Influence of water regime on growth and resource allocation in aquatic macrophytes of the Lower River Murray, Australia

by

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Thesis addendum

1. Application of average irradiance to the growth of *Vallisneria americana* in shallow, turbid water (Chapter 7)

The data presented indicates that average irradiance ($\bar{I}$) is of considerable value in explaining growth in *V. americana* under a range of rates of light attenuation (K_d) and depth (z_m). Relationships between $\bar{I}$ and relative growth rate (RGR), and shoot and leaf production support this view (see Figs Chapter 3). Whilst $\bar{I}$ is arguably of greatest theoretical and practical use for shallow, turbid waterbodies (z_m<2m, K_d>~5 ln units m^{-1}) when photosynthetic tissue extends through much of the water column, reduced growth is clearly predicted by the models presented at very low $\bar{I}$ when the ratio of plant height to depth is <1.0, although prediction accuracy is likely to be poorer in this case. In a strong vertical light gradient absolute average irradiance at the top of the canopy, or indeed at any depth, does not take into account z_m or the irradiances experienced at other depths in the canopy. Both of these factors are of great import to plant growth, and are incorporated into $\bar{I}$.

As this study shows, RGR *v* $\bar{I}$ relationships have considerable potential for quite accurately predicting the effects of water regime and K_d on submersed macrophyte growth over the medium-term in shallow, turbid water. By extension, such an approach may prove highly useful in researching and managing macrophytes under similar conditions elsewhere.

2. Multivariate analyses (Chapter 3)

Multivariate techniques do not yield completely objective data clusters, but rather alllow one to select sufficient species groups to allow a meaningful ecological analysis without resolving the data set into an unwieldy number of groups (see Ludwig and Reynolds, 1988: *Statistical ecology. A primer on methods and computing.* Wiley and Sons, Sydney). Whilst breaks in the number of groups *v* dissimilarity relationship can be used to impart a measure of objectivity to the proceedure, it should not override this principal aim. As similar species relationships were determined using the four techniques presented in Chapter 3 (SHS, UPGMA, MST and nearest neighbour anaylses), it is concluded that the clusters are ecologically meaningful.

Groups 1 and 2 are well defined in the UPGMA (see Fig. 3.3), with groups 3-5 less so, as vegetation does not form highly discreet units along water regime gradients in the Lower Murray (nor indeed along many environmental gradients). The decision to choose five rather than three groups (*ie.* by resolving species in groups 3-5 into one large third group) reflects real differences in the water regime requirements of species grouped within these last three clusters. To have chosen just three groups would have sacrificed considerable information about their ecology and produced a large, third group with species that I know occur in quite different water regimes.

1st July 1998

Stuart Blanch

You can not step in the same river twice.

Heraclitus

Opposite our camp the river is of noble breadth and depth,
its waters clear and soft with an undiminished current.

Explorer Captain Charles Sturt on the River Murray, 1830

The water at this time of the year was particularly clear and a rich growth
of water plants extended out from the bank for some twenty and thirty feet.

Harris (1963) near Blanchetown on the Lower Murray

On the last and greatest day of the Feast, Jesus stood and said in a loud voice,
"If anyone is thirsty, let him come to me and drink. Whoever believes in me,
as the Scripture has said, streams of living water will flow from within him".

John, Chapter 7

Summary

Water regime is the principal factor determining pattern and process in vegetation in rivers and wetlands in semi-arid environs. It is a complex variable, encompassing the depth, duration, frequency and timing of flooding and exposure, and the rate of change in water level. The influence of water regime on macrophytes of the Lower River Murray, Australia, was investigated at the level of the community, population and tissue. The aim of the study was to examine the effects of water regime on growth, vegetative recruitment, resource allocation and photosynthesis in selected perennial species, and the adaptations permitting them to tolerate sub-optimal regimes.

The composition of littoral plant assemblages along weir Pool 5 was correlated with gradients in water regime established by weirs. Species with competitive and ruderal traits (cf. Grime, 1979) occurred in the hydrologically stable lower pool (*Vallisneria americana, Typha domingensis*), whilst species with stress-tolerant and ruderal traits predominated in mid and upper pools where flooding and exposure were common (*Cyperus gymnocaulos, Cynodon dactylon, Muehlenbeckia florulenta*). Vegetation was significantly correlated with the number of days flooded to 0-20 and 20-60 cm, and days exposed to ≥100 cm. Five species groups were suggested by clustering, reflecting broad water regimes and species abundance: common (*e.g. Paspalidium jubiflorum, Muehlenbeckia*) and uncommon floodplain species (*Eleocharis acuta, Pseudoraphis spinescens*), species from the infrequently (*Phyla canescens, Bolboschoenus caldwellii*) and permanently flooded littoral (*Vallisneria, Typha*), and widespread, common species broadly tolerant of flooding and exposure (*Phragmites australis, Cyperus* and *Bolboschoenus medianus*). Half of the 26 species occurred in four or more of seven water regime groups suggested by clustering of sites based on indices of water regime, suggesting selection for adaptations to a variable hydrologic regime are common. In contrast, 4 species occurred only in the stable lower pool.

Growth and resource allocation in the emergent sedge *Bolboschoenus medianus* (Cyperaceae) and submersed herb *Vallisneria americana* (Hydrocharitaceae) were examined in response to changes in water regime in pond and field experiments. Morphological and photosynthetic adaptations to resource limitation were studied: access to CO_2, O_2 and water in *Bolboschoenus*, and to light in *Vallisneria*. Results were used to interpret the changes in community composition of littoral vegetation along gradients of water regime in the Lower Murray, Australia.

Experiments determined optimum water regimes for *Bolboschoenus* and *Vallisneria*, and how they responded to sub-optimal conditions. RGR was greatest when the water surface was within ±20 cm of the sediment in *Bolboschoenus* in a pond experiment. With increasing depth, net assimilation rate (NAR) and hence RGR declined. Leaf area ratio (LAR) remained remarkably constant however, due to stem elongation, more vertical orientation of submersed leaves and higher leaf recruitment when partially flooded. Tuber biomass and emergent leaf area were inversely linearly related, indicating below-ground biomass is allocated to stems as depth increases, producing up to a three-fold increase in above:below ground biomass. Carbon assimilation and stomatal conductance of emergent leaves were highest in partially flooded plants. Assimilation declined due to lower conductance in plants exposed by 20 cm, which reduced culm recruitment. A field experiment found RGR, culm recruitment and flowering was greatest in plants shallowly flooded then slowly exposed at 2.5 cm day^{-1}. The temporal juxtaposition of top-flooding followed by rapid exposure (10-12 cm d^{-1}) reduced growth and reproduction.

Vallisneria was grown at turbidities of 90, 209 and 504 NTU (producing rates downwelling light extinction of 6.48, 12.59 and 21.92 m^{-1}, respectively) at various depths in a pond experiment. RGR declined with decreasing light penetration and increasing depth, calculated as $\bar{I}$, the average irradiance between the water surface and sediment. The whole-plant RGR-$\bar{I}$ response followed a P-I curve, and integrates photosynthesis at all irradiances across all depths in the canopy over time. The reduction in RGR was due to lower NAR as less of the canopy received greater than compensating irradiances. However, LAR peaked at low $\bar{I}$ due to the production of long thin leaves, indicating morphological plasticity at low light. The RGR-$\bar{I}$ model successfully simulated growth in field populations under a range of extinction coefficients and depths. Such models may be useful for predicting the effects of elevated turbidity levels on submersed macrophytes.

Oxygen evolution experiments with leaf pieces found similar or lower I_c and I_k than reported elsewhere for *Vallisneria* (3-35, and 40-180 µmol m^{-2} s^{-1} respectively), presumably due to adaptation to low light penetration in the Murray. Photosynthetic efficiency α was relatively high: 0.005-0.1 mg C g dw^{-1} h^{-1} (µmol m^{-2} s^{-1})$^{-1}$. Carbon assimilation depended on leaf age and depth. No evidence of shade acclimatization (increasing α with depth) was observed.

Modelled daily canopy carbon assimilation indicates the importance of canopy formation in highly turbid water. Plants in shallow water (24 cm) placed 42% of their canopy at the surface, and had high canopy carbon assimilation (21.2 mg C d^{-1}). Plants at 82 cm had 87% of the canopy below the maximum depth of penetration of compensating irradiances, and had a negative carbon balance (-2.2 mg C d^{-1}). Carbon balances correlated well with observed growth: RGRs of 15 and -2 mg g d^{-1}, respectively.

Vallisneria died when exposed for >14 days in spring and summer in a field experiment which investigated growth in stable and variable water regimes. RGR was greatest at 0.5 m in stable conditions, and declined in shallower and deeper water due to exposure and light-limitation, respectively. These data concur with the distribution of *Vallisneria* in the Murray in the early 1990's: depths of 10-80 cm in lower weir pools.

A computer model used by South Australian water agencies for flood forecasting, the *River Murray Hydraulic Model*, was evaluated for its use in researching the effects of flooding on littoral vegetation in the Murray. Prediction accuracy for water levels was often within 10 cm, but linear interpolations between weirs proved simpler and more effective when stage data are available. Recommendations are made for improving the model or future models for ecological research and environmental flow management.

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Declaration

To the best of my knowledge and belief, this thesis contains no material previously submitted for a degree or any other award, in any university by any person, or any material previously published or written by any other person, except where due reference is made in the text. I consent to the thesis being made available for copying and loan if accepted for the award of the degree.

18 August, 1997

Stuart James Blanch

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Chapter 1

Introduction

1.1 Water regime and aquatic macrophytes in semi-arid rivers and wetlands

Water regime is the principal factor determining pattern and process in wetland vegetation in semi-arid regions (Mitchell and Rogers, 1985; Rea and Ganf, 1994a). It is a complex variable, encompassing the depth, duration, frequency and timing of flooding and exposure, and the rate of change in water level (Rea and Ganf, 1994a,b,c). In xeric environments, all facets of water regime are characterised by high variability (Finlayson and McMahon, 1988; Hughes and James, 1989), reflecting aseasonal and long-term weather patterns (Brock 1991; Simpson *et al.*, 1993). Flow variability is much higher across all time scales, from hourly to multi-year, than in mesic environments (Braune, 1985). For example, the average coefficient of variation of annual river flow for Australia is 0.7, compared to 0.2 and 0.3 for Europe and North America, respectively. Seasonal influences also occur in waterbodies receiving runoff from rivers which rise in mountainous regions (Walker, 1986; Mackay, 1990). In semi-arid southeastern Australia, most wetlands are associated with floodplain rivers of the Murray-Darling Basin (Fig. 1.1). Aquatic macrophytes inhabiting these ecosystems must tolerate flooding and exposure of varying duration and depth. Mature plants may persist in sub-optimal regimes for many years, but conditions amenable to recruitment from the propagule bank and by vegetative growth may occur infrequently (Brock, 1991; Squires and van der Vaalk, 1992; Rea and Ganf, 1994b).

Two common plant growth forms found in wetlands and rivers of the Murray-Darling Basin are emergent (mainly Cyperaceae, Poaceae, Polygonaceae, Typhaceae and Juncaceae) and submersed macrophytes (mainly Hydrocharitaceae, Potamogetonaceae and Haloragaceae). In both emergent and submersed macrophytes, water regime influences biomass production, resource allocation, recruitment, and photosynthesis (Briggs and Maher, 1985; Brock, 1988; Brock and Casanova, 1991; Casanova, 1994; Denton and Ganf, 1994; Froend and McComb, 1994; Rea and Ganf, 1994a,b,c; Walker *et al.*, 1994; Chambers *et al.*, 1995; Nielsen and Chick, 1997). Morphological and physiological adaptations which enable plants to persist in aquatic ecosystems with variable water regimes are diverse and occur across many families, and are discussed below.

Figures and Plates are placed at the end of each chapter, and Tables within the text. Species nomenclature is given in Appendix 1.

