm increase were similar at STAT and shallow drawdown treatments (0.64-0.73 culm d^{-1}) but declined by 47% and 66% for plants exposed to slow and rapid deep drawdown ($F_{8,42}$=12.9, $P < 0.0001$: Figure 8.1). The weight allocated to tubers (Figure 8.2) and the weight per ramet (Figure 8.3) remained constant across all drawdown treatments.

C. gymnocaulos

The rate of culm increase declined from 0.44 culm d^{-1} at STAT to < 0.12 culm d^{-1} for shallow flooded plants ($F_{8,40}$=22.6, $P < 0.0001$: Figure 8.4). Slow deep flooded plants added an average of 0.01 culms d^{-1} and only one plant at RF60 increased culm density. All ramet weights across flooded treatments were less than recorded at STAT (Figure 8.5). The allocation to rhizomes was higher for flooded plants than those at STAT because of the dieback of submerged culms (Figure 8.6).

Culm production remained constant for plants exposed to drawdown (Figure 8.4). Ramet weight was greatest at SD60 (1.5 g) and ranged from 0.83-1.05 g for other drawdown treatments ($F_{8,40}$=21.0, $P < 0.0001$: Figure 8.5). The maintenance of culm increase was paralleled by a constant allocation of biomass to rhizomes for all drawdown treatments ($F_{8,42}$=9.6, $P < 0.0001$: Figure 8.6).

Total bulbil weight was reduced to < 1 g for flooded treatments and bulbil number declined from 25 at STAT to less than 3 per plant for flooded treatments. Only two plants at SF60 (3 and 1 bulbils each) and one plant at RF60 (2) possessed bulbils. Despite the low total weight of bulbils on flooded plants, the weight per bulbil was constant and similar to plants subject to drawdown (Table 8.2). Most bulbils produced on flooded plants were eventually abscised.

The weight of bulbils was greatest at SD60, nearly double that recorded at STAT and at least three times greater than for other drawdown treatments (Table 8.2). However, the number of bulbils differed little with only SD60 having more than plants at SD20 (Table 8.2). The greater total weight at SD60 was because individual bulbils were at least three times heavier than for other drawdown treatments (Table 8.2).

J. aridicola

The rate of culm increase declined from 0.33 culms d^{-1} at STAT to 0.07 and 0.01 culms d^{-1} for slow and rapid deep flooded plants (Figure 8.7). Ramet weight declined only for slow deep flooded plants compared to those at STAT ($F_{8,39}$=3.3, P=0.005: Figure 8.8). The proportion of weight allocated to below ground tissue remained constant for flooded treatments.

The rate of increase in culm density was greater for plants at SD60 than RD60 ($F_{8,39}$=9.1, $P < 0.0001$: Figure 8.7). However, the ramet weight was the same for all plants exposed to STAT and drawdown (Figure 8.8) and there was no change in the proportion of biomass allocated to below ground tissues (25-30%, $F_{8,40}$=2.1, P=0.06).

S. validus

Flooding caused a reduction in the number of culms produced per day compared to plants at STAT for all treatments except RF20 ($F_{8,42}$=7.7, $P < 0.0001$: Figure 8.9). In contrast, ramet weight (Figure 8.10) and the proportion of weight allocated to rhizomes remained constant for flooded treatments (Figure 8.11).

Drawdown favoured culm increase at all but RD60, with rates of increase at other drawdown treatments the same as at STAT (0.22-0.31 culms d^{-1}: Figure 8.9). The ramet weight was the same for all drawdown treatments ($F_{8,42}$=8.1, $P < 0.0001$: Figure

8.10) compared with the proportional allocation to rhizomes that increased from shallow to deep drawdown treatments ($F_{8,42}$=64.8, $P < 0.0001$: Figure 8.11).

8.4.3 Impact of flood and drawdown on sexual reproduction

B. caldwellii

Investment in sexual reproduction was variable across treatments and there was no trend between flood and drawdown and weight or weight per flower (Table 8.2). The only response was at SD60 where the number of flowers per culm was at least double most other treatments ($F_{8,42}$=3.8, P=0.002: Figure 8.12).

C. gymnocaulos

No flowers were recorded, with culms producing bulbils instead.

J. aridicola

Shallow flooding reduced the total weight, number and weight per flower by at least half compared to plants and STAT, and by an order of magnitude compared to deep flooded plants (Table 8.2). Sixty to eighty percent of culms for STAT and shallow flooded plants had flowers compared to 7% for deep flooded plants ($F_{8,37}$=12.9, $P <$ 0.0001: Figure 8.13).

The number and total weight of flowers was the same for plants at STAT and all drawdown treatments (Table 8.2). The weight per flower was approximately the same across drawdown treatments although a reduction was recorded for plants at RD60 (Table 8.2). The percentage of culms with flowers remained constant for all drawdown and STAT treatments.

S. validus

Flooding reduced the total weight and number of flowers compared to plants at STAT (Table 8.2). In contrast, the weight per flower and the proportion of culms with flowers was variable and did not differ across flooded treatments. The proportion of weight allocated to flowers remained constant under STAT and shallow flooding but declined for deep flooded plants, with only 4% of weight allocated to flowers at RF60 (Figure 8.14).

The total weight, number and weight per flower declined significantly from STAT to deep drawdown treatments (Table 8.2). Similarly, the proportional allocation of weight to flowers declined under drawdown to -60 cm ($F_{8,42}$=11.6, $P < 0.0001$: Figure 8.14). The proportion of culms with flowers was at least 56% for plants exposed to STAT and shallow drawdown but fell below 25% for those drawndown to -60 cm ($F_{8,42}$=10.5, $P < 0.0001$: Figure 8.15).

8.5 Discussion

8.5.1 Growth and asexual reproduction

Investment in asexual reproduction changed in concert with biomass accumulation for *J. aridicola* and *C. gymnocaulos*. This response is common among emergent macrophytes (e.g. *Miscanthus sacchariflorus*, *Phragmites australis*, *Zizania latifolia*: Yamasaki and Tange 1981; *Typha domingensis*, *Typha latifolia*: Grace 1989). Stevenson and Lee (1987) suggested that declines in asexual reproduction with increasing depth may be explained by the greater effort put into reaching the water surface reducing the time available for reproduction.

Asexual reproduction for *B. caldwellii* was linked with growth, however, unlike *J. aridicola* and *C. gymnocaulos*, the weight per ramet and proportional allocation to tubers varied between treatment regimes. Grace (1993) suggested that there are six major selective forces operating on clonal propagules: numerical increase, dispersal, resource acquisition, storage, protection and anchorage. The response of *B. caldwellii* suggests differential investment in the functions served by clonal propagules. When subject to slow deep flooding allocation to tubers decreased, but rates of culm and numerical increase were maintained. In contrast, under deep drawdown, growth and asexual reproduction declined but plants increased allocation to tubers. These responses suggest that *B. caldwellii* is able to trade-off between carbohydrate storage and the maintenance of rates of numerical increase.

S. validus was the only species not to mirror growth with investment in asexual reproduction, with culm production declining for deep flooded plants despite maintenance of growth. The continuous investment of biomass in rhizomes suggests a strategy that places greater importance on protection and storage than numerical increase. The importance of storage for *S. validus* was further demonstrated for deep drawdown treatments where the weight per ramet was reduced but the proportional allocation of biomass to rhizomes increased.

Table 8.2. The total weight and number of flowers and the weight per flower (± SD) for *B. caldwellii*, *J. aridicola* and *S. validus*. Data for *C. gymnocaulos* relate to bulbils. Superscripts indicate treatments with similar responses (α=0.05). Treatment codes are described in Table 7.1.

B. caldwellii		Weight (g)	Flowers (#)	Weight/flower (g)	*C. gymnocaulos*	Weight (g)	Bulbils (#)	Weight/bulbil (g)
F (df), *P*		2.3 (8,42), 0.04	2.1 (8,42), 0.06	4.1 (8,40), 0.001	*F* (df), *P*	13.1 (7,37), <0.0001	14.3 (7,37), <0.0001	4.6 (7,31), 0.001
	SD60	5.9^{ab} (2.5)	19.7^{a} (7.4)	0.30^{b} (0.05)		17.9^{a} (6.5)	30.6^{a} (4.3)	0.61^{a} (0.28)
	RD60	1.0^{b} (1.3)	3.5^{a} (3.2)	0.20^{b} (0.14)		5.0^{bc} (4.9)	26.7^{ab} (12.8)	0.19^{b} (0.19)
	SD20	18.0^{a} (14.9)	19.0^{a} (14.0)	0.90^{a} (0.25)		2.6^{bc} (2.7)	14.3^{bc} (5.2)	0.15^{b} (0.11)
	RD20	3.9^{ab} (2.7)	6.3^{a} (3.2)	0.55^{ab} (0.26)		4.1^{bc} (4.0)	30.8^{a} (18.0)	0.13^{b} (0.14)
	STAT	6.2^{ab} (9.6)	10.0^{a} (15.8)	0.62^{ab} (0.34)		9.3^{b} (5.9)	25.0^{ab} (8.9)	0.41^{ab} (0.26)
	SF20	5.4^{ab} (8.7)	7.3^{a} (5.6)	0.56^{ab} (0.42)		0.2^{c} (0.3)	2.5^{c} (2.1)	0.08^{b} (0.09)
	RF20	7.0^{ab} (5.5)	10.5^{a} (9.3)	0.72^{ab} (0.29)		0.6^{c} (1.2)	2.5^{c} (3.3)	0.16^{b} (0.12)
	SF60	6.2^{ab} (6.3)	15.8^{a} (11.7)	0.33^{b} (0.23)		0.0^{c} (0.1)	0.7^{c} (1.2)	0.08^{b} (0.04)
	RF60	2.9^{ab} (4.0)	5.7^{a} (8.1)	0.56^{ab} (0.09)		0.1	2.0	0.03
J. aridicola		Weight (g)	Flowers (#)	Weight/flower (g)	*S. validus*	Weight (g)	Flowers (#)	Weight/flower (g)
F (df), *P*		7.5 (8,41), <0.0001	5.9 (8,41), <0.0001	6.0 (7,32), 0.0001	*F* (df), *P*	7.4 (8,42), <0.0001	10.5 (8,42), <0.0001	4.9 (8,41), 0.0003
	SD60	12.0^{a} (6.1)	58.7^{a} (33.2)	0.21^{ab} (0.04)		3.3^{cd} (2.5)	9.3^{cde} (4.3)	0.33^{b} (0.27)
	RD60	5.5^{abcd} (6.1)	35.6^{abc} (27.3)	0.13^{bc} (0.04)		0.4^{d} (0.5)	1.7^{e} (2.3)	0.20^{b} (0.05)
	SD20	11.8^{ab} (3.1)	57.2^{ab} (14.2)	0.21^{abc} (0.03)		20.8^{abc} (10.6)	25.2^{ab} (9.4)	0.84^{ab} (0.31)
	RD20	10.2^{abc} (10.1)	48.2^{ab} (43.2)	0.20^{abc} (0.03)		15.2^{bcd} (9.9)	20.7^{abc} (8.5)	0.71^{ab} (0.30)
	STAT	10.6^{abc} (6.6)	41.2^{ab} (21.0)	0.25^{a} (0.05)		35.7^{a} (19.0)	28.7^{a} (7.2)	1.21^{a} (0.46)
	SF20	2.2^{bcd} (0.9)	17.6^{bc} (8.4)	0.14^{bc} (0.08)		12.9^{bcd} (11.9)	15.2^{bcd} (8.3)	0.81^{ab} (0.35)
	RF20	2.2^{cd} (1.0)	18.8^{bc} (6.3)	0.12^{bc} (0.05)		23.2^{ab} (8.3)	19.5^{abc} (3.7)	1.23^{a} (0.48)
	SF60	0.2^{d} (0.4)	2.0^{c} (4.0)	0.07^{c} (0.03)		7.8^{bcd} (4.1)	11.7^{cde} (2.9)	0.65^{ab} (0.30)
	RF60	0^{d} (0.1)	0.5^{c} (1.2)	0.07 (-)		3.9^{cd} (3.4)	4.5^{de} (3.6)	0.78^{ab} (0.32)

Reducing culm production while maintaining biomass accumulation appears to be a characteristic of plants tolerant of deep flooding. For example, Coops *et al.* (1996) found that of four species from the shoreline of the estuarine section of the River Rhine, *Scirpus lacustris*, which had a population spanning depths of 50-90 cm, maintained biomass accumulation but reduced culm density. To achieve this however, *S. lacustris* reduced allocation to rhizomes at depths > 50 cm. This compares to *S. validus* that maintained allocation to rhizomes even at 60 cm, suggesting that in their respective environments, *S. validus* may be better adapted to deeper water.

8.5.2 Sexual reproduction and its relationship with asexual reproduction

A shift from asexual to sexual reproduction has been demonstrated for numerous emergent macrophytes, primarily in response to increasing depth (e.g. Lieffers and Shay 1981; Sun *et al.* 2001). On the basis of these studies, it was predicted that reduced growth and asexual reproduction would result in increased flowering. This hypothesis was rejected for all species that flowered supporting Rea and Ganf's (1994a) proposal that the unpredictable nature of fluctuating water levels means that asexual and sexual reproduction cannot be seen as strict trade-offs.

Each species demonstrated contrasting patterns of investment in sexual and asexual reproduction. For *J. aridicola*, investment in flowering coincided with culm increase and optimal growth. Concomitant changes in growth, clonal expansion and flowering have also been observed for *Zizania aquatica* (Stevenson and Lee 1987), *Typha domingensis* and *Typha latifolia* (Grace 1989). In contrast, *S. validus* reduced investment in flowering across treatments for which growth was maintained. The allocation of biomass to rhizomes over flowers for *S. validus* at RD60 suggests it may have a preference for investing in the protection offered by perennating organs to persist through periods of stress, rather than re-establishment from the seed bank.