1.1.1 Emergent macrophytes

Flooding affects emergent plants both directly and indirectly. Access to atmospheric O_2 and CO_2 falls as the proportion of the plant protruding above the surface declines (Blom *et al.*, 1990). Meristematic activity is constrained as carbon assimilation declines, causing shoot and root production to slow. The pool of labile sugars available for sequestering in storage organs also declines, reducing the potential for regrowth (Armstrong *et al.*, 1994). Gas exchange through the water column is minimal as diffusion is 10^4 times slower in water than in air (Armstrong *et al.*, 1994). Dissolved oxygen concentrations are also 30 times lower than in the gaseous state. Thus, an increase in depth causes a decrease in oxygen concentration in the sediments as the pathlength for diffusion increases, *via* both the water column and plant. Microbial and chemical oxygen demand further reduces oxygen concentrations and only the uppermost few millimetres may remain aerobic (Armstrong *et al.*, 1994). Some soil nutrients are speciated into the reduced state as oxygen concentrations fall, and are highly phytotoxic; particularly those of iron, manganese and sulphur (Ernst, 1990). Flooding in the warmer months rapidly reduces soluble carbohydrate concentrations in tubers and rhizomes in some species (*e.g.* Pip and Stepaniuk, 1988), leading to carbon starvation (Cizkova-Koncalova *et al.*, 1992). Ethanol is a product of anaerobic metabolism, and upon re-exposure of the plant to air is converted to acetaldehyde, which damages cell membranes (Crawford and Braendle, 1996). However, many rhizomatous species stimulate the activity of anti-oxidants and enzymes under anoxic conditions to reduce post-anoxic injury from superoxides, which are involved in acetaldehyde production (Crawford and Braendle, 1996).

Sediments become oxic upon exposure. Wetting and drying stimulates organic matter decomposition and nutrient release (Conner and Day, 1991; van der Vaalk *et al.*, 1991). Stomatal conductance is impaired under low soil moisture (Kirkman and Sharitz, 1993), reducing carbon acquisition and growth (Furness and Breen, 1980). Production of new shoots declines and carbohydrates are instead stored below-ground. Re-flooding stimulates shoot and rhizome/stolon production, particularly in warm weather.

Adaptations which enable survival when flooded or exposed are common. The stems or leaves of many emergents extend when flooded to maintain contact with the atmosphere (Blom *et al.*, 1990; Waters and Shay, 1990), stimulated by an increase in concentration of the growth hormone ethylene (Armstrong *et al.*, 1994). Stem elongation may result from enhanced cell division and/or cell elongation (Armstrong *et al.*, 1994). Labile carbohydrates, which are sequestered in tubers and rhizomes over winter and during drought, are allocated to stems during flooding to support elongation (Grace, 1989; Zakravsky and Hroudova, 1994). Morphological plasticity is highly developed amongst the sedges, bulrushes and some grasses, and numerous studies have correlated stem height and depth across an elevation gradient (Bernard, 1975; Pip and Stepaniuk, 1988; Grace, 1989; Hultgren, 1989; Waters and Shay, 1990; Squires and van der Vaalk, 1992; Neill, 1992, 1993; Kirkman and Sharitz, 1993).

Changes in growth form and the distribution of biomass between tissues at different depths are interpreted as resource allocation strategies to redress a resource imbalance (Chapin *et al.*, 1987, 1993; Tilman, 1988; Rea and Ganf, 1994c). Changes in above- to below-ground biomass ratios in a variable water regime reflect such strategies. Two to three fold increases have been observed in wetland grasses during flooding (Kirkman and Sharitz, 1993; Neill, 1993), indicating a strategy to maintain sufficient access to atmospheric gases to meet respiratory requirements.

Many species possess tall rigid stems or leaves (*e.g. Phragmites australis, Schoenoplectus validus* and *Typha domingensis*) that can withstand fluctuations in water level of a metre or more yet maintain photosynthetic area above the surface. Stems produced in deep water are generally wider and comprise aerenchymatous tissue with low resistance to gaseous diffusion and low respiratory demand. In species with cylindrical stems or long leaves capable of pressurisation, air may be transported to the roots *via* convective flow (Brix *et al.*, 1992; Armstrong *et al.*, 1994). This permits plants to maintain oxygen concentrations at close to atmospheric levels in the rhizome; much higher than possible from passive diffusion (Armstrong *et al.*, 1994). For example, a humidity gradient across the stomata in

Phragmites australis causes O_2 to diffuse into the leaf at up to 15 cm^3 min^{-1} (Armstrong *et al.*, 1994). Radial diffusion of oxygen from the roots elevates oxygen concentrations in the sediments and, if of sufficient volume, maintains nutrients in an oxidised state.

Roots may also contain high proportions of aerenchyma tissue and cell configurations with high gas-space provision (Armstrong *et al.*, 1994). Root morphology may change to avoid anoxia in flooded soils. For example, Blom *et al.* (1990) found that *Rumex* roots become very fine and branched, and are placed near the (oxic) sediment surface.

The high temporal variability of water regime in semi-arid wetlands has selected for strategies permitting rapid establishment and colonisation. These are most prevalent amongst the Monocotyledonae, in which clonal growth *via* rhizomes, stolons and runners is the prime mode of reproduction (Callaghan *et al.*, 1992; Grace, 1993; Johansson, 1993; Dong and de Kroon, 1994), with dispersal by stem fragments (Brock, 1991) and pseudovivipary also important. Along with tubers, these organs also provide anchorage and protect meristems from physical damage. Integration across environmental gradients in clonal plants allows resources to be allocated to daughter shoots placed at sub-optimal depths (Rozema and Blom, 1977; Evans and Whitney, 1992; Hester *et al.*, 1994). In pseudoviviparous plants, clonal propagules replace seeds within the flower, ensuring greater reproductive success. In *Cyperus gymnocaulos*, the parent stem then bends to the sediment surface ('layering', cf. Grace, 1993), placing the young plant in a favourable environment nearby (Black, 1980).

1.1.2 Submersed macrophytes

Submersed species have a narrower colonisable depth range than emergents in variable, turbid waterbodies. Light limitation prevents significant growth below c. 2 m depth, whilst fluctuating water levels expose tissues to desiccation. Photosynthetically active radiation (PAR; 400-700 nm) is attenuated approximately exponentially through the water column, as described by the Lambert-Beer relationship (cf. Equation (3), Chapter 7). Net photosynthesis occurs when photon flux densities exceed the compensation irradiance, I_c. I_c is species-specific, and is dependent upon leaf age (Mazzella and Alberte, 1986), depth (Maberly, 1993; van der Bijl *et al.*, 1989), previous light history (Kirk, 1983; Pizzaro and Montecino, 1992), and inorganic carbon and nutrient supply (Barko and Smart, 1981; Chambers and Kalff, 1987; Sand-Jensen, 1989; Madsen and Sand-Jensen, 1994). Values of

I_c are lower for submersed macrophytes than for terrestrial species: from 10-100 μmol m^{-2} s^{-1}, but usually <60 μmol m^{-2} s^{-1} (Bowes and Salvucci, 1989). Other parameters of the photosynthesis-irradiance (P-I) relationship are shown in Fig. 1.2 (Jassby and Platt, 1976; Bannister, 1979). Relative photosynthetic activity amongst species can be compared with these parameters, with low I_c and I_k and high α, indicating high physiological shade-tolerance. Physiological shade-tolerance confers an advantage in turbid waters and where prolonged, deep flooding occurs (Madsen *et al.*, 1991; Howard-Williams *et al.*, 1995). Michaelis-Menten curves are also used to model P-I relations (*e.g.* Madsen *et al.*, 1991; van der Bijl *et al.*, 1989), with relative shade tolerance indicated by the half-saturation irradiance , K_m.

A plant's carbon balance depends upon the depth distribution of leaves relative to the vertical light gradient and the photosynthetic and respiratory characteristics of the various tissues (Titus and Adams, 1979; Mazzella and Alberte, 1986; van der Bijl *et al.*, 1989). In general, growth and recruitment decline with depth, although photoinhibition near the surface may reduce canopy area at high light (Spence, 1982; Kirk, 1983; Chambers and Kalff, 1985; Tanner *et al.*, 1993; Kimber *et al.*, 1995b; Rørslett and Johansen, 1995; Middelboe and Markager, 1997). Many species produce longer leaves or stems in deep water, however, to maintain a positive carbon balance. Formation of a surface canopy may also confer a competitive advantage over other species (Titus and Adams, 1979; Madsen *et al.*, 1991).

Growth-irradiance relationships, analogous to P-I relationships but measuring changes in biomass production with irradiance, have been determined experimentally for a few species and found to describe a similar form of curve (Sand-Jensen and Madsen, 1991; Olesen and Sand-Jensen, 1993). At high light, relative growth rates become asymptotic as a greater proportion of the canopy photosaturates. I_c values are generally higher for growth than photosynthesis due to respiratory demand of non-photosynthetic tissues and night-time leaf respiration (Sand-Jensen, 1989). In field studies, the maximum depth of colonisation has been correlated with the rate of light extinction, K_d, and Secchi depth (Spence, 1982, Chambers and Kalff, 1985; Schwarz *et al.*, 1996; Middleboe and Markager, 1997).

Various carbon balance models have been developed to simulate growth based on P-I relationships (Titus *et al.*, 1975; Verhagen and Nienhuis, 1983; Cosby *et al.*, 1984; Wetzel and Neckles, 1986; Dennison, 1987; Collins and Wlosinski, 1989; Scheffer *et al.*, 1993; Chen and Coughenour, 1996). Models are useful for predicting the effects of changes in depth, ambient irradiance and light extinction through the water column, but accuracy is constrained by the temporal density of input light data (Zimmerman *et al.*, 1994) and representativeness of P-I relationships across tissues of different ages and depths.

Acclimatization to transient periods of low light is indicated by an increase in chlorophyll concentration, which increases photosynthetic efficiency, α (Sondergaard and Bonde, 1988; Boston *et al.*, 1989; Frost-Christensen and Sand-Jensen, 1992; Pizarro and Montecino, 1992; Howard-Williams *et al.*, 1995). Hence, α more than doubled in *Potamogeton perfoliatus* within 6 days of shading, and returned to normal levels when shading was removed (Goldsborough and Kemp, 1988). However, no acclimatization occurred in the conspecific *P. pectinatus* (van der Bijl *et al.*, 1989). Light harvesting efficiency is inversely proportional to leaf thickness, as thin leaves expose more of their photosynthetic pigments to quanta (Frost-Christensen and Sand-Jensen, 1992; Agusti *et al.*, 1994; Enriquez *et al*, 1995). Consequently, many submersed species have leaves <10 cells thick.

At very high light (generally >1500 μmol m^{-2} s^{-1}), photosynthesis is inhibited, probably due to damage to quinone-based molecules in the reaction centre of photosystem II (Kirk, 1983, p 232). Shade-adapted plants may be exposed to these irradiances when the water level falls, placing leaves at the surface, or if turbidity declines rapidly. *Vallisneria americana* has been shown to protect its photosystems from high light levels by moving its chloroplasts away from the light source within 30 mins of being exposed (Sinclair and Hall, 1995).

The low diffusibility of inorganic carbon in water has selected for high plasticity in carbon acquisition and photosynthetic carbon reduction strategies amongst submersed species (Bowes and Salvucci, 1989; Madsen and Sand-Jensen, 1991). The principal adaptations include the utilization of bicarbonate ions and sediment CO_2, and carbon concentration mechanisms similar to C_4 pathways in terrestrial species (Bowes and Salvucci, 1989; Robe and Griffiths, 1990; Madsen *et al*, 1993; Singer *et al*, 1994; Newman and Raven, 1995; Vadstrup and Madsen, 1995). Malate or similar sugars may be used as an alternate carbon source when CO_2/HCO_3^- availability is low (Helder and van Harmelen, 1982). Carbon dioxide compensation points are also highly variable, which permits rapid adjustment to changes in carbon concentration.

Submersed species are desiccation-intolerant as they possess negligible cuticle, thin leaves and minimal vasculature and structural support. Hence, submersed vegetation is usually rare or absent in semi-arid wetlands in which large changes in water level are frequent. When rivers or wetlands are impounded, however, they provide ideal habitats, particularly if water level fluctuations are reduced and plants are able to maintain a significant surface canopy.

1.2 The Murray-Darling Basin and Lower River Murray

The Murray-Darling Basin lies between latitudes 24 and 38°S in southeastern Australia (Fig. 1.1). The eastern section experiences a temperate-mediterranean climate, whilst the west and north-west are arid to semi-arid (Eastburn, 1990; Mackay, 1990). The Murray and Darling Rivers have a combined length of 5 300 km, placing them fourth in world standing, and the Basin drains 14% of mainland Australia (1.073 million km^2; Walker, 1986; and Fig. 1.1). By world standards, mean annual discharge from the basin is low: approximately 10-12 million megalitres, or less than one day's average discharge from the Amazon (Mackay, 1990). Variability in flow, however, is extreme: ranging from 0.6-49.3 million megalitres at Blanchetown from 1950-80 (Walker, 1986). The Basin drains four States and one Territory: Queensland, New South Wales, Victoria, South Australia, and the Australian Capital Territory. Annual production from the basin is approximately $10 billion, mainly from agriculture, grazing and horticulture. Canberra is the only major city (population >100, 000) situated within the basin, and industrial development is low. Irrigation uses nine-tenths of the total flow (Walker, 1992). Interbasin transfers from the Murray provide 50-90% of Adelaide's metropolitan water supply.

The Lower River Murray is formed by the junction of the Murray and Darling Rivers at Wentworth in western New South Wales (Fig. 1.1), and its flow and turbidity regimes reflect the differing climatic patterns operating in the two sub-catchments. The hydrograph is predominantly seasonal due to Murray flows, but with variable Darling influences superimposed. Murray flows are dominated by winter rains and snowmelt from the Eastern Highlands, with one-third of the total annual discharge contributed by the uppermost 1.5%

of the catchment (Eastburn, 1990). The headwaters of the Darling, and those of its tributaries, arise across a broad section of eastern Australia, stretching from the Dividing Range in New South Wales to desert in western Queensland. Rainfall is erratic over most of the catchment, while the northern tributaries also experience monsoonal weather patterns (*e.g.* Culgoa/Condamine and Warrego Rivers). The Darling's catchment is twice that of the Murray (650 000 and 310 000 km^2, respectively; Walker, 1986), but it contributes on average only 12% of flows to the Lower Murray. No major tributaries enter the Murray below Wentworth, and the contribution from runoff is negligible. Flows are also influenced by cyclic patterns in sea surface temperature in the eastern tropical Pacific Ocean (the El Niño Southern Oscillation; Simpson, *et al.*, 1993), producing periods of 1-3 y of above or below average rainfall (Nicholls, 1989). Sequences of low and high flows are evident for downstream of Lock 6 in Fig. 1.3. Eleven oscillations have been recorded this century, and are correlated with drought and flooding.

Light attenuation is much higher in the Darling than the Murray, due to high suspended loads of fine clays from its floodplain (mainly montmorillonites and illites; Woodyer, 1979). Median turbidities from 1978-95 in the two rivers were 95 and 24 NTU respectively (at Burtundy and Merbein; data from M. Shaffron, Murray-Darling Basin Commission, Canberra). A relatively low median turbidity (42 NTU) at Lock 9 reflects the greater contribution of Murray water. However, periods of very high turbidity may occur for 1-2 y following a Darling flood *e.g.* 1983-84 (see Fig. 1.7) (see also Mackay *et al.*, 1988). Irradiances sufficient for photosynthesis in submersed macrophytes penetrate <2 m, and frequently <1 m.

The Lower Murray's channel is 80-300 m wide and 3-7 m deep. The gradient is low (1-5 cm km^{-1}) and water may take 2-3 weeks to traverse its length (Eastburn, 1980; Jacobs, 1989). For nearly half its 825 km length, it supports a floodplain 5-10 km wide, dominated by *Eucalyptus camaldulensis* (redgum) and *E. largiflorens* (blackbox) woodlands and grasslands/shrublands (Pressey, 1986; Thompson, 1986, O'Malley, 1990). Its widest point is in Pools 4-6, where it spans up to 22 km. The floodplain supports diverse hydrologic environments, including creeks, anabranches, billabongs (oxbows) and deflation basin wetlands (Pressey, 1986; Walker, 1986; Roberts and Ludwig, 1990). Within Pools 1 and 2, the river cuts through a limestone gorge and the floodplain is constrained to <2 km wide (Walker and Thoms, 1993).

1.3 Flow regulation in the Lower Murray

Significant flow regulation commenced in 1922 with the construction of Lock 1 (Jacobs, 1990). By 1935 the river between Wentworth and Blanchetown was a series of 10 stepped pools, 29-88 km long (Plate 1.1). Headwater dams, off-stream storages and diversions for intensive irrigation have also greatly reduced flows (Walker and Thoms, 1993). Whilst the magnitude and frequency of large floods are little affected (Jacobs, 1989), those of small-medium flows have been reduced by 70% (Maheshwari *et al.*, 1995). Levels rarely fall below pool level, thus maintaining a base flow year-round (Fig. 1.3). Many low-lying wetlands are now permanently flooded, frequently containing drowned redgums (*Eucalyptus camaldulensis*) and extensive submersed vegetation communities, whilst those high on the floodplain fill less frequently than prior to locking (Jacobs, 1989). Small to medium sized flows are usually stored in Lake Victoria and/or routed down the river under control of the weirs to meet irrigation, domestic or navigation requirements.

During flows < c. 35-50 GL/day, the water level on the upstream of a weir is maintained to within 5 cm of the design weir level. This is achieved by adding and removing 0.4 m high concrete 'stoplogs' and Boulé panels (weir specifications are shown in Fig. 1.4). In contrast, levels vary frequently by 10-20 cm per day on the downstream side, and occasionally by as much as 1 m (Walker *et al.*, 1992). Amplitudes of fluctuations decrease with distance downstream of a weir (Fig. 1.5), creating gradients of water regime (Walker and Thoms, 1993; Walker *et al.*, 1994; Blanch and Walker, in press). Plants growing at pool level at Loxton in Pool 3 are flooded to twice the depth and two to three times the duration of those at Lock 3 (Fig. 1.5 and Plate 1.1).

Fig. 1.3 illustrates the influence of locking on water regimes at Lock 6. Pre-1931, river levels rose and fell more or less continuously, producing a moving littoral zone both within the channel and on the floodplain (Junk *et al.*, 1989). Completion of the weir created a largely permanent pool, but the river frequently fell below pool level up to the 1960's. Extension of the Murray's headwater dam (Hume Dam; stage one completed in 1936; Jacobs, 1990) in 1961 and construction of another major dam on a headwater tributary in 1979 (Dartmouth Dam on the Mitta Mitta River) has further reduced variability to such an extent that river levels along most of the Lower Murray now remain within a 20 cm elevation range for half to three quarters of most years (Maheshwari *et al.*, 1995).

Lake Victoria, a large lowland off-stream impounded lake near Lock 7 (Fig. 1.6), is used to augment late-summer and autumn flows to ensure South Australia receives its minimum annual entitlement flow of 1 850 GL (Murray-Darling Basin Act, 1993). Water is harvested from both Murray and Darling flows *via* Frenchmans Creek above Lock 9, mixed in the lake, and returned to the river *via* Rufus River. These operations increase the duration of elevated turbidities in the Lower Murray downstream of Lock 7, as turbid floodwaters are harvested in late winter-spring and re-released in late summer-autumn (Mackay *et al.*, 1988). Submersed vegetation experiences prolonged periods of reduced light, particularly following a Darling flood.

1.4 Aquatic and littoral vegetation of the Lower Murray

Little published information exists concerning aquatic and littoral vegetation of the Lower Murray prior to flow regulation. Period photographs and anecdotal evidence suggest that vegetation richness and diversity were greater on the floodplain and in temporary wetlands and billabongs than in the main channel, where continually rising and falling river levels limited vegetation development (Fig. 1.3). Nineteenth century explorers noted reeds and rushes growing along the main channel, probably *Phragmites australis, Schoenoplectus validus* and *Typha domingensis*, and extensive *Muehlenbeckia florulenta* and sedge vegetation on the floodplain (Sturt, 1833; Mitchell, 1839). Little or no mention is made of submersed vegetation within the channel. Herbarium collections from last and early this century confirm these observations. Sturt's records also reveal the highly variable turbidity regime in the Murray; on one occasion he notes the 'transparent water', and later 'its waters became so turbid, that it was impossible to see objects in it, not withstanding the utmost diligence on the part of the men.' (see also Tate, 1884).

The creation of hydrologically stable weir pools allowed vegetation to colonise the main channel, whilst reduced flooding led to a constriction in floodplain vegetation. Zimmer (1938) recorded aquatic species in a billabong near Mildura, 60 km upstream of Wentworth on the Murray, in the early years of flow regulation. A diverse submersed and emergent vegetation is described, including *Pseudoraphis spinescens*, *Juncus pauciflorus*, *Centipeda minima*, *Vallisneria americana* (called *V. spiralis*), *Potamogeton crispus* and *P. tricarinatus*. The two lilies noted, *Nymphoides crenata* and *Ottelia ovalifolia*, are presently rare in the Lower Murray (O'Malley, 1990), with the former being recorded only once within the South Australian section in the last 70 y (Black, 1980).

Fourty years after the completion of Lock 1, Harris (1963) described the submersed vegetation within the main channel 20 km upstream of Blanchetown. Apart from *Hydrilla verticillata*, which is now rare in the Lower Murray, all species reported are also presently common, including *Myriophyllum verrucosum*, *Ceratophyllum demersum* and *Vallisneria americana*. Harris noted that 'a rich growth of water plants extended out from the bank twenty or thirty feet', considerably more than was observed during the present study. Emergent species were *Isolepis inundata* (then named *Scirpus inundatus*; cf. Black, 1980), *Paspalidium jubiflorum* and *Phragmites*. Conditions were favourable for submersed vegetation over the 15 month prior to the survey (April 1962): turbidity was low; <25 nephelometric turbidity units (Fig. 1.7), and water levels relatively stable (Fig. 1.3). Water clarity is widely considered to have generally declined since the early 1970s (but see Tate, 1884), which is variously attributed to the large floods of 1974-75, the introduction of the benthivorous carp (*Cyprinus carpio*) (Roberts *et al.*, 1995), widespread clearing, poor catchment practices, and Lake Victoria operations.

Thompson (1986) noted the presence of common reeds, rushes and submersed species in wetlands within the South Australian section from 1983-86. Most species recorded have wide tolerances to water regime, however, and are of little discriminatory value. Vegetation was surveyed principally to determine the conservation value of wetlands for waterbirds and fish, and only the most obvious macrophytes were noted. The qualitative data briefly describe vegetation patterns only, with little indication of processes.

The first major ecological studies of vegetation dynamics in the Lower Murray's littoral and floodplain were conducted in 1988. Walker *et al.* (1994) examined the distribution of 11 perennial species along Pools 2 and 3 after 3 y of mainly stable water levels. *Phragmites*, *Cyperus gymnocaulos* and *Paspalum ?vaginatum* (probably mostly *P. distichum*) were widespread and abundant, indicating broad tolerances to flooding and drying. *Typha domingensis* occurred mainly within the lower pool sections (0-20 km upstream of the weirs), whilst *Myriophyllum verrucosum* favoured the fluctuating water levels in the mid and upper pools (approximately 20-50 and 50-70 km upstream, respectively). Longitudinal vegetation patterns were correlated with peak flood heights for the six years prior to the survey, suggesting concomitant gradients in vegetation and water regime.

Roberts and Ludwig (1990, 1991) studied the phytosociology of aquatic and riparian plants of creeks, billabongs and channels in the Chowilla floodplain complex in Pool 6. They defined four vegetation types, characterised as *Eucalyptus camaldulensis+Phragmites*, *E. camaldulensis*+sedges+*Typha domingensis*, *Cyperus gymnocaulos+Cynodon dactylon +Paspalidium*, and *Cynodon +Paspalidium*. Scouring by flooding 4-6 months prior to the study removed most of the submersed vegetation. The processes producing these associations are difficult to determine from the study. Semi-quantitative scores for current and wave action were determined using a five point scale, and regressed against site ordination scores. Both were significantly correlated, though correlations were low. However, factors not accounted for may have been at least as or more important in structuring vegetation. For example, aspects of water regime such as flooding depth and frequency may be more important for the sedges and rushes which dominated in anabranches and backwaters, where wave action and currents were minimal.

A parallel study (O'Malley, 1990) examined vegetation communities at higher elevations on the Chowilla floodplain, and concluded that they were distributed along an axis of flooding frequency/soil moisture. Common species in deflation basin wetlands and high creeks were the shrubs *Muehlenbeckia florulenta* and *Senecio cunninghamii*, grasses *Paspalidium*, *Cynodon* and *Phragmites*, and sedges/rushes *Bolboschoenus medianus*, *Cyperus gymnocaulos* and *Typha domingensis*. Margules and Partners (1990) and Beovich (1994) also related species diversity and regeneration to aspects of water regime. Free-floating species are small (*e.g. Azolla filiculoides, Lemna* spp.), but are often abundant within isolated waterbodies.