B. caldwellii was the only species that maintained the number of flowers it produced across the treatment regimes and only recorded a decline in flower weight at RD60. This was despite significant reductions in relative growth rate at RF60 and deep drawdown treatments. This response is consistent with other species tolerant of flooding to depths of 20-60 cm (e.g. *T. domingensis*, *T. latifolia*, Grace 1989). The observation that plants flowered despite a decline in growth rate implies that they are continually investing in maximising the genetic variability of their offspring, which may enhance their ability to persist in unpredictable environments (Hutchinson 1975).

The number of flowers produced per culm differed between species suggesting a difference in the relative importance of flowering. It was highest for *J. aridicola*, ranging from 56 to 82% of culms for all except deep flooded treatments. This is likely to be important for short as well as long distance dispersal for *J. aridicola* given that its rhizomes only form tufts. In contrast, *B. caldwellii* and *S. validus*, both of which can fuel local population growth by rhizome extension, produced flowers on < 26% and 40-65% of culms, respectively.

A distinctive feature of all species was the variability in the number and weight of flowers across treatment regimes. This was illustrated by two slow, shallow flooded *B. caldwellii* plants which had relative growth rates of 55.3 and 55.7 mg g^{-1} d^{-1} and produced 43 and 7 flowers respectively, with minimal difference in the weight per flower. While this may reflect variable plant performance, an alternate hypothesis is that variable investment between genotypes may be a strategy for persistence at the population scale.

8.5.3 Bulbil production for C. gymnocaulos

As bulbils increased in weight culms bent and made contact with the ground. This stimulated root production leading to bulbil anchoring and abscission from the parent plant. In contrast, bulbils on flooded plants abscised. In the field this would enable them to float and lodge at the water's edge and subsequently anchor and establish. Either way, their formation provides a faster method of local population growth than afforded by the type of rhizome extension *C. gymnocaulos* displays.

To investigate *C. gymnocaulos*' investment in asexual versus sexual reproduction may require different water regimes than used for this study. Field observations suggest that plants high on the elevation gradient tend to flower whereas those closer to the water edge develop bulbils (J. Nicol, University of Adelaide, pers. comm.). This suggests that soil moisture levels or depths to groundwater lower than that experienced in the pond experiment may be needed to stimulate flowering.

8.5.4 Predictive model of the impact of water regime on floristic composition

This study re-affirms that species characteristic of different locations across the littoral zone have different patterns of investment in reproduction when subject to contrasting water regimes. A model predicting the influence of water regime on floristic composition is presented in Figure 8.16. The model predicts which mixture of the four species would develop at an elevation subjected to the water regimes used for the pond experiment. It assumes that a) the final depth of the treatment regime is maintained for the entire growth season, b) mudflats are bare and c) other abiotic and biotic factors (e.g. salinity, sediment fertility and grazing) are benign.

Predictions consider the growth rate, investment in asexual reproduction, potential interspecific interactions and the distance between culms. For *B. caldwellii* and *S. validus* culms are separated by about 5-15 cm, whereas *C. gymnocaulos* and *J. aridicola* culms are separated by ≤ 5 mm.

Slow and rapid deep drawdown – Outcomes 1 and 2

Based solely on growth, *B. caldwellii* is likely to be dominant. However, these regimes also promote bulbil production for *C. gymnocaulos*, which would enable faster colonisation than the types of clonal expansion afforded to the other study species. The ability of *B. caldwellii* to out compete *C. gymnocaulos* would be reduced given that under these regimes it invests in storage and protection rather than numerical increase. It is predicted that *C. gymnocaulos* would ultimately dominate sites exposed to slow and rapid deep drawdown.

Static 0 cm and shallow drawdown – Outcome 3

All species achieved optimal growth and clonal increase under these regimes and thus competitive interactions are likely to be high. Bulbil production for *C. gymnocaulos* would still provide an advantage in colonising space 50-100 cm from the parent plant, however, the growth and culm production of *B. caldwellii* suggests it would dominate competitive interactions. *B. caldwellii* dominated interactions between it and *Bolboschoenus medianus* when drawn down to 20 cm below the sediment surface and flooded to 0 cm (Siebentritt and Ganf 2000). Notably, the growth rate of *B. medianus* for these depths was about double that of *C. gymnocaulos*, *J. aridicola* and *S. validus*.

Shallow flooding – Outcome 4

Shallow flooding favoured the growth of *B. caldwellii* and *S. validus*, but for the same reasons outlined for plants exposed to depths of 0 cm and –20 cm, the competitive dominance of *B. caldwellii* suggests it would dominate. The extent to which

B. caldwellii excludes *J. aridicola* and *C. gymnocaulos* may be even greater given their much reduced rates of growth and culm addition.

Slow and rapid deep flooding – Outcome 5

Deep flooding should result in the co-dominance of *B. caldwellii* and *S. validus*. Under rapid flooding in particular, it is unlikely that competitive interactions would be high because the allocation to asexual reproduction is low and plant responses are directed toward survival through the production of emergent tissue. *J. aridicola* and *C. gymnocaulos* are likely to persist in the short term in low abundances given their ability to tolerate at least 90 days of total submergence. This is supported by observations that emergent macrophytes from the upper and lower littoral zone may co-occur at depths of 70 cm for up to 2 years (Squires and van der Valk 1992).

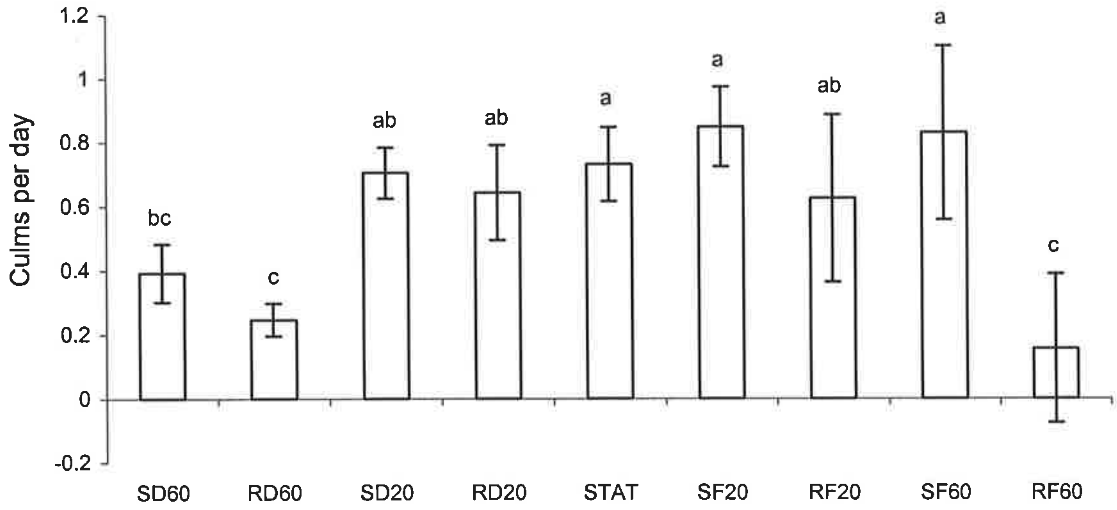
Influence of prolonged flood or drawdown on floristic composition – Outcomes A-F

It is anticipated that the floristic composition would change if the conditions at the end of each growing season were maintained through to the beginning of the next (Outcomes A-F Figure 8.16).

B. caldwellii culms and roots senesce at the end of each growing season and plants re-establish in the following season from tubers. In contrast, the above ground material of the other species persists. Hence, if water levels remained, for instance, at 60 cm above or below the sediment surface, tubers would need to support culm extension to produce emergent photosynthetic tissue or root extension to reach groundwater or moist soil. The inability of a number of rapid deep flooded and drawndown plants, which had already established above and below ground tissue, to do this in the pond experiment suggests such a response is improbable. *B. caldwellii* is even more unlikely to achieve this at deep flooded sites given its low investment in tubers and the importance of carbohydrate storage for successful emergence at the start of a new growing season (Sun *et. al.* 2001). The other species may therefore be able to avoid competition with *B. caldwellii* if they are able to persist through to subsequent growing seasons.

Figure 8.1. The mean rate of culm increase per day for *B. caldwellii* across the water regime treatments (± SD). n=6 for all except RF60 where n=3. Superscripts indicate treatments with similar responses (α=0.05).

Figure 8.2. The proportional allocation of biomass to *B. caldwellii* tubers (± SD) across the water regime treatments. n=6 for all except RF60 where n=3. Superscripts indicate treatments with similar responses (α=0.05).


Culms per day
1.2
1
0.8
0.6
0.4
0.2
0
-0.2
bc
c
ab
ab
a
a
ab
a
c
SD60
RD60
SD20
RD20
STAT
SF20
RF20
SF60
RF60

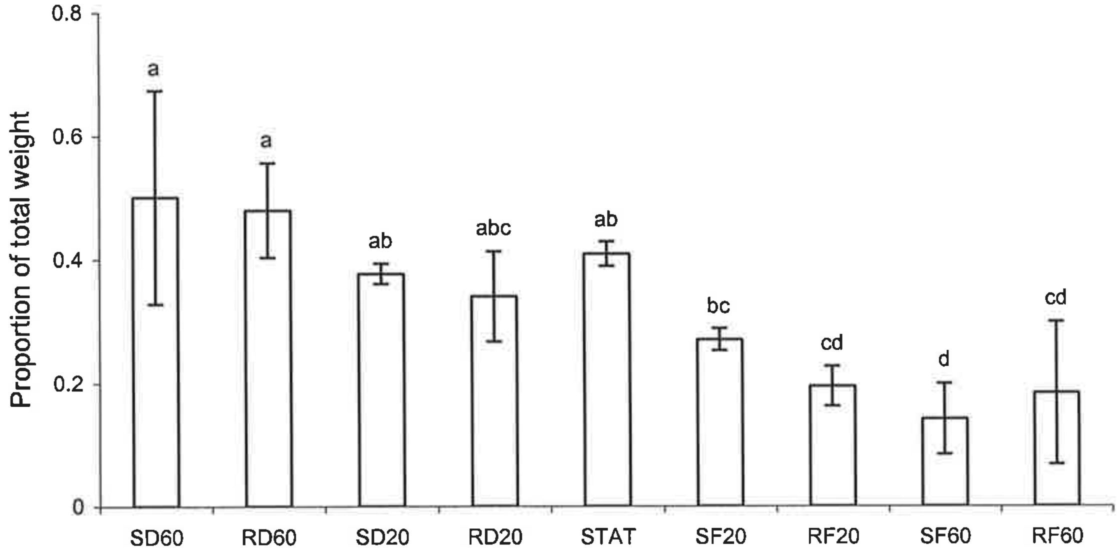
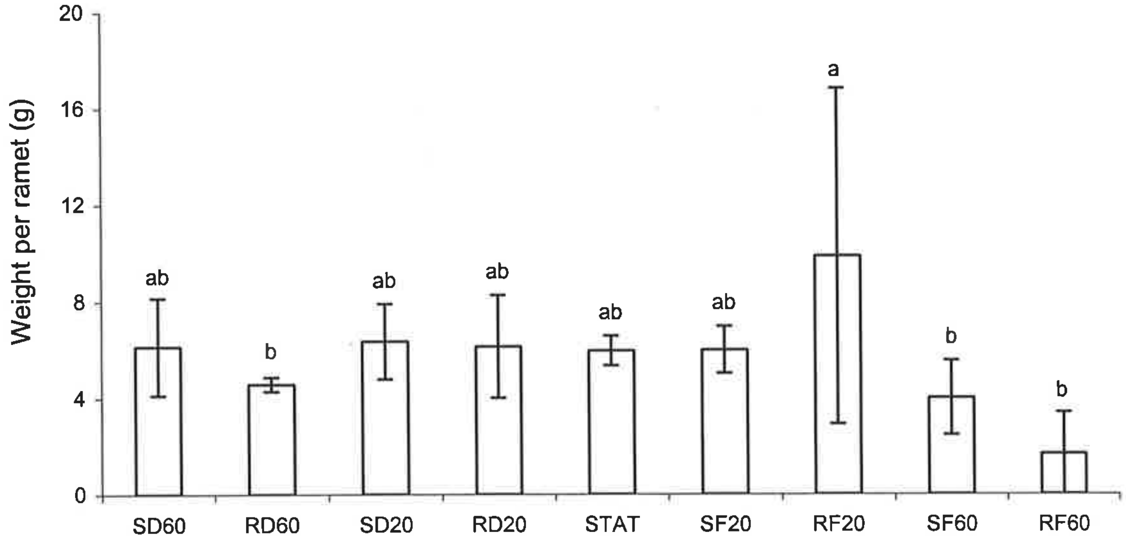

Proportion of total weight
0.8
0.6
0.4
0.2
0
a
a
ab
abc
ab
bc
cd
d
cd
SD60
RD60
SD20
RD20
STAT
SF20
RF20
SF60
RF60

Figure 8.3. The mean ramet weight (± SD) for *B. caldwellii* across the water regime treatments. *n*=6 for all except RF60 where *n*=3. Superscripts indicate treatments with similar responses (α=0.05).

Figure 8.4. The mean number of culms (± SD) produced per day for *C. gymnocaulos* across the water regime treatments. *n*=6 for all except RD20, STAT, SF20 and RF60 where *n*=5. Superscripts indicate treatments with similar responses (α=0.05).