1.5 Thesis outline

This thesis examines the influence of aspects of water regime on the ecology of aquatic and littoral plants in the Lower Murray. Its aims are to examine the effects of water regime on growth, vegetative recruitment and resource allocation in selected species, and to investigate the adaptations permitting plants to tolerate sub-optimal regimes.

Chapters 2 and 3 investigate vegetation-water regime patterns in Pool 5, and determine broad correlations between water regime and plant life history strategies and physiological tolerances to flooding and drying. The study complements earlier studies (see above), and was used to select two common species which exhibit contrasting water regime 'preferences' for experimentation: the emergent sedge *Bolboschoenus medianus* and the submersed herb *Vallisneria americana*. Pond, field and laboratory studies examining the effects of water regime on growth, clonal reproduction, resource allocation and photosynthesis in the two species are related in Chapters 5-10. Specifically, I investigate to what extent a reduction in resource availability in emergent and submersed species (access to atmospheric gases, soil moisture, light) stimulates biomass allocation to the tissue(s) responsible for the acquisition of the limiting resource.

Chapter 4 relates an evaluation of a computer simulation model, used for flood forecasting by water resource agencies, for its application to ecological research on the Lower Murray, *e.g.* as in Chapters 2 and 3.

Resource allocation strategies and morphological response mechanisms to flooding are investigated for *Bolboschoenus* grown across a depth gradient in Chapter 5, to elucidate how emergent plants react to flooding. Chapter 6 relates a field study of the effects of natural flooding to different depths and rates of exposure in *Bolboschoenus*, to examine responses of emergents to sequential resource limitation (CO_2 and O_2, then soil moisture).

Growth, vegetative recruitment and morphological plasticity in *Vallisneria* are examined across a range of irradiances in Chapter 7 to interpret the influence of flooding depth and turbidity on submersed macrophytes. Chapter 8 examines physiological shade-tolerance in *Vallisneria* using P-I characteristics determined from oxygen evolution studies in the laboratory. The data are used to model carbon assimilation under different light regimes in Chapter 9, and complements the pond experiment examining growth-irradiance relationships (Chapter 7). Chapter 10 tests the hypothesis that distribution patterns of submersed vegetation in the Lower Murray are related to water level variability and light limitation, as suggested by Chapters 2 and 3, and Chapters 7-9, respectively, in a field study using *Vallisneria*.

Chapter 11 is a summary and synthesis, and suggests directions for research into water regime and aquatic plants in semi-arid rivers and wetlands. General recommendations are made regarding possible means of enhancing littoral and floodplain vegetation diversity in the Lower Murray.

This thesis has been written as a series of independent papers to facilitate publication, and there is some unavoidable repetition in the opening remarks of each chapter. The aims and hypotheses tested are stated in the introduction to each chapter. Results of the literature survey are also developed more fully in each introduction.

1.6 Papers bound in support of the thesis

- Blanch, S. and Walker, K.: Life history strategies and water regime gradients in the Lower River Murray, South Australia. *Internationalen Vereinigung fur Theoretische und Angewandte Limnologiae*, in press (cf. Appendix 2).

- Blanch, S.J., Walker, K.F. and Ganf, G.G., 1994: *An evaluation of the River Murray Hydraulic Model and its value in environmental flow management.* Proceedings of a seminar on 'Environmental Flows' convened by the Australian Water and Wastewater Association, Canberra, 25-26 August, 1994 (cf. Appendix 2).

Figure 1.1. The Murray-Darling Basin and Lower River Murray.

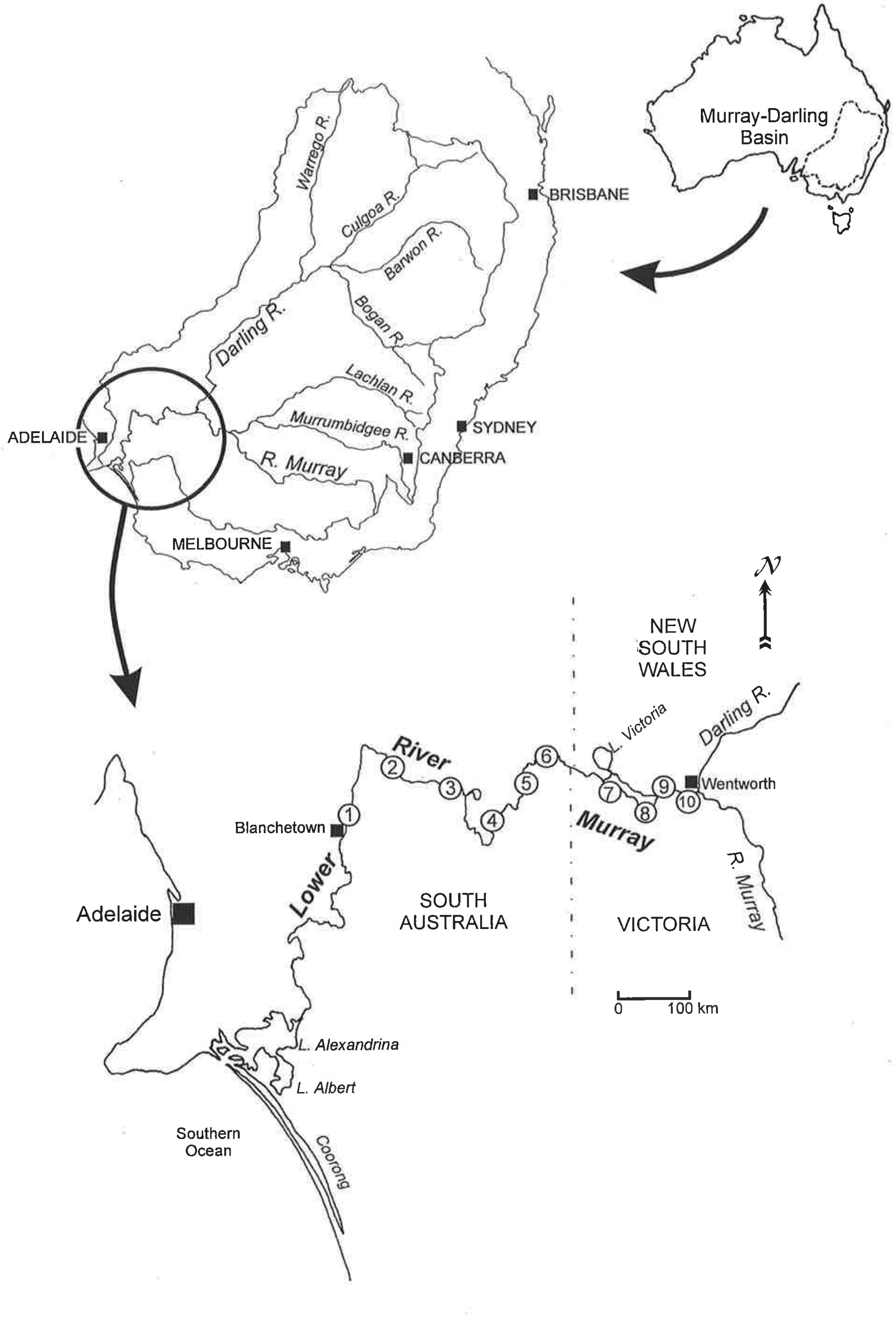

Murray-Darling Basin
Warrego R.
Culgoa R.
Barwon R.
Bogan R.
Darling R.
Lachlan R.
Murrumbidgee R.
R. Murray
BRISBANE
SYDNEY
CANBERRA
ADELAIDE
MELBOURNE
N
NEW SOUTH WALES
L. Victoria
Darling R.
River
Murray
Lower
①
②
③
④
⑤
⑥
⑦
⑧
⑨
⑩
Wentworth
Blanchetown
R. Murray
Adelaide
SOUTH AUSTRALIA
VICTORIA
0
100 km
L. Alexandrina
L. Albert
Southern Ocean
Coorong

Figure 1.2. Parameters describing a photosynthesis-irradiance response curve; P_{max}, maximum rate of net photosynthesis; R, rate of dark respiration; α, photosynthetic efficiency; I_{c}, compensation irradiance; I_{k} ($=\alpha/P_{\mathrm{max}}$), onset of light-saturated photosynthesis.

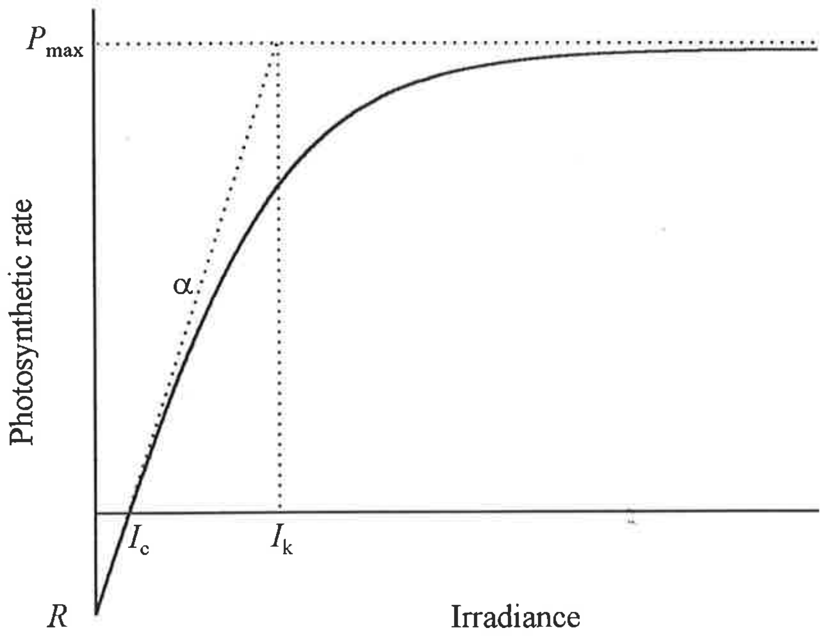

P_{max}
Photosynthetic rate
α
I_c
I_k
R
Irradiance

Plate 1.1. Upper panel: Low-level weir (3-m high) on the Lower Murray, showing the hydrologically stable weir pool on the left, and bank erosion on the downstream side. Boat traffic navigates the weir through the lock (bottom). Middle panel: Littoral zone in a mid-pool reach, supporting grasses, sedges and herbs tolerant of flooding and exposure. Lower panel: Dense *Phragmites australis* (behind) and *Schoenoplectus validus* (shallow water) growth in a lower pool.

Figure 1.3. Stage hydrograph on the upstream (upper trace) and downstream sides of Lock 6, June 1927-February 1994. Construction of Lock 6 was completed in 1931. Hydrographs are presented in 10 y periods, commencing on 1 January for each decade. Data were provided by SA Water and compiled by K. Walker.