Weight per ramet (g)
20
16
12
8
4
0
ab
b
ab
ab
ab
ab
a
b
b
SD60
RD60
SD20
RD20
STAT
SF20
RF20
SF60
RF60

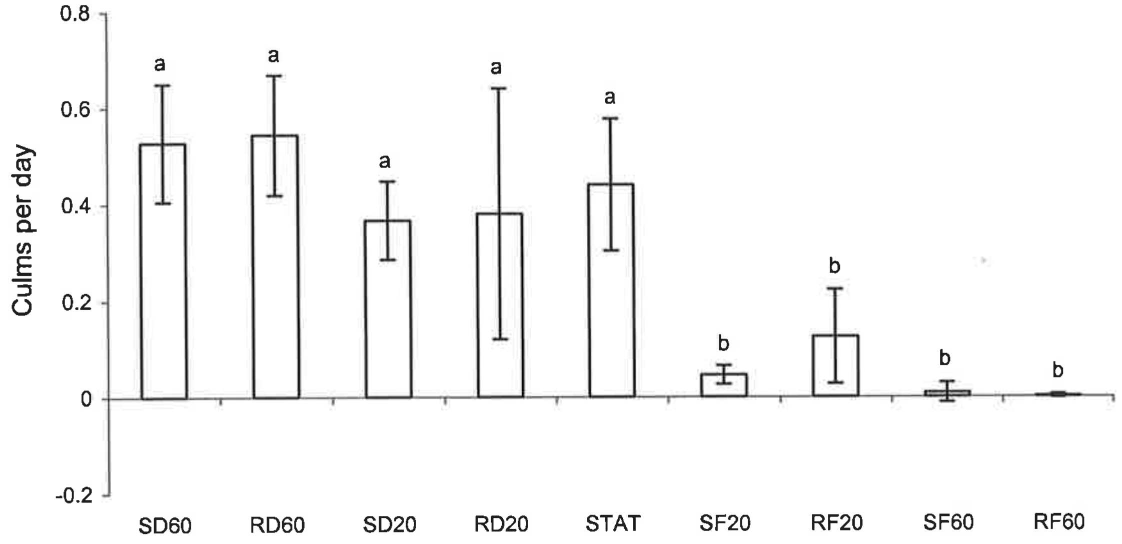
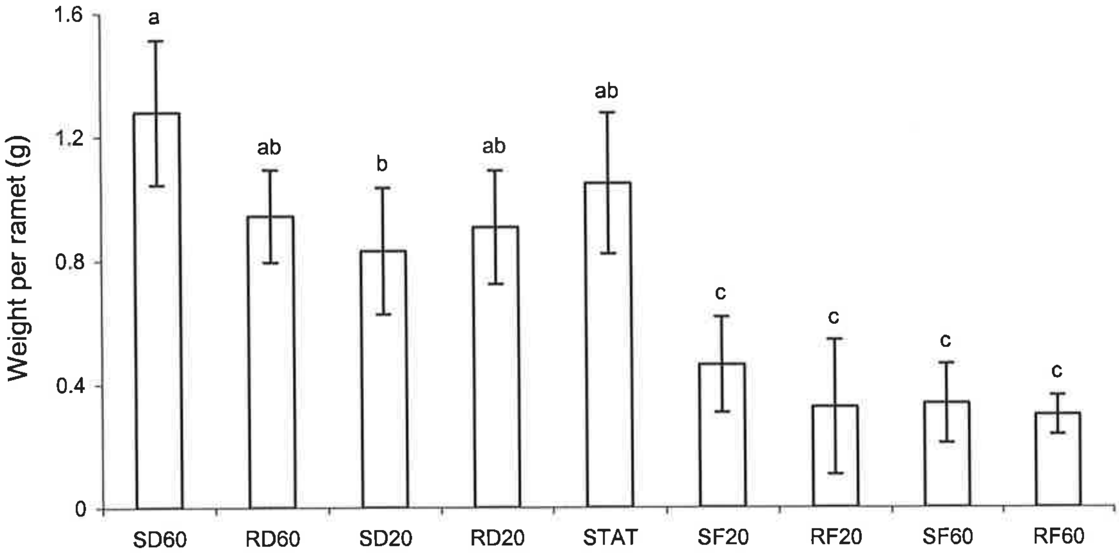

Culms per day
0.8
0.6
0.4
0.2
0
-0.2
a
a
a
a
a
b
b
b
b
SD60
RD60
SD20
RD20
STAT
SF20
RF20
SF60
RF60

Figure 8.5. The mean ramet weight for *C. gymnocaulos* (± SD). n=6 for all except RD20, STAT, SF20 and RF60 where n=5. Superscripts indicate treatments with similar responses (α=0.05).

Figure 8.6. The mean proportion of weight (± SD) allocated to rhizomes across water regimes for *C. gymnocaulos*. n=6 for all except RD20, STAT, SF20 and RF60 where n=5. Superscripts indicate treatments with similar responses (α=0.05).


Weight per ramet (g)
1.6
1.2
0.8
0.4
0
a
ab
b
ab
ab
c
c
c
c
SD60
RD60
SD20
RD20
STAT
SF20
RF20
SF60
RF60

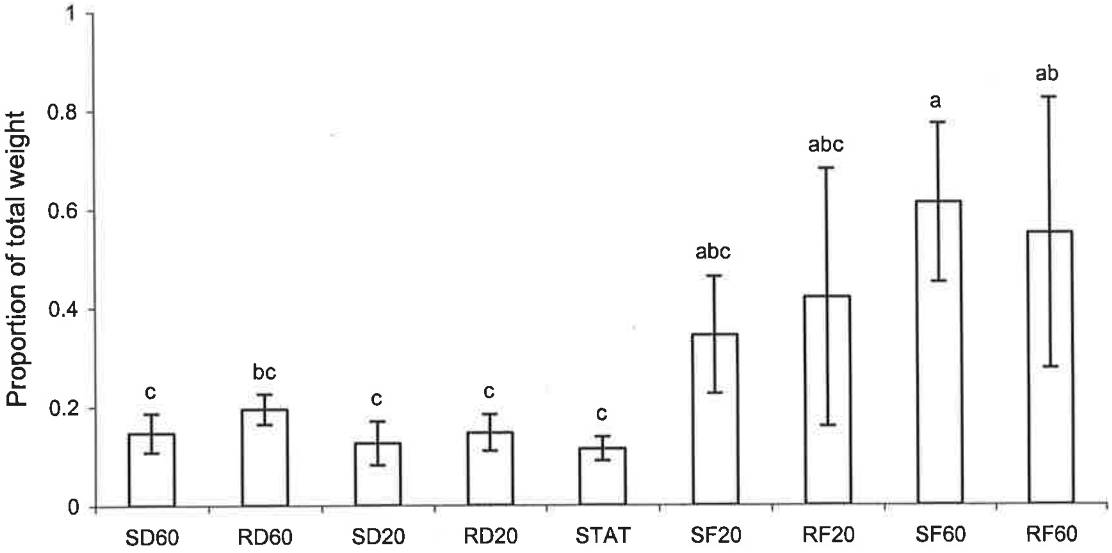
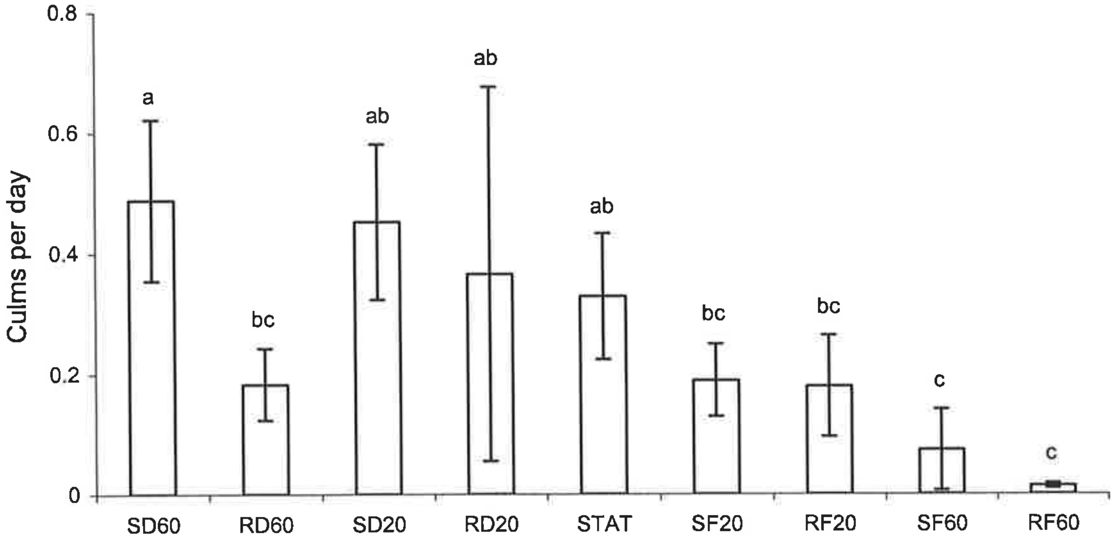

Proportion of total weight
1
0.8
0.6
0.4
0.2
0
c
bc
c
c
c
abc
abc
a
ab
SD60
RD60
SD20
RD20
STAT
SF20
RF20
SF60
RF60

Figure 8.7. The mean increase in the number of culms per day (± SD) for *J. aridicola* across treatment water regimes. *n*=6 for all except RD20, RD60, SD20 and SF20 where *n*=5. Superscripts indicate treatments with similar responses (α=0.05).

Figure 8.8. The weight per ramet (± SD) for *J. aridicola* across treatment water regimes. *n*=6 for all except RD20, RD60, SD20 and SF20 where *n*=5. Superscripts indicate treatments with similar responses (α=0.05).


0.8
0.6
0.4
0.2
0
Culms per day
a
bc
ab
ab
ab
bc
bc
c
c
SD60
RD60
SD20
RD20
STAT
SF20
RF20
SF60
RF60

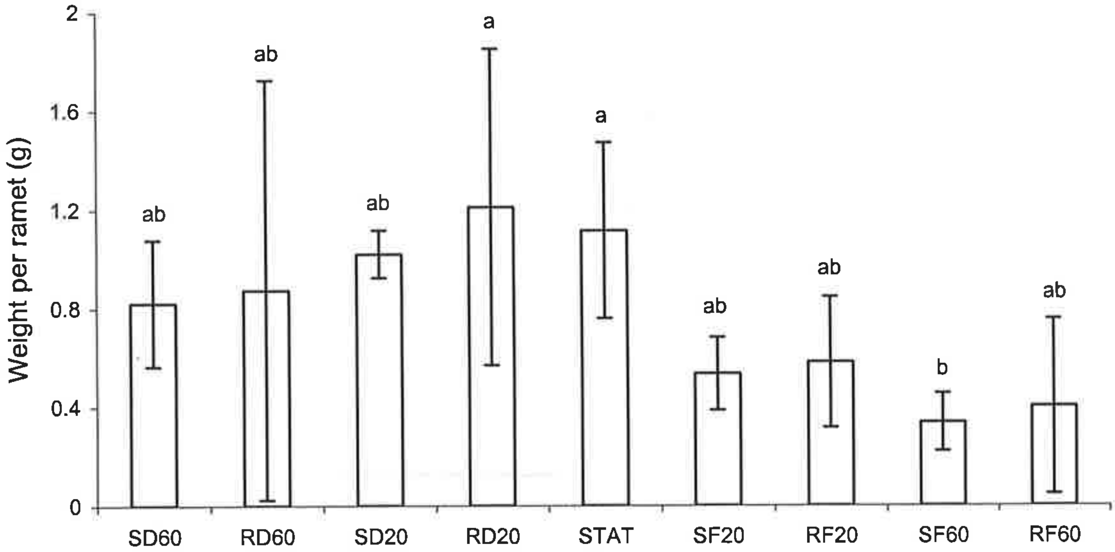
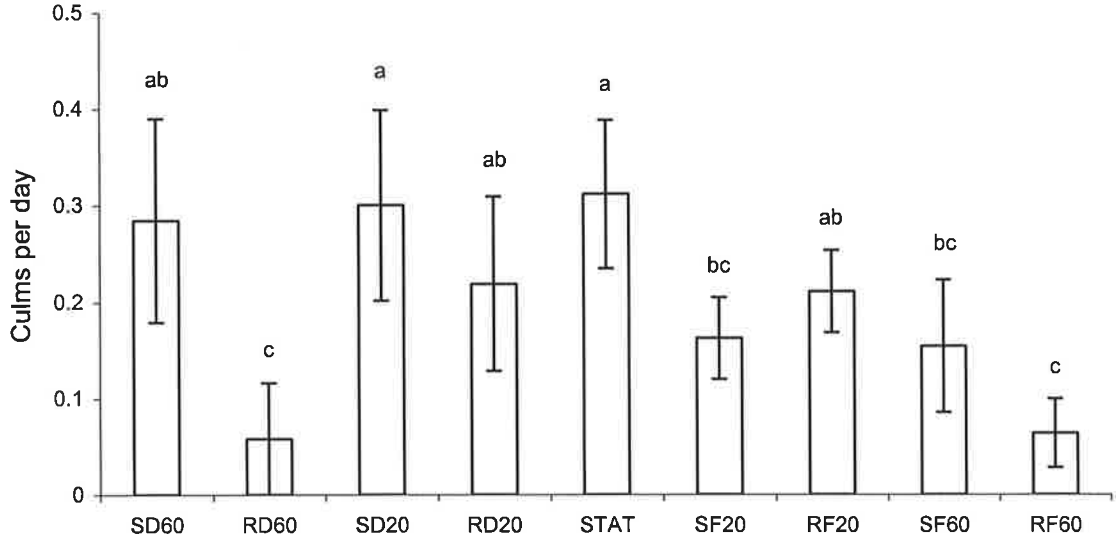

2
1.6
1.2
0.8
0.4
0
Weight per ramet (g)
ab
ab
ab
a
a
ab
ab
b
ab
SD60
RD60
SD20
RD20
STAT
SF20
RF20
SF60
RF60

Figure 8.9. The number of culms produced per day (± SD) by *S. validus* across treatment water regimes. *n*=6 for all except RF60 where *n*=5 and RD60 where *n*=4. Superscripts indicate treatments with similar responses (α=0.05).