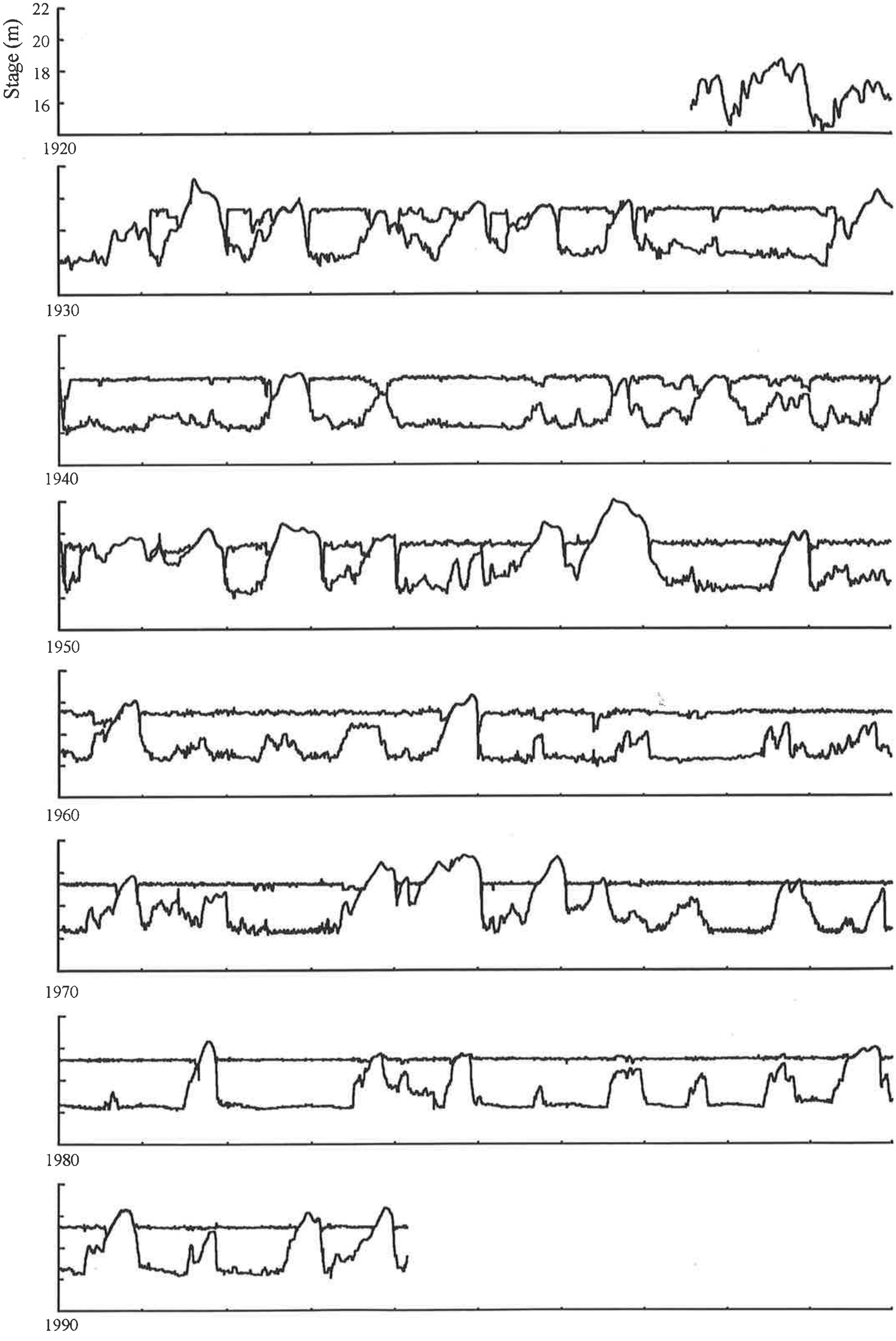

Stage (m)
22
20
18
16
1920
1930
1940
1950
1960
1970
1980
1990

Figure 1.4. Lengths (km) and elevations ('EL' (m)) of pools in the Lower Murray. Drawn by SA Water, Berri, South Australia.

File RMLOCKS1

RIVER MURRAY LOCKS

POOL LEVELS AND LOCK CHAINAGES

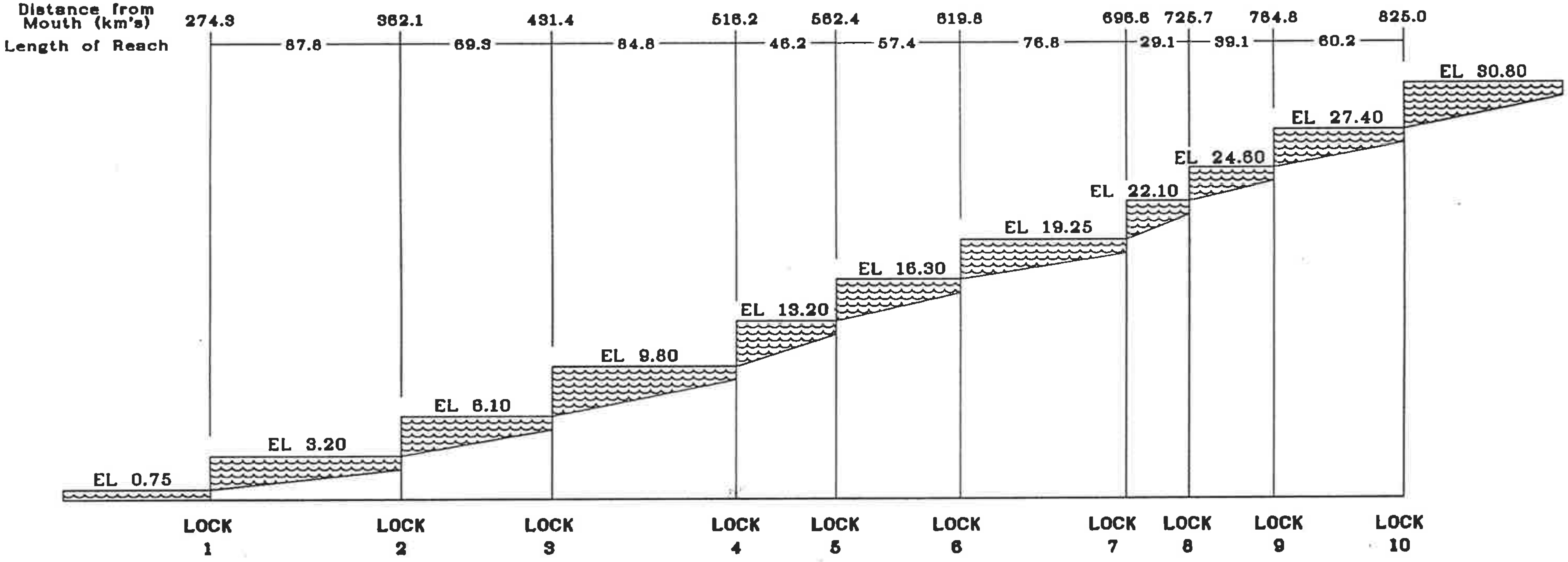


Figure 1.5. Decline in amplitude of a stage hydrograph along Pool 3. The upper trace is for the upstream side of Lock 4. Loxton is 23 km downstream of Lock 4, and Cobdogla 75 km downstream (hence 10 km upstream of Lock 3). Pool levels are 13.20 m and 9.82 m AHD.

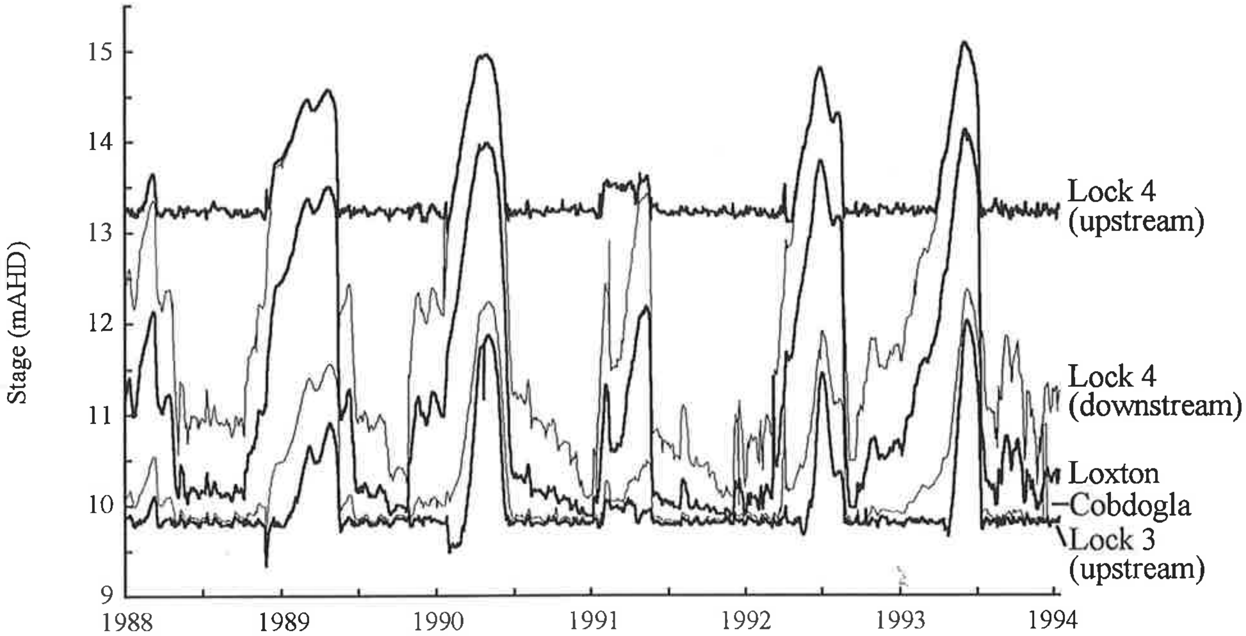

Stage (mAHD)
15
14
13
12
11
10
9
1988
1989
1990
1991
1992
1993
1994
Lock 4 (upstream)
Lock 4 (downstream)
Loxton
Cobdogla
Lock 3 (upstream)

Figure 1.6. Lake Victoria and its relationship to the Lower Murray. Water is gravity-fed to the Lake *via* Frenchmans Creek, and returns *via* Rufus River. Capacity is 680 GL (modified from Mackay *et al.*, 1988).

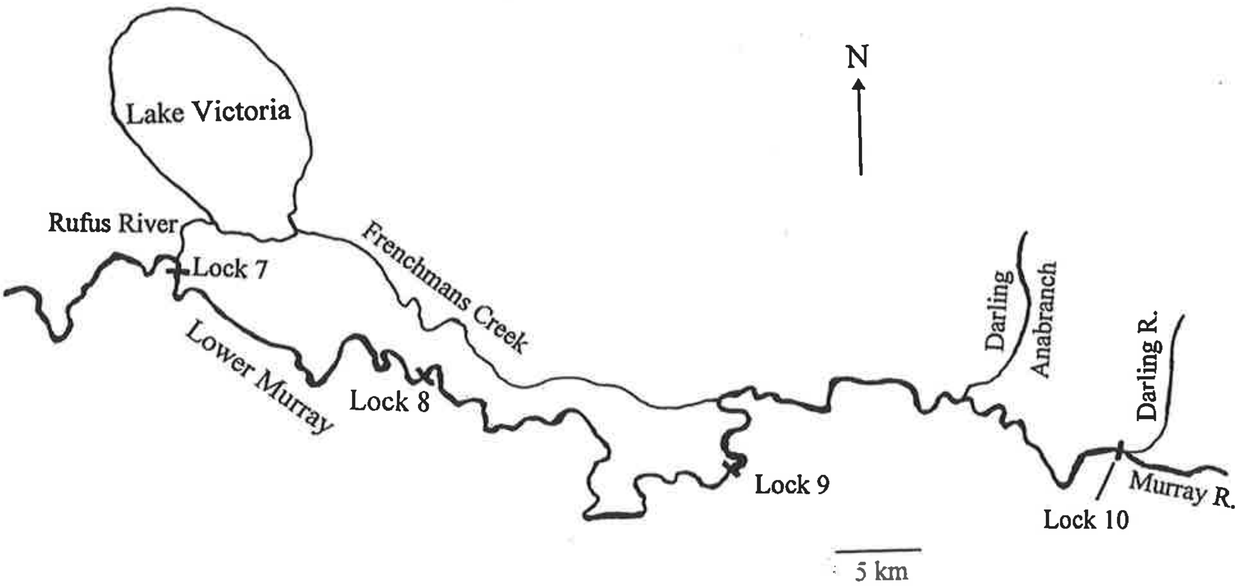
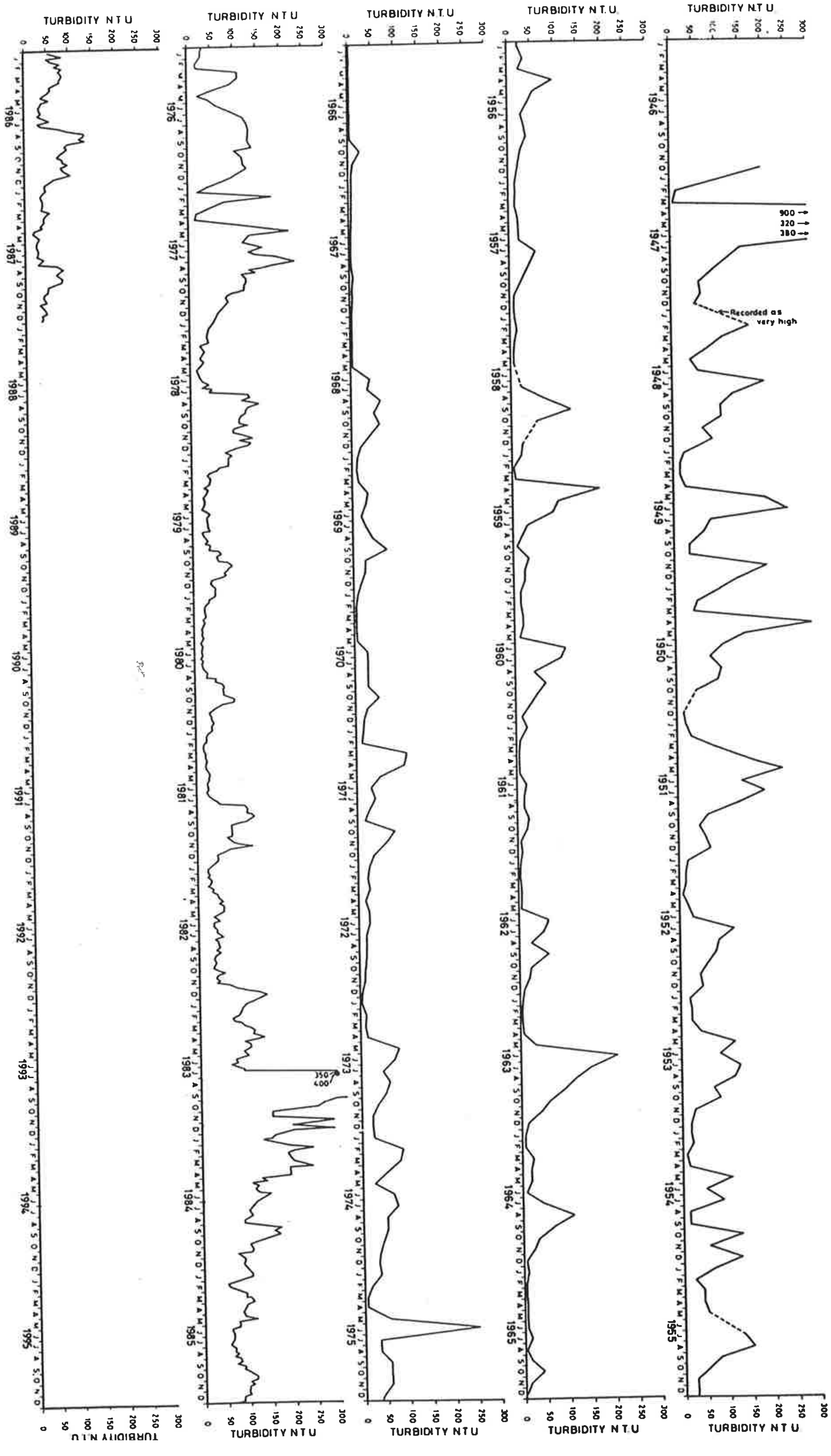