Figure 8.10. The weight per ramet (± SD) for *S. validus* across treatment water regimes. *n*=6 for all except RF60 where *n*=5 and RD60 where *n*=4. Superscripts indicate treatments with similar responses (α=0.05).


Culms per day
0.5
0.4
0.3
0.2
0.1
0
ab
c
a
ab
a
bc
ab
bc
c
SD60
RD60
SD20
RD20
STAT
SF20
RF20
SF60
RF60

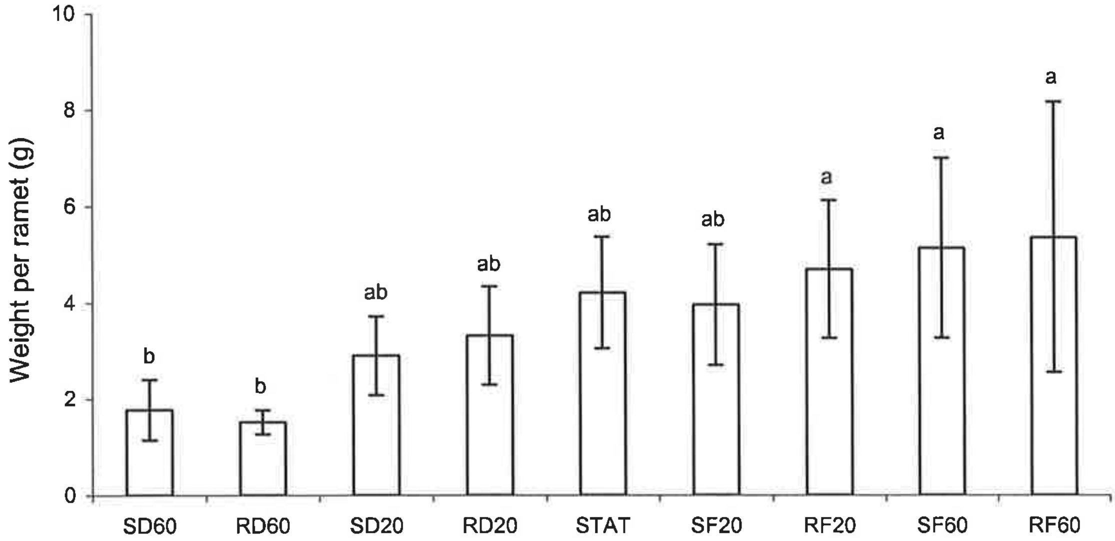
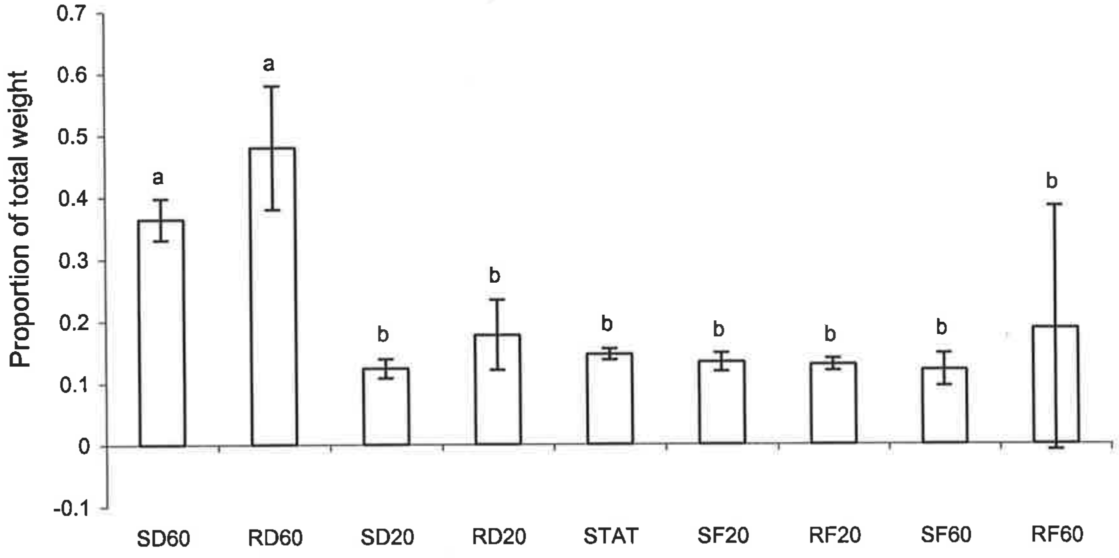

Weight per ramet (g)
10
8
6
4
2
0
b
b
ab
ab
ab
ab
a
a
a
SD60
RD60
SD20
RD20
STAT
SF20
RF20
SF60
RF60

Figure 8.11. The mean proportion of weight (± SD) allocated to rhizomes for *S. validus* across treatment water regimes. *n*=6 for all except RF60 where *n*=5 and RD60 where *n*=4. Superscripts indicate treatments with similar responses (α=0.05).

Figure 8.12. The mean number of flowers per culm (± SD) for *B. caldwellii* across treatment water regimes. *n*=6 for all except RF60 where *n*=3. Superscripts indicate treatments with similar responses (α=0.05).


Proportion of total weight
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
-0.1
a
a
b
b
b
b
b
b
b
SD60
RD60
SD20
RD20
STAT
SF20
RF20
SF60
RF60

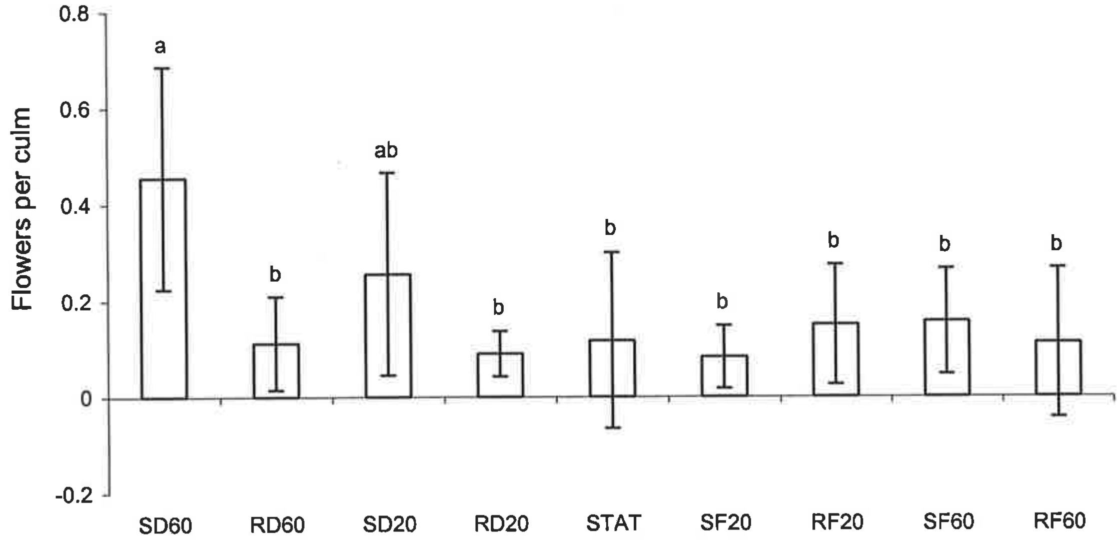
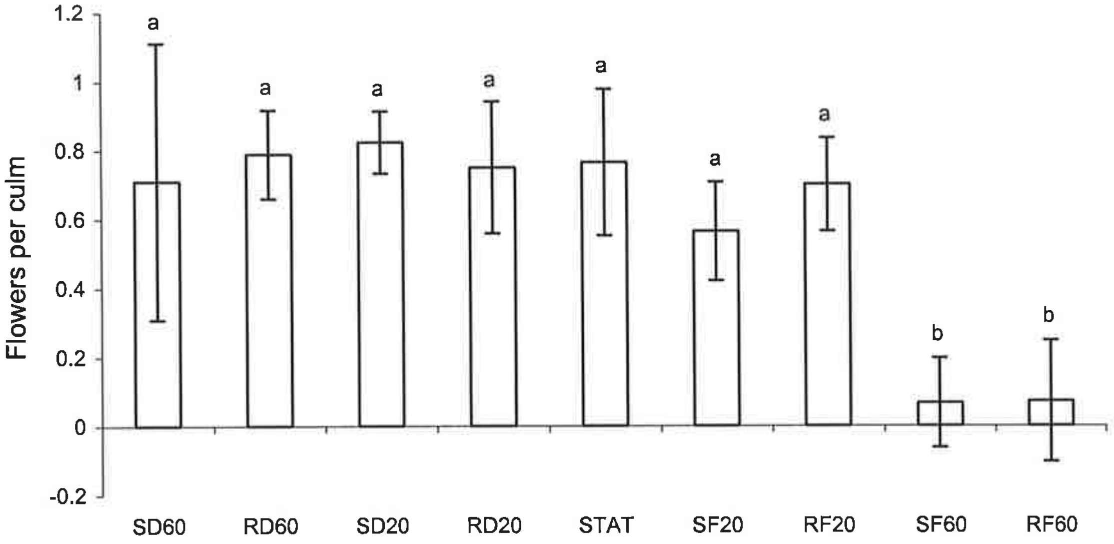

Flowers per culm
0.8
0.6
0.4
0.2
0
-0.2
a
b
ab
b
b
b
b
b
b
SD60
RD60
SD20
RD20
STAT
SF20
RF20
SF60
RF60

Figure 8.13. The mean number of flowers per culm (± SD) for *J. aridicola* across the treatment water regimes. *n*=6 for all except RD20, RD60, SD20 and SF20 where *n*=5. Superscripts indicate treatments with similar responses (α=0.05).

Figure 8.14. The mean proportion of total weight allocated to flowers (± SD) for *S. validus* across treatment water regimes. *n*=6 for all except RF60 where *n*=5 and RD60 where *n*=4. Superscripts indicate treatments with similar responses (α=0.05).


Flowers per culm
1.2
1
0.8
0.6
0.4
0.2
0
-0.2
a
a
a
a
a
a
a
b
b
SD60
RD60
SD20
RD20
STAT
SF20
RF20
SF60
RF60

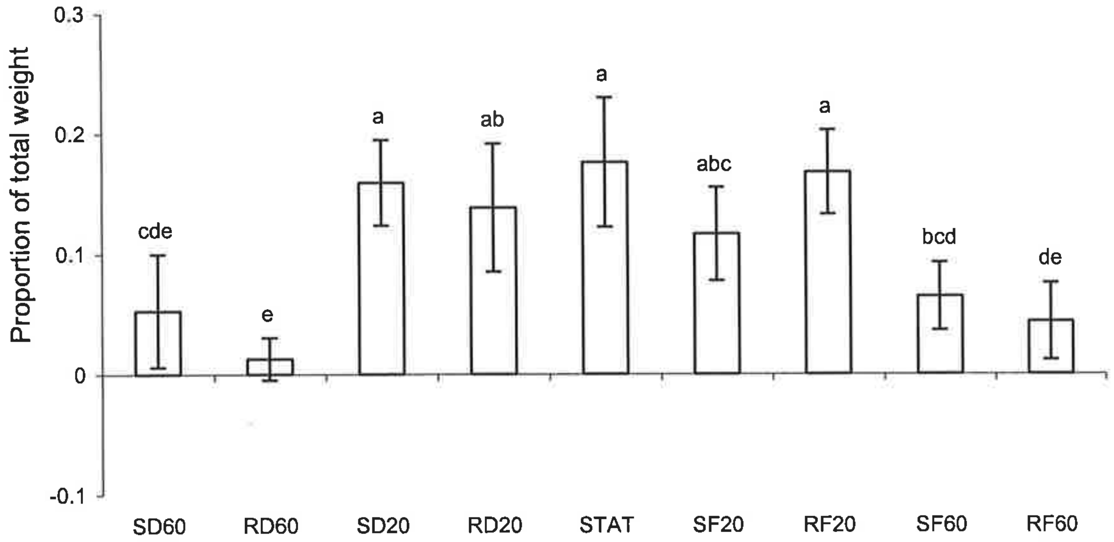

Proportion of total weight
0.3
0.2
0.1
0
-0.1
cde
e
a
ab
a
abc
a
bcd
de
SD60
RD60
SD20
RD20
STAT
SF20
RF20
SF60
RF60

Figure 8.15. The mean number of flowers per culm (± SD) for *S. validus*. $n=6$ for all except RF60 where $n=5$ and RD60 where $n=4$. Superscripts indicate treatments with similar responses ($\alpha=0.05$).

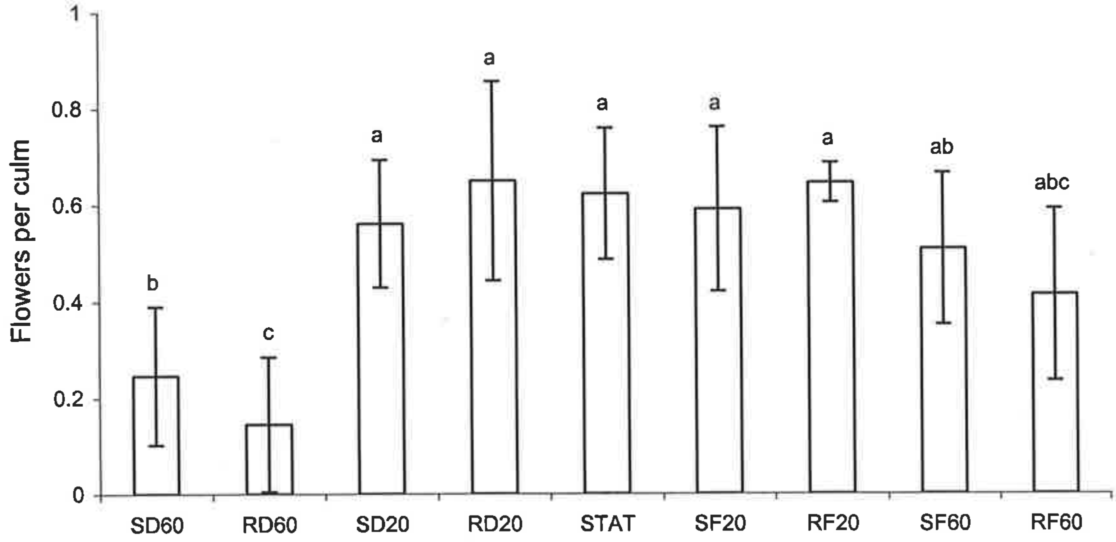
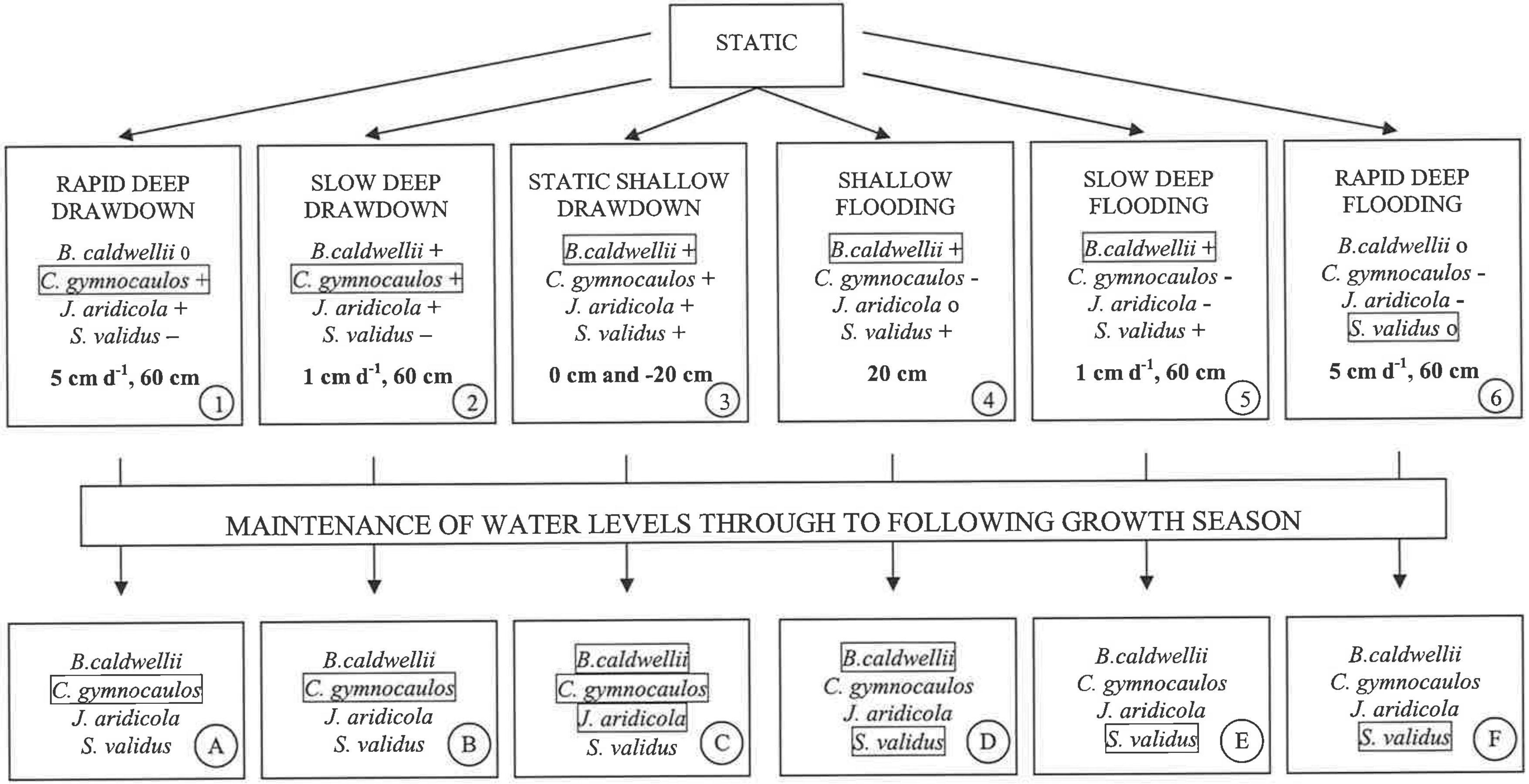

Flowers per culm
1
0.8
0.6
0.4
0.2
0
b
c
a
a
a
a
a
ab
abc
SD60
RD60
SD20
RD20
STAT
SF20
RF20
SF60
RF60

Figure 8.16. Predictions of the floristic composition that would develop if mixtures of the four test species were subject to the water regimes used in the pond experiment. STATIC refers to conditions with water levels at the sediment surface. Species with a border are those that are predicted to dominate as a result of the water regime. The first level of boxes containing species names relate to the predicted outcome of species interactions at the end of the first growing season, the second layer predicts the outcome if water levels remain at their respective depths until the following growth season. The circled numbers and upper case letters relate to the outcome of a box that is referred to in the text.


STATIC
RAPID DEEP DRAWDOWN
B. caldwellii 0
C. gymnocaulos +
J. aridicola +
S. validus –
5 cm d-1, 60 cm
1
SLOW DEEP DRAWDOWN
B.caldwellii +
C. gymnocaulos +
J. aridicola +
S. validus –
1 cm d-1, 60 cm
2
STATIC SHALLOW DRAWDOWN
B.caldwellii +
C. gymnocaulos +
J. aridicola +
S. validus +
0 cm and -20 cm
3
SHALLOW FLOODING
B.caldwellii +
C. gymnocaulos -
J. aridicola o
S. validus +
20 cm
4
SLOW DEEP FLOODING
B.caldwellii +
C. gymnocaulos -
J. aridicola -
S. validus +
1 cm d-1, 60 cm
5
RAPID DEEP FLOODING
B.caldwellii o
C. gymnocaulos -
J. aridicola -
S. validus o
5 cm d-1, 60 cm
6
MAINTENANCE OF WATER LEVELS THROUGH TO FOLLOWING GROWTH SEASON
B.caldwellii
C. gymnocaulos
J. aridicola
S. validus
A
B.caldwellii
C. gymnocaulos
J. aridicola
S. validus
B
B.caldwellii
C. gymnocaulos
J. aridicola
S. validus
C
B.caldwellii
C. gymnocaulos
J. aridicola
S. validus
D
B.caldwellii
C. gymnocaulos
J. aridicola
S. validus
E
B.caldwellii
C. gymnocaulos
J. aridicola
S. validus
F

CHAPTER 9

GENERAL DISCUSSION

9.1 The influence of water regime upon floristic composition

The field studies and pond experiment demonstrated the significance of depth and other components of water regime (e.g. rate, duration and timing of flood and drawdown) in influencing the distribution and abundance of wetland plants.

The responses of plant assemblages to contrasting water regimes were assessed by examining:

1) the morphological and physiological response of individual plants;
2) the influence of water regime on regeneration (establishment, growth and reproduction) and extirpation; and
3) changes in floristic composition at the scale of the wetland.

The following discussion draws on a subset of the results presented.

9.1.1 Morphological and physiological responses

The pond experiment supports the results of similar studies conducted in North America, Europe and Australia that the distribution of plants across the littoral zone is influenced by water depth tolerances (Grace 1989; Waters and Shay 1991; Squires and van der Valk 1992; Coops *et al.* 1996; Siebentritt and Ganf 2000). However, the results also suggest that in wetlands subject to periodic drawdown, plant distribution is as much a result of tolerance to drawdown as it is of flooding.

As observed for other studies, culm extension is a key to the survival of emergent macrophytes subject to flooding (Stevenson and Lee 1987; Squires and van der Valk 1992; Blanch et al. 1999). Culm extension was of particular importance during the initial stages of inundation. Drawdown tolerance also requires specific strategies. Greater stomatal control, a mechanism for tolerance of low soil moisture, was recorded for species characteristic of more infrequently flooded elevations. Together with Kirkman and Sharitz (1993), this provides one of the few examples of a drought tolerance mechanism among wetland plants. An alternate mechanism for tolerating drawdown is avoidance of low soil moisture by extending roots to groundwater. This thesis provides the first record of this response, as quantified through a pond experiment, as a mechanism for tolerating falling water levels among wetland plants.

Along with the research of Nicol and Ganf (2000), the pond experiment provides one of the few assessments of the impact of the combined effects of the water regime components rate and depth on plant performance. The rate of flood and drawdown interacted with rates of culm and root extension, respectively, to determine the ability of plants to maintain access to the resources necessary to support growth. The effect of both factors was most pronounced for plants flooded or drawndown to 60 cm suggesting that it is most significant where plants are at the limit of depth tolerances.

9.1.2 Establishment and extirpation

Establishment and extirpation are the outcomes of morphological and physiological responses and at the wetland scale are the processes that shape differences in plant distribution and abundance patterns. For both studies these processes were influenced by not just whether an elevation was wet or dry, but by the characteristics of flood and drawdown.

Observations from the field studies concur with others that exposure of mudflats provide an opportunity for the establishment of mudflat annuals and emergent macrophytes (Galinato and van der Valk 1986; Deswart *et al.* 1994; ter Heerdt and Drost 1994; Gergley *et al.* 2001). The results of the floodplain wetland study in particular highlight the importance of the characteristics of drawdown in determining the floristic composition that develops.

Where the season of drawdown was appropriate for triggering germination, the species mixture that developed was influenced by the rate of drawdown, with a greater proportion of emergent macrophytes establishing in Big Mussel under slow drawdown compared to Little Duck and Pilby Creek. Harris and Marshall (1963), Salisbury (1970) and ter Heerdt and Drost (1994) suggested that accelerated mudflat drying resulting from summer drawdown promotes the preferential establishment of mudflat annuals over emergent macrophytes. These results lead to a similar hypothesis: greater rates of drawdown increase the rate of soil moisture depletion and favour mudflat annual establishment.

Most descriptions of vegetation change in the literature focus on the role of flood or drawdown in promoting establishment. This thesis suggests that extirpation plays just as significant a role in shaping floristic composition. Extirpation was observed during the two field studies and the pond experiment and in summary was influenced by the:

- type of plant (e.g. emergent macrophyte, submerged macrophyte, mudflat annual) and its life history strategies;
- depth, duration, rate and timing of flood and drawdown;
- developmental stage of the plant e.g. seedling versus adult;
- previous water regime conditions; and
- ability of other factors to modify the response to flood and drawdown.

At re-flooded sites extirpation drove vegetation change, from the loss of mudflat annuals on the bed of re-flooded wetlands to the death of *Atriplex vesicaria* during the enhanced flood. Plant death from flooding was typically rapid and led to significant changes in floristic composition between surveys.

Studies on drawdown initiated extirpation are generally of submerged macrophytes (Cooke 1980; Briggs *et al.* 1985; van Wijck and de Groot 1993). In this regard, the floodplain wetland study found that the death of submerged macrophytes upon drawdown was not a formality, and that where winter drawdown occurs, the below ground tissue of submerged macrophytes and thus the entire plant can persist.

Models of vegetation change suggest that as drawdown continues and soil moisture reserves are exhausted, extirpation of drought intolerant species drives vegetation change (e.g. Harris 1963; Segal 1971; van der Valk and Davis 1980). A feature of the floodplain wetland study was the lack of extirpation of emergent macrophytes during drawdown, presumably because of groundwater access.

In Lower Murray wetlands, drawdown is not a simple transition from water logged to dry sediment. Instead, water levels may remain within 1-2 m of the sediment surface. The extension of roots by emergent macrophytes down the soil column to maintain contact with groundwater was demonstrated in the pond experiment. There was further evidence of this in the field studies for *Paspalum distichum* and *Typha domingensis*. This ability to maintain access to groundwater may disrupt classical patterns of vegetation change. I suggest that future models of vegetation change take into account groundwater depths. Where groundwater levels remain close to the sediment surface the transition from less to more drought tolerant species may be slowed or even prevented.

9.1.3 Changes and differences in floristic composition

The initial premise of this thesis was that periodic flood and drawdown would promote regenerative processes leading to the establishment of more unique and diverse plant assemblages than those present in permanently inundated wetlands. This was extended to the enhanced flood study, with the expectation that the enhanced flood would stimulate establishment and growth of floodplain plant populations and promote vegetation change at flooded elevations. To this extent, the results of the two field studies support those of other researchers that alternating periods of wet and dry can promote regeneration and lead to contrasting plant assemblages (van der Valk 1981; van der Valk 1987; ter Heerdt and Drost 1994; Kadlec 1962; Harris and Marshall 1963). This thesis concludes, however, that floristic composition is influenced by more than whether an elevation or wetland is wet or dry, but by the characteristics of flood and drawdown such as depth, duration, rate and timing.

Where the characteristics of water regime are similar, responses are also likely to be similar. This was demonstrated in the enhanced flood study where *S. mitchellii* expansion and *A. vesicaria* dieback was a common response across floodplain areas separated by at least 10 km. Where the characteristics of flood and drawdown differ, unique *cycles* of vegetation change develop. Some components of these cycles may have a high degree of similarity, as was observed between managed and permanently inundated wetlands when the former returned to the flooded phase.

9.2 Further studies

Differences in floristic composition were examined by considering the impact of water regime on establishment, growth, reproduction and extirpation. Future studies need to be directed at improving our understanding of the relationship between establishment and water regime, extirpation and water regime and should consider the ability of salinity to modify plant response to water regime. All future work also needs to be supported by better characterisation of water regime.