N
Lake Victoria
Rufus River
Lock 7
Frenchmans Creek
Lower Murray
Lock 8
Lock 9
Darling Anabranch
Darling R.
Murray R.
Lock 10
5 km

Figure 1.7. Turbidity at Morgan (in Pool 1) in the Lower Murray, 1947-1987. Data are in nephelometric turbidity units (NTU) (from Mackay *et al.*, 1988).


TURBIDITY N.T.U
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50
100
150
200
250
300
1946
1947
1948
1949
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1951
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1954
1955
1956
1957
1958
1959
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1990
1991
1992
1993
1994
1995
J F M A M J J A S O N D
900 →
320 →
380 →
Recorded as very high
350
400

Chapter 2

Littoral plant life history strategies and water regime gradients in the River Murray, South Australia*

2.1 Abstract

The distribution and relative abundance of littoral plants were surveyed along a water regime gradient established between two weirs on the Lower Murray to test the hypothesis that 'competition' (C) and 'ruderal' (R) traits would predominate in stable reaches, and plants with 'stress-tolerant' (S) and 'ruderal' traits in more variable reaches. The distribution and abundance of plants in Pool 5 (Locks 5-6) were related to river distance (hence water regime) and bank and bend attributes. *Cynodon dactylon*, *Cyperus gymnocaulos*, *Phragmites australis* and *Xanthium ?occidentale* occurred at most sites. CR strategists (*Schoenoplectus validus*, *Typha domingensis*, *Vallisneria americana*) occurred in stable reaches and S- and R-species dominated where levels were variable. Perennials were more sensitive to water regime than annuals, which reflected site characteristics.

2.2 Introduction

The distribution of plants in littoral regions of rivers and lakes is strongly influenced by water regime, which is the depth, frequency, timing and rate of inundation (cf. Rea and Ganf, 1994c). For example, Rørslett (1989) showed that plants were distributed along water depth gradients in Norwegian hydropower lakes experiencing fluctuating levels. Rørslett used a modification of Grime's (1979) CSR model whereby plants are grouped according to life history strategies, namely competitive (C), stress-tolerant (S) and ruderal (R) traits (Table 2.1). Shallow-water species demonstrated rapid clonal growth, vigorous seed

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*The material in Chapter 2 was presented at the XXVI Congress of the International Society for Limnology, 23-29 July, 1995, São Paulo, Brasil. The paper is currently in press in the Proceedings (Blanch and Walker, in press), and a preprint is bound in support of the thesis (see Appendix 2).

Table 2.1. Plant characteristics used by Rørslett (1989) to classify aquatic plants into life-history strategy groups following Grime (1979).

Strategy	Characteristics
R =ruderal	Annual, vigorous seed production
	Vegetative (clonal) reproduction
	Extensive bud/propagule formation
	Fast growth/early reproduction
S = stress-tolerant	Crassulacean Acid Metabolism
	CO_2 from sediment or water
	Slow biomass turnover
	Enhanced shoot:root ratio
	Perennial or evergreen
C = competitive	Large peak biomass
	HCO_3^- utilization (submerged species)
	CO_2 from air (floating-leaved and emergent species)
	Canopy forming (rapidly-elevating monolayer)
	Winter-annual or short-lived perennial
	Fast biomass turnover
	Low shoot:root ratio

production and had protected rhizomes (S, SR traits), enabling them to tolerate alternating periods of inundation and exposure. Deep-water species showed rapid canopy formation and elevation, fast turnover and low root:shoot ratios (CR traits). Day *et al.* (1988) found a relationship between plant traits and water regime in the Ottawa River, Canada, and Wilcox and Meeker (1991) correlated plant form with amplitudes of water level change in Minnesota Lakes.

Water regime gradients occur between weirs in the regulated River Murray in South Australia (Figs 1.1 and 1.5). Water levels are comparatively stable immediately above weirs and become more variable with greater distance upstream of a weir (Maheshwari *et al.*, 1993). A pilot study of the littoral vegetation in Pools 2 and 3 in 1988 showed a broad correlation between the composition of the plant assemblages and the distance below a weir (hence the amplitude of water level fluctuation) (Walker *et al.*, 1994).

The distribution and relative abundance of littoral plants in Pool 5 in South Australia was surveyed in January 1994, and correlated with environmental data such as distance downstream of Lock 6, bank and bend physical attributes. Rørslett's (1989) model for characterising life history strategies was tested for it's applicability to Lower Murray littoral plants. Using this model we tested the hypothesis that CR strategists would occur in the comparatively stable water levels immediately upstream of Lock 5, whilst S and R-traits would typify plants found in water regimes characterised by greater variability. Analyses of longitudinal vegetation patterns in this Chapter present an initial investigation of the influence of water regime on littoral species in Pool 5, and guided exminations of species distributions across elevation and longitudinal gradients in Chapter 3.

2.3 Materials and Methods

Relative abundances of littoral plants were estimated using a simple six-point scale (0=absent, 5=dense and widespread). Survey sites were determined from 1:50 000 topographic maps and river charts. Twelve sites were surveyed at 5 river-km intervals over 55 km. All plants from 2 m below the water level to the top of the bank were scored along 100 m of bank. Position on the bend was recorded, and bank and bend shape (using a five-point scale). Nomenclature is given in Appendix 1.

Daily water levels were generated for the 12 survey sites using linear interpolation between the two weirs. Two indices of relative water level stability were generated for each site. *Rates of river fall* decline with greater proximity to Lock 5. Frequency of small (-0.1 to 0 m) and large (-2.0 to -1.0 m) falls in level over 7 days were determined over 6 years. A Microsoft QBASIC program was constructed to determine the *maximum continuous time in which the river level remained within a 0.2 and 1.0 m depth range* over 6 years.

Relative abundance data was examined using Semi-strong Hybrid mutlidimensional Scaling (SHS, Belbin, 1991, 1993). Non-parametric Spearman rank correlations between vegetation patterns and the above environmental data were determined. Flexible UNpaired Geometric Mean Analysis (UPGMA, an agglomerative, polythetic, hierarchical fusion strategy; Belbin, 1993) clustering suggested groupings amongst sites and species. Vegetation patterns of perennial species are more likely to reflect the preceding 6 years of water level changes than annuals. Hence abundance data for perennials alone and perennials + annuals was examined.

Table 2.2. Spearman correlations between environmental variables and scores on the first two ordination axes for perennial species ($n = 12$). Numbers in brackets indicate correlations when annuals are included.

	Axis 1		Axis 2	
Axis 1	1.000	(1.000)	-	-
Axis 2	-0.035	(-0.014)	1.000	(1.000)
River distance below Lock 6	-0.937	(-0.615)	-0.147	(0.252)
Bend shape	0.259	(0.161)	-0.084	(-0.088)
Bank shape	0.363	(0.592)	0.244	(-0.356)
Position on bend	-0.154	(0.205)	0.358	(-0.615)

2.4 Results

2.4.1 Vegetation-environment correlations

River distance downstream of Lock 6 was highly correlated with the distribution and abundance of perennials (-0.937 on Axis 1, Table 2.2). The correlation was lower when annuals were included (-0.615, Table 2.2). Twenty-three species of littoral plants, sixteen perennials and seven annuals, occurred across the 12 sites (Table 2.3, Fig. 2.2). Six sedges and 6 grasses constituted 75% of the perennial species. *Cynodon dactylon*, *Cyperus gymnocaulos*, *Phragmites australis* and *Xanthium ?occidentale* occurred at over 83% of sites. *Paspalidium jubiflorum* and *Centipeda ?cunninghamii* were most abundant in upper and mid-pool sites. *Schoenoplectus validus*, *Typha domingensis* and *Vallisneria americana* only occurred in the first 10 km upstream of Lock 5.

Axis 1 of the SHS ordination shows a right-left pattern of increasing river distance below Lock 6 (Fig. 2.3a). Sites were clustered into 4 groups, principally determined by river distance on Axis 1 (Fig. 2.3b). Factors other than river distance appear to be important determinants of vegetation patterns in the mid sections of the pool (25 - 40 km downstream).

Flexible UPGMA clustered species into 5 groups (Fig. 2.4). The principal dichotomy split species into a group of 4, three of which were CR strategists (*Schoenoplectus, Typha* and *Vallisneria*), and a group of 19 species which generally possessed S and R traits. A

Table 2.3. Aquatic plants recorded in Pool 5, January 1995. Habit, growth form and height are also indicated (see also Appendix 1).

Species	habit and gowth form	height (m)
PERENNIALS		
Cyperaceae		
Bolboschoenus medianus (V. Cook) Sojak	rhizomatous sedge	0.7 - 2.0
Cyperus bulbosus Vahl.	tufted sedge	0.5
C. exaltatus Retz.	tufted sedge	1.0- 1.5
C. gymnocaulos Steudel.	rhizomatous sedge	0.2 - 0.6
Eleocharis acuta R.Br.	rhizomatous sedge	0.3 - 0.6
Schoenoplectus validus (Vahl) A. Love & D. Love	rhizomatous sedge	1.0-2.0
Hydrocharitaceae		
Vallisneria americana Michx.	stoloniferous, submersed	0.1 - 1.0
Poaceae		
Cynodon dactylon (L.) Pers.*	stoloniferous, creeping	0.05 - 0.4
Paspalidium jubiflorum (Trin.) Hughes	tufted grass	0.4 - 0.8
Paspalum ?distichum L. *	stoloniferous, creeping	0.05 -0.4
Phragmites australis (Cav.) Trin. ex Steudel	rhizomatous grass	1.0- 3.0
Pseudoraphis spinescens (R.Br.) Vick.	stems floating	0.2 - 3.0
Sporobolus mitchellii (Trin.) C.E. Hubb. ex S.T. Blake	creeping to erect stems	0.3
Polygonaceae		
Muehlenbeckia florulenta Meissner	shrub	2.0 - 2.5
Typhaceae		
Typha domingensis (Pers.) Steudel	rhizomatous	1.0- 3.0
Verbenaceae		
Phyla canescens (Kunth.)E. Greene.*	creeping stems	0.05
ANNUALS OR SHORT-LIVED PERENNIAL HERBS		
Aizoaceae		
Glinus lotoides L.	herb	0.3
Asteraceae		
Centipeda ?cunninghamii (DC.)A. Braun & Asch.	herb	0.05 - 0.2
Eclipta platyglossa F. Muell.	herb	0.1 - 0.25
Epaltes australis Less.	herb	0.05 - 0.3
Pseudognaphalium luteo-album (L.) Hilliard & B.L. Burt.	herb	0.2 - 0.4
Xanthium ?occidentale Bertol.*	herb	0.5 - 2.0
Scrophulariaceae		
Stemodia florulenta W.R. Barker	herb	0.2 - 0.8

* Species introduced to the Lower River Murray, according to Black (1980).

lack of experimental data prevented the accurate assessment of traits for most species according to Rørslett's (1989) model.