9.2.1 Establishment

Submerged macrophyte establishment is influenced by the quantity and quality of light reaching the sediment, which is modified by depth and optical properties such as turbidity, suspended solids and colour (Baskin and Baskin 2001). In the turbid Lower Murray, re-filling provides an opportunity for submerged macrophytes to establish in shallow water under improved light conditions. The rate of filling determines the period of time for which this opportunity is available.

One method of examining the influence of flooding on submerged macrophyte establishment is through controlled pond experiments. These would commence with exposed pots (water surface below sediment surface) containing either a) known quantities of submerged macrophyte seed or b) sods of wetland sediment known to contain submerged macrophyte seed. Pots would be flooded at rates of 1, 5 and 10 cm d^{-1}, to reflect the range of flooding rates in Lower Murray wetlands, and to depths of 25-100 cm to mimic the depth distribution of submerged macrophytes across the Lower Murray. Turbidity would be mimicked using a clay suspension, as has been done by Blanch *et al.* (1998) and Cenzato and Ganf (2001), and set at levels known to occur in the Lower Murray e.g. 10 –100 NTU.

The results of this experiment would be used to develop a model of the colonisable depth for seedlings of selected submerged macrophytes. The model would provide a predictive relationship between a) the depth of colonisation, b) the rate and depth of flooding and c) turbidity. This would complement Blanch's (1997) model for predicting the maximum colonisable depth of mature *V. americana*.

Another significant establishment event in floodplain wetlands was of mudflat annuals and emergent macrophytes during drawdown. As indicated by Seabloom *et al.* (1998), high soil moisture conditions present during the initial stages of drawdown provide establishment opportunities for a range of species. There is evidence from this study and others, however, that the mixture of species is influenced by characteristics of drawdown such as rate and timing (Harris and Marshall 1963; Salisbury 1970; ter Heerdt and Drost 1994).

The relationship between floristic composition and the characteristics of drawdown could be examined through a combination of field studies and controlled pond experiments. For field studies, the vegetation that develops on the wetland bed could be analysed using multivariate techniques such as ordination, overlayed with a matrix of environmental variables describing different characteristics of drawdown. The number of wetlands surveyed would be maximised to improve the accuracy of the relationship between drawdown characteristics and floristic composition.

An alternate to field studies would be a controlled pond experiment in which wetland sods would be flooded to 0 cm and then exposed to different rates and depths of drawdown. The drawdown regimes used in Chapters 7 and 8 would be suitable for this purpose. To account for the influence of timing on floristic composition the experiment could be repeated during spring, summer, autumn and winter.

9.2.2 Extirpation

The value of field studies for examining the influence of water regime on extirpation was demonstrated in Chapter 4. More frequent monitoring and collection of water level data would improve the accuracy of water regime preference estimates. In addition, longer term monitoring is necessary to better estimate the preferences of emergent macrophytes, given that they are able to tolerate 2-3 years of sub-optimal flooding before dying back (Millar 1973; Sjoberg and Danell 1983; Squires and van der Valk 1992).

The ability of emergent macrophytes to withstand sub-optimal conditions was demonstrated in the pond experiment. The survival of deep (> 50 cm) flooded plants is influenced by the amount of carbohydrate in storage tissue. The relationship between carbohydrate storage and survival could be examined by selecting planting material, such as tubers (*B. caldwellii*) and rhizomes (*C. gymnocaulos* and *S. validus*) that vary in weight and subject them to the same water regimes described in Chapters 7 and 8. Use of carbohydrate could be measured using a technique such as bomb calorimetry. Specific questions to be addressed by this experiment would be a) what is the relationship between carbohydrate use and the depth and duration of flooding, b) does increased carbohydrate storage enable greater tolerance/survival under sub-optimal flooding and c) do heavier initial perennating organs confer greater tolerance to sub-optimal flooding.

A major gap in understanding the influence of water regime on floristic composition is the impact of drawdown, in particular depth to groundwater, on emergent macrophyte survival. Methods of drought tolerance such as root extension require further investigation across a wider range of plants, including potential nuisance species such as *Paspalum distichum* and *Typha domingensis*. Pond experiments proved to be a useful method for exploring this relationship. However, future studies need to expand on the treatment regimes to include drawdown depths of 1 m below the sediment surface and rates of 10 cm d^{-1}.

9.2.3 Salinity

Although saline soils are a natural feature of Lower Murray floodplains, vegetation clearance on land above the floodplain has resulted in further salinisation (Mackay and Eastburn 1990; Sharley and Huggan 1995). The presence of *Sarcocornia quinqueflora* and *Wilsonia rotundifolia*, both halophytic species (Jessop and Toelken 1986), implies that soil salinity influences floristic composition at Banrock Station and the enhanced flood study sites.

The influence of salinity on floristic composition could be examined by comparing plant distribution with measures of soil salinity similar to those recorded during the enhanced flood study. Such data would be suitable for use in an ordination analysis with salinity used as a variable in the environmental matrix. An overlay of joint plots (*sensu* Jongman *et al.* 1987) could then be used to indicate the direction and strength of the relationship between floristic composition and salinity.

Pond experiments could also be used to examine the relationship between salinity and water regime. The interaction between drawdown and salinity is of particular interest given that both affect water acquisition. A two-way factorial design would be used to examine interactions between different levels of salinity and drawdown regimes. Salinity levels would mimic those found in study wetlands, especially Banrock Station, and drawdown regimes would be the same as those used in Chapter 7. The objective would be to determine if increasing salinity exacerbates the effect of drawdown on plant growth and reproduction and to assess how combinations of drawdown and elevated soil salinity will affect floristic composition.

9.2.4 *Water regime characterisation*

Accurate water regime data is mandatory for investigations akin to those in this study. Different wetland managers have different data needs and thus the frequency of data collection varied from daily measurements to those coinciding with the opening and closing of regulators. Future studies should avoid this discrepancy by installing water level loggers.

A further improvement would be measurement of groundwater levels through the installation of piezometers with water level loggers attached. The relationship between soil moisture levels and drawdown also needs to be elicited further. This could be achieved by placing soil moisture probes, such as those described in Chapter 7, at different depths down the soil profile to enable continuous measurement of moisture levels, or, by frequent collection of soil cores and subsequent soil moisture analysis through gravimetric procedures.

9.3 Recommendations for wetland restoration

In guidelines informed by the results of this study, Tucker *et al.* (2002) suggest that wetland restoration should focus on establishing and maintaining a range of vegetative wetland habitats including: submerged plants, emergent plants, dry wetland bed plants (mudflat annuals) and riparian plants. The results of this thesis point to a number a number of recommendations for promoting these vegetation types in the Lower Murray. These recommendations also serve as hypotheses for management.

The establishment of submerged macrophytes requires slow flooding between late spring to early autumn at rates < 3 cm d^{-1}. An improvement to this regime would be staged filling at < 3 cm d^{-1}, initially to a depth of 20-30 cm for 3-4 weeks to encourage germination and establishment, then to the final depth at the same rate to enable leaf and stem extension to the water surface. Adjustment of these rates may be required as a better understanding of the relationship between turbidity, flooding and colonisable depth is developed.

The mixture of mudflat annuals and emergent macrophytes can be manipulated by varying the rate and depth of drawdown. Evaporative drawdown of approximately 1 cm d^{-1} will promote the establishment and expansion of emergent macrophytes. On the other hand, drawdown of at least 5-10 cm d^{-1} to depths of 1.5-2 m should favour mudflat annual establishment. The timing of drawdown is likely to have a similar effect with preferential establishment of mudflat annuals during drawdown initiated in summer compared to spring.

An alternate approach to managing for specific floristic responses is to use the natural flow regime as a template for restoration (Poff *et al.* 1997). The natural flow or water regime may be reconstructed using historical data or by association with similar rivers (Walker 2002). In the Lower Murray, this approach has led to the adoption of annual flood and drawdown cycles. As demonstrated for the study wetlands, this can promote diverse species assemblages but also encourage the spread of nuisance species. I would argue, however, that the strict application of annual cycles reflects the mis-interpretation of the natural water regime. While the natural regime might on average have had annual flood and drawdown, it would also have included extended flood and drawdown resulting from successive wet or dry years stimulated by climatic phenomena such as the El Nino Southern Oscillation (Simpson *et al.* 1993).

As discussed in Chapter 3, managers may need to offset annual cycles by periodically increasing the depth and duration of flood and drawdown. Given the limitations of implementing flood and drawdown in some managed wetlands (e.g. drawdown depth in Big Mussel was influenced by the possibility of saline incursions), an alternating regime of 2-3 years of partial drawdown with 2 or more years of flooded conditions, is likely to be preferred. A similar regime may be applied if management, targeted at floristic responses, results in the establishment of nuisance species.

Regardless of whether water regime is designed to illicit specific floristic responses or mimic the natural flow regime, if the same water regime is applied equally to all wetlands, it is likely to result in similar floristic assemblages at the scale of a river reach. This only mimics the problem that has been created by the permanent inundation of Lower Murray wetlands.

A more appropriate outcome of wetland management would be the restoration of a mosaic of habitats across the river reach, from the river channel to the edges of the floodplain. Habitat mosaics are a feature of natural river systems, where the variable flow regime and range of elevations across the floodplain create a variety of water regimes and thus vegetation types.

Weir pool variability, whether through weir rasing or lowering, provides an ideal tool for establishing and maintaining habitat mosaics. The natural variability in commence to flow heights in floodplain wetlands means that a single action of raising or lowering a weir pool will produce a variety of water regimes.

Mimicking this result through managing individual wetlands is difficult because wetlands are managed to produce site-specific not reach-specific outcomes. This could be overcome by co-ordinating wetland management across a river reach. Wetlands could be surveyed to determine the range of habitat types present and then the management of individual wetlands tailored to ensure a diversity of vegetation types exists at the reach scale.

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APPENDIX 1

A list of the 72 species recorded during the floodplain wetland study (Chapters 2-4). Of these, 44 had a % total cover and abundance for all surveys in all wetlands of > 0.1% and were used to describe the floristic composition of wetlands in Chapters 2 and 3. Plant presence and absence is denoted by 1 and 0 respectively. BA – Banrock Station; BM – Big Mussel; CC – Chambers Creek; LD – Little Duck; OP – Old Petes; PI – Pilby Creek. * denotes an introduced species.

Species name	Common name	BA	BM	CC	LD	OP	PI
Acacia stenophylla	River cooba	0	0	0	1	0	1
*Agrostis avenaceae**	Fairy grass	1	1	1	0	1	0
Alternanthera denticulata	Lesser joyweed	1	1	0	1	0	1
*Aster subulatus**	Bushy starwort	1	1	1	1	1	0
Atriplex semibaccata	Creeping saltbush	1	1	0	0	1	1
Atriplex prostrata	Mat saltbush	1	1	0	0	0	0
Azolla filiculoides	Azolla	1	1	1	1	1	1
Bolboschoenus caldwellii	Three-cornered rush	1	1	0	0	1	1
Bolboschoenus medianus	Marsh club-rush	0	0	0	1	0	0
Brachycome basaltica	Swamp daisy	0	1	0	0	1	1
Calotis cuniefolia	Purple burr-daisy	1	1	0	0	0	1
Callitriche umbonata *	Common starwort	0	0	0	0	0	1
Centipeda cunninghamii	Common sneeze-weed	0	1	0	1	0	1
Centipeda minima	Spreading sneeze-weed	0	1	0	1	0	1
Chenopodium pumilio	Crumbweed	0	0	0	1	0	1
Cotula australis	Common cotula	0	0	0	0	0	1
Cotula coronopifolia	Waterbuttons	1	1	0	0	1	1
Crassula helmsii	Australian stonecrop	1	0	0	0	0	0
Cynodon dactylon *	Couch grass	1	1	0	1	1	1
Cyperus eragrostis *	Umbrella sedge	0	0	0	0	0	1
Cyperus gymnocaulos	Spiny sedge	1	1	1	1	1	1
Disphyma clavellatum	Austral pigface	0	0	1	0	0	0

Species name	**Common name**	**BA**	**BM**	**CC**	**LD**	**OP**	**PI**
Dittrichia graveolens	Stinkwort	1	0	0	0	1	0
Einadia nutans	Climbing saltbush	1	0	0	0	0	1
*Elatine gratioloides**	Waterwort	1	0	0	0	0	0
Eleocharis acuta	Common spike-rush	1	1	0	0	1	0
Enchylaena tomentosa	Ruby saltbush	1	0	0	0	1	0
Epaltes australis	Spreading nut-heads	1	1	0	0	1	0
Eragrostis australasica	Canegrass	0	1	0	0	0	1
Eragrostis dielsii	Mulka grass	1	1	0	0	0	0
Eucalyptus camuldulensis	River red gum	0	1	1	1	1	1
Heliotropum curassavicum *	Smooth heliotrope	1	1	1	1	1	0
Juncus aridicola	Tussock rush	1	1	1	1	1	1
Lemna minor	Duck weed	1	1	1	1	1	1
Limosella australis	Australian mudwort	0	1	0	0	0	1
*Ludwigia peploides**	Water primrose	1	1	1	1	0	1
Lythrum hyssopifolia	Lesser loosestrife	1	0	0	0	0	0
Mimulus repens	Creeping monkey-flower	1	1	0	0	0	1
Muehlenbeckia florulenta	Tangled lignum	1	1	1	1	1	1
Myriophyllum papillosum	Common water milfoil	0	0	1	0	1	0
Myriophyllum verrucosum	Red water milfoil	1	1	1	0	0	0
Paspalidium jubiflorum	Warrego summer-grass	0	0	0	1	0	1
Paspalum distichum	Water couch	1	1	1	1	1	1
Persicaria decipiens	Slender knotweed	1	1	0	0	0	0
Persicaria lapathifolium	Pale knotweed	0	1	0	1	0	1
Persicaria prostratum	Creeping knotweed	0	0	0	0	0	1
Phragmites australis	Common reed	1	1	1	1	1	1
Polygonum aviculare	Wireweed	1	1	0	0	0	1
Polypogon monspiliensis *	Annual beardgrass	1	1	1	0	0	0
Phyla canescens *	Lippia	0	1	0	0	0	0
Potamogeton crispus	Curly pondweed	0	1	1	0	0	0
Potamogeton ochreatus	Blunt pondweed	0	1	0	0	0	0
Potamogeton tricarinatus	Floating pondweed	1	0	1	0	0	0
Pseudognapthalium luteo-album	Cudweed	1	1	0	0	0	1
Pseudoraphis spinescens	Spiny mud-grass	1	0	0	0	0	0
Ranunculus sceleratus *	Celery buttercup	0	0	0	0	0	1
Ricciocarpus natans	Ricciocarpus	0	1	0	0	0	0
Rorippa palustris	Marsh watercress	0	1	0	1	0	1

Species name	**Common name**	**BA**	**BM**	**CC**	**LD**	**OP**	**PI**
Rumex bidens	Mud dock	0	0	0	1	0	0
Sarcocornia quinqueflora	Samphire	1	1	0	0	1	0
Schoenoplectus pungens	Pyramid club-rush	0	1	0	0	0	0
Schoenoplectus validus	River club-rush	1	1	1	0	1	0
Solanum nigrum	Black nightshade	1	0	0	0	0	0
Sonchus spp.	Sow thistle	1	1	1	1	1	1
Spergularia diandra	Lesser sandspurrey	1	1	0	0	1	0
Sporobolus mitchellii	Rats tail couch	1	1	1	1	1	1
Typha domingensis	Cumbungi	1	1	1	1	1	1
Vallisneria americana	Ribbon weed	1	1	1	0	1	0
Wahlenbergia communis	Tufted bluebell	1	1	0	0	0	0
Wilsonia rotundifolia	Round-leaved wilsonia	1	0	0	0	0	0
*Xanthium californicum**	California burr	1	1	0	1	1	1
Xanthium spinosum *	Bathurst burr	0	0	0	0	1	0

APPENDIX 2

Water regime preferences for species with total cover/abundance > 0.1% and with at least 5 individuals recorded. Preferences were used in the model described in Chapter 4. The number of water regime phases used to calculate the preferences is indicated in brackets next to the species name.

Agrostis avenaceae (16)	25-percentile	Median	75-percentile
≥ 0 cm	47	52	58
0 to 20 cm	7	13	38
20 - 60 cm	25	40	69
60 - 100 cm	0	0	0
> 100 cm	0	0	0
< 0 cm	68	79	81
0 to -20 cm	5	19	44
-20 to -60 cm	7	29	46
-60 to -100 cm	19	25	40
< -100 cm	14	23	35

Alternanthera denticulata (17)	25-percentile	Median	75-percentile
≥ 0 cm	27	53	57
0 to 20 cm	6	6	21
20 - 60 cm	47	49	51
60 - 100 cm	1	1	1
> 100 cm	0	0	0
< 0 cm	34	58	110
0 to -20 cm	3	5	26
-20 to -60 cm	6	17	27
-60 to -100 cm	22	25	88
< -100 cm	8	11	14

Aster subulatus (61)	25-percentile	Median	75-percentile
≥ 0 cm	52	57	79
0 to 20 cm	6	11	52
20 - 60 cm	45	50	57
60 - 100 cm	14	26	38
> 100 cm	0	0	0
< 0 cm	76	91	187
0 to -20 cm	5	18	59
-20 to -60 cm	9	48	79
-60 to -100 cm	22	50	68
< -100 cm	2	15	25

Atriplex semibaccata (5)	25-percentile	Median	75-percentile
≥ 0 cm	3	3	3
0 to 20 cm	3	3	3
20 - 60 cm	0	0	0
60 - 100 cm	0	0	0
> 100 cm	0	0	0
< 0 cm	91	94	173
0 to -20 cm	5	5	44
-20 to -60 cm	30	90	120
-60 to -100 cm	47	47	47
< -100 cm	12	13	16

Bolboschoenus caldwellii (51)	25-percentile	Median	75-percentile
≥ 0 cm	56	82	113
0 to 20 cm	6	19	59
20 - 60 cm	13	33	70
60 - 100 cm	5	15	48
> 100 cm	0	0	0
< 0 cm	28	78	108
0 to -20 cm	3	20	57
-20 to -60 cm	14	39	66
-60 to -100 cm	21	50	70
< -100 cm	0	0	0

Bolboschoenus medianus (8)	25-percentile	Median	75-percentile
≥ 0 cm	13	35	49
0 to 20 cm	6	18	25
20 - 60 cm	8	17	20
60 - 100 cm	3	4	4
> 100 cm	0	0	0
< 0 cm	78	86	194
0 to -20 cm	7	25	97
-20 to -60 cm	20	25	63
-60 to -100 cm	20	35	45
< -100 cm	16	23	43

Brachycome basaltica (9)	25-percentile	Median	75-percentile
≥ 0 cm	167	167	167
0 to 20 cm	137	137	137
20 - 60 cm	30	30	30
60 - 100 cm	0	0	0
> 100 cm	0	0	0
< 0 cm	79	94	339
0 to -20 cm	1	9	25
-20 to -60 cm	10	79	116
-60 to -100 cm	13	19	36
< -100 cm	78	94	364

Centipeda cunninghamii (27)	25-percentile	Median	75-percentile
≥ 0 cm	52	52	56
0 to 20 cm	5	6	6
20 - 60 cm	44	47	50
60 - 100 cm	0	0	0
> 100 cm	0	0	0
< 0 cm	73	78	87
0 to -20 cm	3	5	7
-20 to -60 cm	6	6	46
-60 to -100 cm	14	25	44
< -100 cm	58	78	78

Centipeda minima (17)	25-percentile	Median	75-percentile
≥ 0 cm	57	57	61
0 to 20 cm	5	6	6
20 - 60 cm	51	51	56
60 - 100 cm	0	0	0
> 100 cm	0	0	0
< 0 cm	78	79	166
0 to -20 cm	2	3	3
-20 to -60 cm	6	27	63
-60 to -100 cm	10	22	58
< -100 cm	76	78	166

Chenopodium pumilio (11)	25-percentile	Median	75-percentile
≥ 0 cm	104	104	104
0 to 20 cm	95	95	95
20 - 60 cm	9	9	9
60 - 100 cm	0	0	0
> 100 cm	0	0	0
< 0 cm	78	83	94
0 to -20 cm	1	1	1
-20 to -60 cm	72	79	87
-60 to -100 cm	67	91	94
< -100 cm	78	78	78

Cynodon dactylon (36)	25-percentile	Median	75-percentile
≥ 0 cm	11	49	64
0 to 20 cm	9	37	49
20 - 60 cm	10	28	46
60 - 100 cm	0	0	0
> 100 cm	0	0	0
< 0 cm	78	105	220
0 to -20 cm	8	55	172
-20 to -60 cm	12	57	102
-60 to -100 cm	19	45	63
< -100 cm	25	49	90

Cyperus gymnocaulos (61)	25-percentile	Median	75-percentile
≥ 0 cm	31	68	135
0 to 20 cm	16	49	73
20 - 60 cm	12	42	72
60 - 100 cm	2	6	19
> 100 cm	0	0	0
< 0 cm	83	350	563
0 to -20 cm	15	61	166
-20 to -60 cm	12	65	202
-60 to -100 cm	26	50	74
< -100 cm	27	65	138

Eragrostis australis (11)	25-percentile	Median	75-percentile
≥ 0 cm	3	11	22
0 to 20 cm	3	11	20
20 - 60 cm	4	5	6
60 - 100 cm	0	0	0
> 100 cm	0	0	0
< 0 cm	89	93	332
0 to -20 cm	41	62	69
-20 to -60 cm	18	90	336
-60 to -100 cm	4	55	56
< -100 cm	50	50	50

Eragrostis dielsii (6)	25-percentile	Median	75-percentile
≥ 0 cm	9	15	20
0 to 20 cm	9	15	19
20 - 60 cm	3	3	3
60 - 100 cm	0	0	0
> 100 cm	0	0	0
< 0 cm	113	176	273
0 to -20 cm	22	36	36
-20 to -60 cm	33	132	202
-60 to -100 cm	47	47	55
< -100 cm	0	0	0

Heliotropium curasvassicum (29)	25-percentile	Median	75-percentile
≥ 0 cm	9	15	22
0 to 20 cm	9	15	22
20 - 60 cm	3	3	3
60 - 100 cm	0	0	0
> 100 cm	0	0	0
< 0 cm	78	88	166
0 to -20 cm	22	53	139
-20 to -60 cm	44	63	78
-60 to -100 cm	15	23	37
< -100 cm	20	36	63

Juncus aridicola (31)	25-percentile	Median	75-percentile
≥ 0 cm	86	166	272
0 to 20 cm	24	63	139
20 - 60 cm	49	79	174
60 - 100 cm	2	24	53
> 100 cm	0	0	0
< 0 cm	78	84	130
0 to -20 cm	15	50	78
-20 to -60 cm	15	41	57
-60 to -100 cm	23	41	59
< -100 cm	13	16	21

Ludwigia peploides (17)	25-percentile	Median	75-percentile
≥ 0 cm	57	77	239
0 to 20 cm	8	25	53
20 - 60 cm	50	67	195
60 - 100 cm	21	61	71
> 100 cm	0	0	0
< 0 cm	30	59	131
0 to -20 cm	3	11	27
-20 to -60 cm	23	43	61
-60 to -100 cm	18	29	64
< -100 cm	9	13	41

Mimulus repens (16)	25-percentile	Median	75-percentile
≥ 0 cm	57	58	60
0 to 20 cm	3	4	6
20 - 60 cm	30	51	54
60 - 100 cm	9	41	49
> 100 cm	0	0	0
< 0 cm	30	106	109
0 to -20 cm	3	3	4
-20 to -60 cm	25	58	78
-60 to -100 cm	12	25	37
< -100 cm	0	0	0

Myriophyllum verrucosum (25)	25-percentile	Median	75-percentile
≥ 0 cm	61	78	78
0 to 20 cm	3	4	8
20 - 60 cm	28	55	78
60 - 100 cm	42	49	88
> 100 cm	33	33	33
< 0 cm	26	30	45
0 to -20 cm	3	3	3
-20 to -60 cm	18	23	36
-60 to -100 cm	10	12	15
< -100 cm	0	0	0

Paspalum distichum (96)	25-percentile	Median	75-percentile
≥ 0 cm	56	99	181
0 to 20 cm	11	43	114
20 - 60 cm	17	48	94
60 - 100 cm	4	11	18
> 100 cm	2	3	8
< 0 cm	80	171	403
0 to -20 cm	8	33	104
-20 to -60 cm	13	49	74
-60 to -100 cm	22	69	94
< -100 cm	13	23	466

Persicaria decipiens (11)	25-percentile	Median	75-percentile
≥ 0 cm	70	98	161
0 to 20 cm	27	63	100
20 - 60 cm	22	54	78
60 - 100 cm	24	50	61
> 100 cm	0	0	0
< 0 cm	11	45	123
0 to -20 cm	8	20	76
-20 to -60 cm	4	12	13
-60 to -100 cm	46	46	47
< -100 cm	0	0	0

Persicaria lapathifolia (38)	25-percentile	Median	75-percentile
≥ 0 cm	58	64	67
0 to 20 cm	4	6	13
20 - 60 cm	49	58	58
60 - 100 cm	2	3	4
> 100 cm	0	0	0
< 0 cm	78	94	260
0 to -20 cm	3	5	10
-20 to -60 cm	7	15	56
-60 to -100 cm	9	15	34
< -100 cm	58	78	190

Phragmites australis (80)	25-percentile	Median	75-percentile
≥ 0 cm	31	131	176
0 to 20 cm	7	33	126
20 - 60 cm	17	47	129
60 - 100 cm	4	12	17
> 100 cm	6	11	53
< 0 cm	255	430	569
0 to -20 cm	8	29	197
-20 to -60 cm	12	53	146
-60 to -100 cm	34	52	116
< -100 cm	21	83	329

Polygonum aviculare (12)	25-percentile	Median	75-percentile
≥ 0 cm	52	56	57
0 to 20 cm	6	6	6
20 - 60 cm	49	51	51
60 - 100 cm	0	0	0
> 100 cm	0	0	0
< 0 cm	78	83	109
0 to -20 cm	3	3	5
-20 to -60 cm	50	63	70
-60 to -100 cm	27	35	44
< -100 cm	78	78	83

Pseudognapthalium luteo-album (9)	25-percentile	Median	75-percentile
≥ 0 cm	24	32	39
0 to 20 cm	5	17	30
20 - 60 cm	18	28	37
60 - 100 cm	0	0	0
> 100 cm	0	0	0
< 0 cm	68	78	94
0 to -20 cm	2	4	10
-20 to -60 cm	17	57	77
-60 to -100 cm	4	5	25
< -100 cm	50	58	78

Rorippa palustris (38)	25-percentile	Median	75-percentile
≥ 0 cm	11	12	12
0 to 20 cm	2	2	9
20 - 60 cm	7	10	10
60 - 100 cm	0	0	0
> 100 cm	0	0	0
< 0 cm	78	78	79
0 to -20 cm	2	9	10
-20 to -60 cm	4	25	63
-60 to -100 cm	4	15	27
< -100 cm	58	78	78

Sarcocornia quinqueflora (19)	25-percentile	Median	75-percentile
≥ 0 cm	60	76	116
0 to 20 cm	37	55	62
20 - 60 cm	19	37	70
60 - 100 cm	0	0	0
> 100 cm	0	0	0
< 0 cm	181	327	453
0 to -20 cm	62	84	153
-20 to -60 cm	12	161	248
-60 to -100 cm	46	50	52
< -100 cm	31	36	41