Bank shape was correlated with relative abundance when annuals were included (0.592) but weakly with perennials only (0.363) on axis 1. The highest correlation on axis 2 occurred for position on bend (all species, -0.615; perennials, 0.358). Position on bend reflects site-specific current velocity effects and is a good measure of the horizontal aspect of the water regime (cf. Roberts and Ludwig, 1991). Hence the distribution and abundance of perennials is determined more so by vertical rather than horizontal components of water regime in Pool 5.

2.4.2 Distance downstream-water regime correlations

Water levels become more stable with increasing distance downstream of Lock 6 (Fig. 2.5a). The maximum continuous time in which river levels remained within a 0.2 m or 1.0 m range increased toward Lock 5 (Fig. 2.5b).

2.5 Discussion

Water regime gradients are established between weirs due to the maintenance of stable water levels on the upstream side and compensatory fluctuations downstream (Fig. 2.1). Composition and abundance of perennials was highly correlated with position along the pool (-0.937, -0.615 when annuals included) indicating they better indicate the medium to long term water regime patterns than annuals. Jean and Bouchard (1993) also found high correlations (up to -0.79) between water level and plant abundance and cover in the Upper St Lawrence River, Quebec.

The distribution of annuals was less influenced by water regime gradients along the pool, with site-specific factors such as position on the bend and bank shape apparently important. Roberts and Ludwig (1991) suggest current and wave action rather than amplitude of fluctuation are the most important factors in determining littoral vegetation in Murray floodplain wetlands.

Maximum continual time in which the level remains between two elevations increases with distance downstream (Fig. 2.5a). Several studies indicate emergents may persist in sub-optimal water regimes if sufficient time for establishment and growth occurs when water levels are more favourable (van der Vaalk, 1994; Rea and Ganf, 1994a,b,c). Thus the increasing stability creates longer 'windows of opportunity' for establishment of emergents.

Large rapid falls in level expose submersed plants to desiccation. Mortality occurs in *Vallisneria* within 14 days of exposure in summer (Blanch, unpub. data; see Chapter 10). Rapid light attenuation limits downward colonisation to approximately 2 m. Extensive *V. americana* colonisation occurred along weir pools during a period of low flows in the 1980's (Walker *et al.*, 1994). In contrast high flows occurred in 4 of the 6 years previous to the present study, restricting growth to the most stable water regimes.

The CR-strategists occurred in the first 10 km upstream of Lock 5 where levels were most stable. Predominantly S and R-trait plants occurred in the mid and upper pool where levels were more variable. These findings are supported by those of Rørslett (1989) and Wilcox and Meeker (1991) in which ruderal and stress-tolerant traits typified littoral plants exposed to repeated inundation and exposure, and competitive and ruderal traits were exhibited in plants where exposure is seldom. Most plants had predominantly stress-tolerant and/or ruderal traits, indicating that despite regulation imposing stability on a naturally variable river, plants able to survive exposure and inundation are widespread. Survey results are consistent with the 'harsh-benign' hypothesis that predicts abiotic factors are more important in determining community structure in highly disturbed sites, whilst biotic controls will predominate in less disturbed areas (Peckarsky *et al.*, 1990).

Accurate assignments of life-history strategies were impossible for most species, due to lack of data. Nevertheless, the groupings of strategies agreed broadly with the UPGMA clusters, suggesting that Rørslett's (1989) models are useful for prediction. Future studies of the ecology of littoral plants along gradients of water regime in the Murray, and other rivers, may benefit from a better understanding of life history strategies.

Figure 2.1. Stage hydrographs for 6 years prior to the survey in Pool 5. Comparatively stable river levels at Lock 5 (thick line) contrast with variable levels immediately below Lock 6.

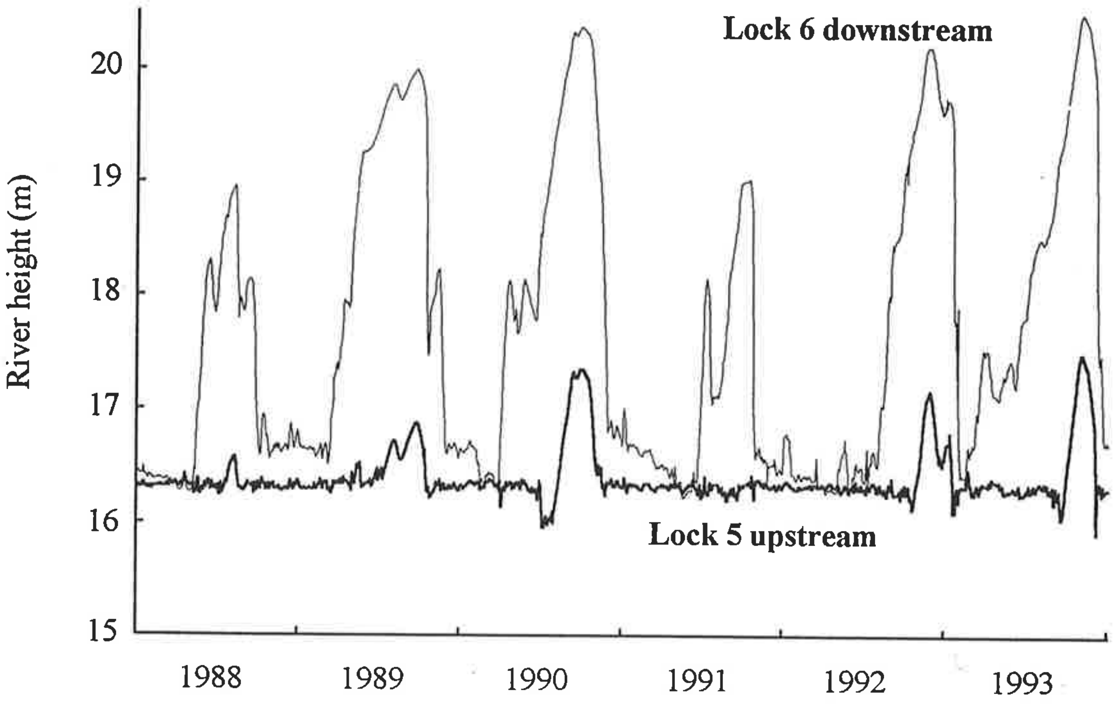

Lock 6 downstream
Lock 5 upstream
River height (m)
15
16
17
18
19
20
1988
1989
1990
1991
1992
1993

Figure 2.2. Distribution and abundance of plants in Pool 5. Abundance was scored (0 = absent, 5 = dense) along 100 m of bank to a depth of 2 m.

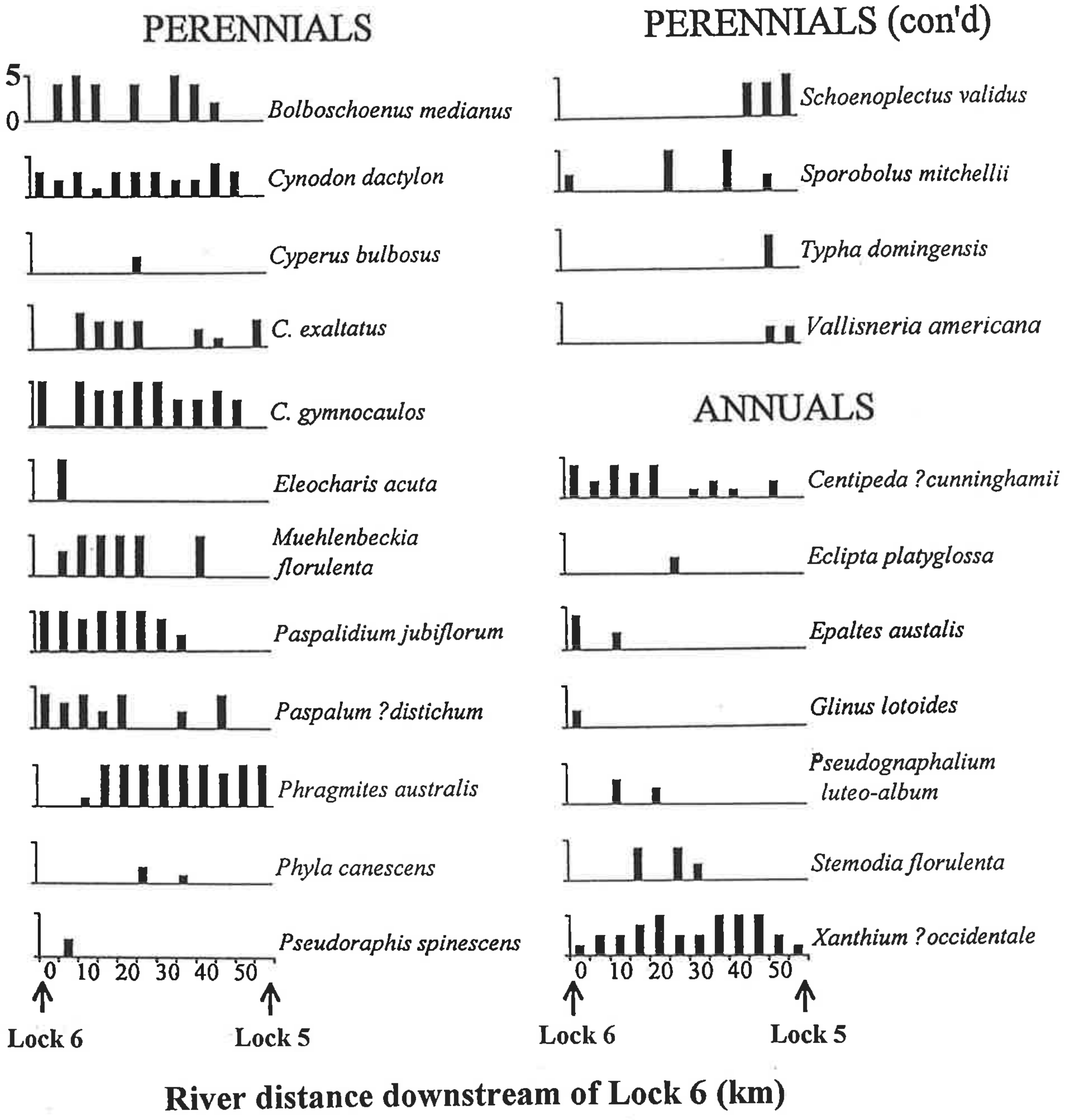

PERENNIALS
5
0
Bolboschoenus medianus
Cynodon dactylon
Cyperus bulbosus
C. exaltatus
C. gymnocaulos
Eleocharis acuta
Muehlenbeckia florulenta
Paspalidium jubiflorum
Paspalum ?distichum
Phragmites australis
Phyla canescens
Pseudoraphis spinescens
0 10 20 30 40 50
Lock 6
Lock 5
PERENNIALS (con'd)
Schoenoplectus validus
Sporobolus mitchellii
Typha domingensis
Vallisneria americana
ANNUALS
Centipeda ?cunninghamii
Eclipta platyglossa
Epaltes austalis
Glinus lotoides
Pseudognaphalium luteo-album
Stemodia florulenta
Xanthium ?occidentale
0 10 20 30 40 50
Lock 6
Lock 5
River distance downstream of Lock 6 (km)

Figure 2.3. (a) SHS ordination of sites and (b) flexible UPGMA dendrogram based on the distribution and relative abundance of 16 perennial species. Sites labelled by distance downstream of Lock 6.