Schoenoplectus validus (19)	25-percentile	Median	75-percentile
≥ 0 cm	94	372	578
0 to 20 cm	23	128	275
20 - 60 cm	35	128	320
60 - 100 cm	15	24	44
> 100 cm	0	0	0
< 0 cm	50	91	170
0 to -20 cm	28	66	151
-20 to -60 cm	9	53	56
-60 to -100 cm	12	24	35
< -100 cm	0	0	0

Spergularia diandra (6)	25-percentile	Median	75-percentile
≥ 0 cm	30	33	35
0 to 20 cm	30	33	35
20 - 60 cm	0	0	0
60 - 100 cm	0	0	0
> 100 cm	0	0	0
< 0 cm	88	114	237
0 to -20 cm	26	36	58
-20 to -60 cm	63	78	95
-60 to -100 cm	15	33	48
< -100 cm	92	92	92

Sporobolus mitchellii (24)	25-percentile	Median	75-percentile
≥ 0 cm	12	25	70
0 to 20 cm	8	22	59
20 - 60 cm	3	6	8
60 - 100 cm	0	0	0
> 100 cm	0	0	0
< 0 cm	176	439	567
0 to -20 cm	42	86	171
-20 to -60 cm	79	154	367
-60 to -100 cm	26	50	56
< -100 cm	56	76	96

Typha domingensis (92)	25-percentile	Median	75-percentile
≥ 0 cm	78	182	471
0 to 20 cm	4	31	121
20 - 60 cm	38	109	319
60 - 100 cm	13	50	87
> 100 cm	5	29	68
< 0 cm	29	64	108
0 to -20 cm	3	7	44
-20 to -60 cm	12	27	53
-60 to -100 cm	22	32	66
< -100 cm	13	13	15

Vallisneria americana (36)	25-percentile	Median	75-percentile
≥ 0 cm	104	412	523
0 to 20 cm	4	6	51
20 - 60 cm	81	172	365
60 - 100 cm	67	107	189
> 100 cm	1	7	16
< 0 cm	48	50	55
0 to -20 cm	5	6	47
-20 to -60 cm	41	48	49
-60 to -100 cm	7	7	7
< -100 cm	0	0	0

Xanthium californicum (21)	25-percentile	Median	75-percentile
≥ 0 cm	11	14	37
0 to 20 cm	8	11	37
20 - 60 cm	3	7	10
60 - 100 cm	9	9	9
> 100 cm	0	0	0
< 0 cm	93	104	219
0 to -20 cm	25	45	93
-20 to -60 cm	15	66	114
-60 to -100 cm	6	6	50
< -100 cm	42	59	60

APPENDIX 3

Water regime preferences for functional groups used for the model described in Chapter 4. The number of species that combine to make the group is indicated in brackets next to the group number. The species composition of each group is outlined in Figure 4.2.

Group 1 (9)	25-percentile	Median	75-percentile
≥ 0 cm	53	57	77
0 to 20 cm	11	14	19
20 - 60 cm	33	48	49
60 - 100 cm	1	11	26
> 100 cm	0	0	0
< 0 cm	78	86	106
0 to -20 cm	11	20	26
-20 to -60 cm	29	43	54
-60 to -100 cm	25	35	50
< -100 cm	11	15	23

Group 2 (6)	25-percentile	Median	75-percentile
≥ 0 cm	37	54	57
0 to 20 cm	3	6	6
20 - 60 cm	32	46	50
60 - 100 cm	0	0	0
> 100 cm	0	0	0
< 0 cm	78	79	79
0 to -20 cm	3	4	4
-20 to -60 cm	11	26	49
-60 to -100 cm	8	18	24
< -100 cm	66	78	78

Group 3 (2)	25-percentile	Median	75-percentile
≥ 0 cm	120	136	151
0 to 20 cm	106	116	127
20 - 60 cm	14	20	25
60 - 100 cm	0	0	0
> 100 cm	0	0	0
< 0 cm	155	217	278
0 to -20 cm	7	13	19
-20 to -60 cm	94	102	109
-60 to -100 cm	51	65	80
< -100 cm	150	221	293

Group 4 (6)	25-percentile	Median	75-percentile
≥ 0 cm	14	15	15
0 to 20 cm	12	14	15
20 - 60 cm	1	3	5
60 - 100 cm	0	0	0
> 100 cm	0	0	0
< 0 cm	94	111	161
0 to -20 cm	29	39	50
-20 to -60 cm	72	105	134
-60 to -100 cm	27	37	49
< -100 cm	39	49	57

Group 5 (4)	25-percentile	Median	75-percentile
≥ 0 cm	55	71	88
0 to 20 cm	26	38	50
20 - 60 cm	28	36	39
60 - 100 cm	0	3	7
> 100 cm	0	0	3
< 0 cm	375	414	459
0 to -20 cm	55	69	77
-20 to -60 cm	72	127	183
-60 to -100 cm	50	51	53
< -100 cm	57	70	78

Group 6 (3)	25-percentile	Median	75-percentile
≥ 0 cm	156	214	293
0 to 20 cm	73	83	119
20 - 60 cm	66	78	94
60 - 100 cm	24	24	37
> 100 cm	0	0	0
< 0 cm	67	88	101
0 to -20 cm	36	52	71
-20 to -60 cm	27	41	47
-60 to -100 cm	32	41	44
< -100 cm	0	0	8

Group 7 (3)	25-percentile	Median	75-percentile
≥ 0 cm	141	205	308
0 to 20 cm	5	6	26
20 - 60 cm	82	109	136
60 - 100 cm	50	50	78
> 100 cm	18	29	31
< 0 cm	40	50	57
0 to -20 cm	5	6	6
-20 to -60 cm	25	27	38
-60 to -100 cm	10	12	22
< -100 cm	0	0	7

APPENDIX 4

The 32 species recorded during the enhanced flood study (Chapters 5 and 6). Plant presence and absence are denoted by 1 and 0, respectively. Ninkle Nook, NN; Jane Eliza, JE; Wide Waters, WW. * denotes an introduced species.

Species name	Common name	NN	JE	WW
*Agrostis avenaceae**	Blown grass	1	1	0
Alternanthera denticulata	Lesser joyweed	1	1	0
Aster subulatus *	Bushy starwort	0	1	0
Atriplex vesicaria	Bladder saltbush	1	1	1
Brachycome basaltica	Swamp daisy	1	1	0
Centipeda cunninghamii	Common sneeze-weed	0	1	1
Cotula australis	Common cotula	1	0	0
Cotula coronopifolia	Waterbuttons	0	1	0
Disphyma clavellatum	Austral pigface	0	0	1
*Dittrichia graveolens**	Stinkwort	0	1	0
Einadia nutans	Climbing saltbush	0	1	0
Eleocharis acuta	Common spike-rush	1	0	0
Enchylaena tomentosa	Ruby saltbush	0	1	1
Eragrostis dielsii	Mulka grass	1	0	1
Eragrostis australasica	Canegrass	1	0	0
Gnephosis foliata	Erect yellow-heads	1	1	1
Heliotropum curassavicum *	Smooth heliotrope	0	1	1
Lepidium campastre *	Field cress	1	1	0
Lythrum hyssopifolia	Lesser loosestrife	0	1	0
Marsilea drummondii	Nardoo	0	1	0
Mesembryanthemum crystallinum *	Ice plant	0	0	1
Mimulus repens	Creeping monkey-flower	0	1	0
Muehlenbeckia florulenta	Tangled lignum	1	1	1
Myriophyllum verrucosum	Red water milfoil	0	1	0
Gnaphalium sphaericum	Japanese cudweed	1	0	0

Species name	**Common name**	**NN**	**JE**	**WW**
Sarcocornia quinqueflora	Samphire	0	1	1
Salsola kali	Roly-poly	1	0	0
Spergularia diandra *	Lesser sandspurrey	0	1	1
Sporobolus mitchellii	Rats tail couch	1	1	1
Wahlenbergia communis	Tufted bluebell	1	0	0
Wilsonia rotundifolia	Round-leaved wilsonia	1	1	1
*Xanthium occidentale**	Noogoora burr	0	1	1

APPENDIX 5

The emergent area for each species was estimated from the relationship between emergent area and the dry weight of emergent tissue. The relationship differed across water regime treatments for each species and thus a separate relationship, presented below, was calculated for each. Leaf area was measured for *Bolboschoenus caldwellii* using a Delta T leaf area meter whereas the remaining species had leafless culms and their area was estimated by recording culm length and diameter and using the equations for the surface area of a cylinder or cone. A = total area; W = total weight. Relationships were not required for *C. gymnocaulos* at RF20, SF60 and RF60 because there were so few emergent culms per plant and *J. aridicola* at RF60 because only one plant had a total of 4 emergent culms.

Bolboschoenus caldwellii		
SD60	A (m^2) = 0.08 + 0.5 W (g)	r^2=0.95, F=654.8, P<0.0001, n=36
RD60	A (m^2) = 0.07 + 0.5 W (g)	r^2=0.93, F=385.8, P<0.0001, n=29
SD20	A (m^2) = 0.006 + 0.6 ×W (g)	r^2=0.91, F=326.9, P<0.0001, n=36
RD20	A (m^2) = 0.1 + 0.6 W (g)	r^2=0.86, F=195.6, P<0.0001, n=36
STAT	A (m^2) = 0.03 + 0.7 W (g)	r^2=0.94, F=520.6, P<0.0001, n=35
SF20	A (m^2) = 0.03 + 0.7 W (g)	r^2=0.94, F=546.1, P<0.0001, n=35
RF20	A (m^2) = -0.009 + 0.9 W (g)	r^2=0.94, F=564.3, P<0.0001, n=36
SF60	A (m^2) = 0.3 + 0.7 W (g)	r^2=0.85, F=193.0, P<0.0001, n=36
RF60	A (m^2) = 0.2 + 0.9 W (g)	r^2=0.93, F=136.5, P<0.0001, n=13

Cyperus gymnocaulos		
SD60	A (m^2) = 0.0004 + 0.006 W (g)	r^2=0.93, F=464.9, P<0.0001, n=35
RD60	A (m^2) = 0.0002 + 0.006 W (g)	r^2=0.95, F=647.3, P<0.0001, n=36
SD20	A (m^2) = 0.0005 + 0.009 W (g)	r^2=0.92, F=422.7, P<0.0001, n=37
RD20	A (m^2) = 0.0008 + 0.007 W (g)	r^2=0.92, F=385.1, P<0.0001, n=30

Cyperus gymnocaulos (continued)

STAT	$A\ (m^2) = 0.0002 + 0.007\ W\ (g)$	$r^2=0.94$, $F=516.9$, $P<0.0001$, $n=36$
SF20	$A\ (m^2) = 0.0004 + 0.01\ W\ (g)$	$r^2=0.91$, $F=422.7$, $P<0.0001$, $n=45$

Juncus aridicola

SD60	$A\ (m^2) = 0.0005 + 0.004\ W\ (g)$	$r^2=0.94$, $F=530.4$, $P<0.0001$, $n=36$
RD60	$A\ (m^2) = 0.0003 + 0.005\ W\ (g)$	$r^2=0.86$, $F=173.9$, $P<0.0001$, $n=31$
SD20	$A\ (m^2) = 0.0004 + 0.006 \times W\ (g)$	$r^2=0.81$, $F=117.1$, $P<0.0001$, $n=30$
RD20	$A\ (m^2) = 0.0006 + 0.006\ W\ (g)$	$r^2=0.66$, $F=55.6$, $P<0.0001$, $n=31$
STAT	$A\ (m^2) = 0.0004 + 0.005\ W\ (g)$	$r^2=0.91$, $F=219.8$, $P<0.0001$, $n=23$
SF20	$A\ (m^2) = 0.0005 + 0.008\ W\ (g)$	$r^2=0.82$, $F=72.8$, $P<0.0001$, $n=18$
RF20	$A\ (m^2) = 0.0005 + 0.007\ W\ (g)$	$r^2=0.96$, $F=516.6$, $P<0.0001$, $n=23$
SF60	$A\ (m^2) = 0.0002 + 0.01\ W\ (g)$	$r^2=0.90$, $F=237.4$, $P<0.0001$, $n=28$

Schoenoplectus validus

SD60	$A\ (m^2) = 0.0004 + 0.005\ W\ (g)$	$r^2=0.91$, $F=250.5$, $P<0.0001$, $n=30$
RD60	$A\ (m^2) = 0.0005 + 0.005\ W\ (g)$	$r^2=0.95$, $F=230.9$, $P<0.0001$, $n=18$
SD20	$A\ (m^2) = 0.003 + 0.006 \times W\ (g)$	$r^2=0.89$, $F=221.7$, $P<0.0001$, $n=36$
RD20	$A\ (m^2) = 0.006 + 0.005\ W\ (g)$	$r^2=0.90$, $F=265.6$, $P<0.0001$, $n=35$
STAT	$A\ (m^2) = 0.0009 + 0.009\ W\ (g)$	$r^2=0.52$, $F=24.2$, $P<0.0001$, $n=24$
SF20	$A\ (m^2) = 0.002 + 0.007\ W\ (g)$	$r^2=0.90$, $F=129.6$, $P<0.0001$, $n=32$
RF20	$A\ (m^2) = -0.003 + 0.006\ W\ (g)$	$r^2=0.92$, $F=237.5$, $P<0.0001$, $n=30$
SF60	$A\ (m^2) = 0.001 + 0.007\ W\ (g)$	$r^2=0.97$, $F=978.2$, $P<0.0001$, $n=36$
RF60	$A\ (m^2) = 0.002 + 0.007\ W\ (g)$	$r^2=0.97$, $F=842.6$, $P<0.0001$, $n=33$