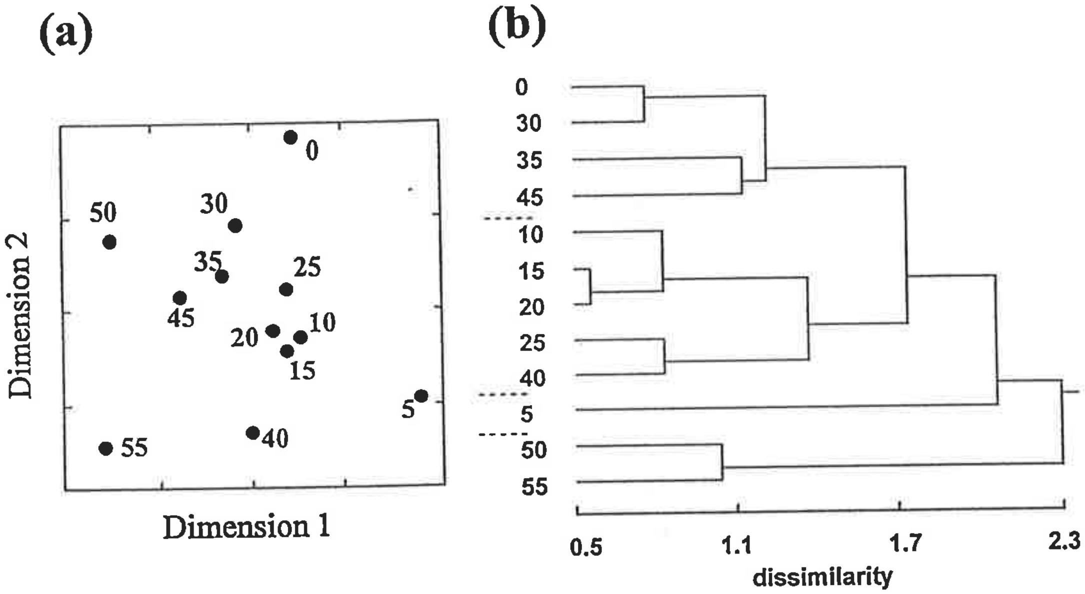

(a)
0
50
30
35
25
45
20
10
15
5
55
40
Dimension 2
Dimension 1
(b)
0
30
35
45
10
15
20
25
40
5
50
55
0.5
1.1
1.7
2.3
dissimilarity

Figure 2.4. Flexible UPGMA dendrogram of species based on relative abundance. Tentative life history strategies are indicated.

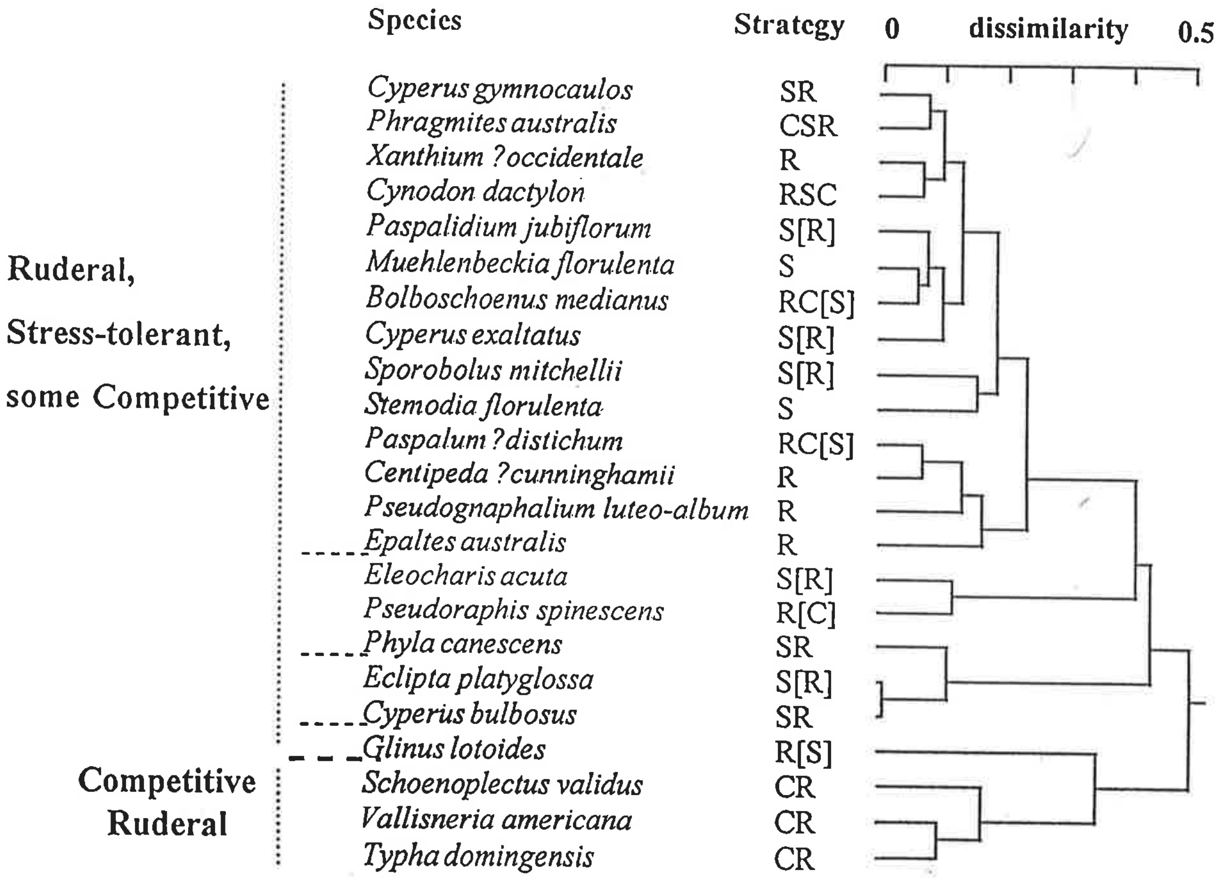
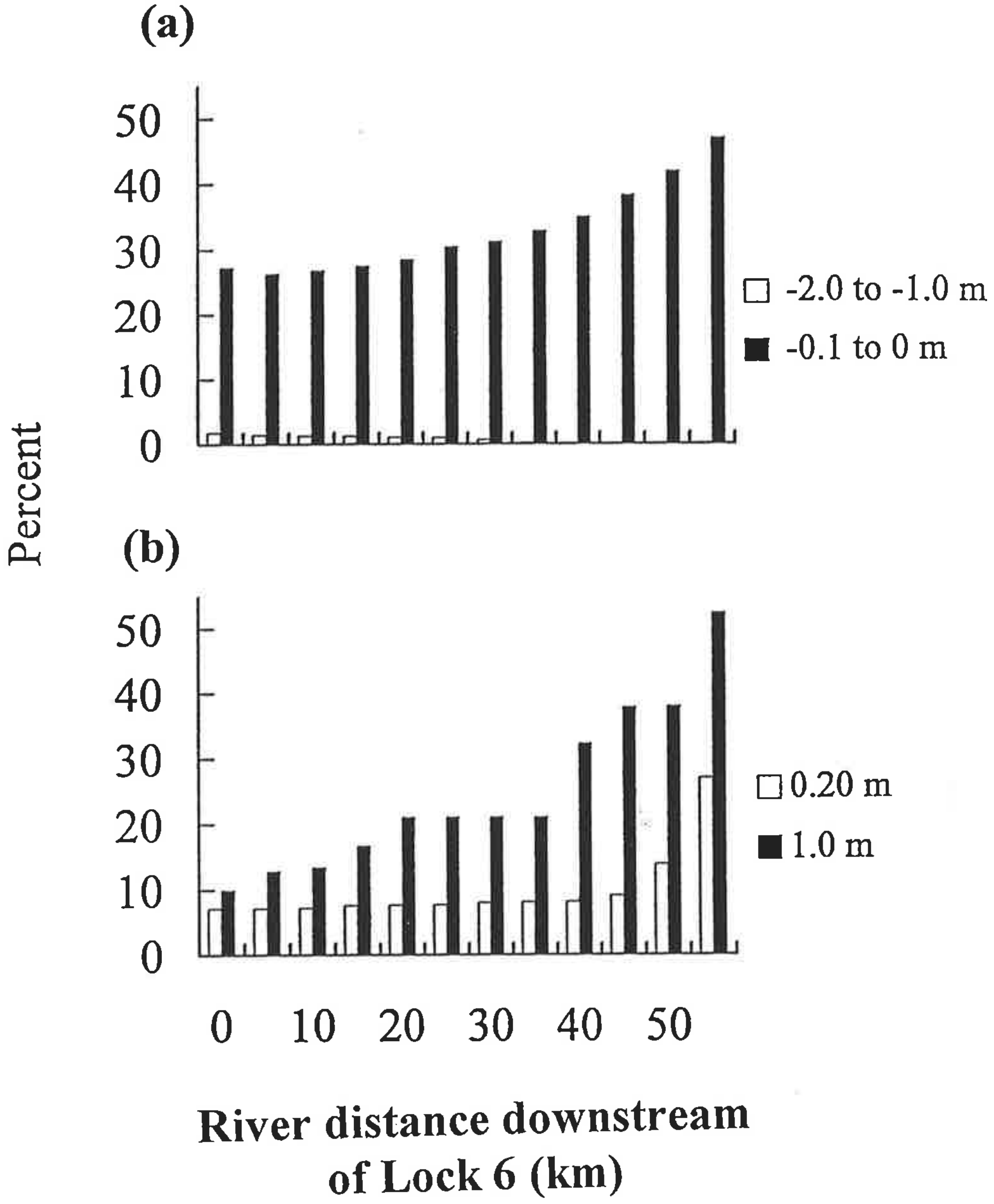

Species
Strategy
0
dissimilarity
0.5
Ruderal,
Stress-tolerant,
some Competitive
Competitive
Ruderal
Cyperus gymnocaulos SR
Phragmites australis CSR
Xanthium ?occidentale R
Cynodon dactylon RSC
Paspalidium jubiflorum S[R]
Muehlenbeckia florulenta S
Bolboschoenus medianus RC[S]
Cyperus exaltatus S[R]
Sporobolus mitchellii S[R]
Stemodia florulenta S
Paspalum ?distichum RC[S]
Centipeda ?cunninghamii R
Pseudognaphalium luteo-album R
Epaltes australis R
Eleocharis acuta S[R]
Pseudoraphis spinescens R[C]
Phyla canescens SR
Eclipta platyglossa S[R]
Cyperus bulbosus SR
Glinus lotoides R[S]
Schoenoplectus validus CR
Vallisneria americana CR
Typha domingensis CR

Figure 2.5. Histograms showing increased river level stability with distance downstream of Lock 6. a. Small (-0.1 to 0 m) and large (-2.0 to -1.0 m) percentage falls in level over seven days, b. Maximum continuous time in which levels remained within small (0.2 m) and large (1.0 m) elevation ranges, expressed as a percent of 6 years.


(a)
50
40
30
20
10
0
☐ -2.0 to -1.0 m
■ -0.1 to 0 m
Percent
(b)
50
40
30
20
10
0
☐ 0.20 m
■ 1.0 m
0
10
20
30
40
50
River distance downstream of Lock 6 (km)

Chapter 3

A characterisation of tolerance to flooding and exposure in littoral plants using indices of water regime

3.1 Abstract

Six quantitative indices of water regime were evaluated for describing the optimum and tolerance ranges to flooding and exposure in littoral and floodplain plants of the Lower River Murray, Australia. Plant cover/abundance was surveyed in transects across the littoral zone and adjacent floodplain at 12 sites along Pool 5. The number of days flooded to 0-20 and 20-60 cm, and days exposed to ≥100 cm were significantly correlated with mutlidimensional scaling axes for vegetation ($P<0.01$). Amongst the 26 perennials recorded, five species groups were suggested by clustering, reflecting broad water regimes and species abundance: common (*e.g. Paspalidium jubiflorum, Muehlenbeckia florulenta*) and uncommon floodplain species (*Eleocharis acuta, Pseudoraphis spinescens*), species from the infrequently (*Phyla canescens, Bolboschoenus caldwellii*) and permanently flooded littoral (*Vallisneria americana, Typha domingensis*), and widespread, common species broadly tolerant of flooding and exposure (eleven species, including *Phragmites australis, Cyperus gymnocaulos* and *Bolboschoenus medianus*). Half of the species occurred in four or more of seven water regime groups suggested by clustering of sites based on the indices, suggesting selection for adaptations to a variable hydrologic regime. In contrast, 4 species occurred only in the stable lower pool. Increasing the frequency of floodplain inundation is likely to increase vegetation diversity in the Lower Murray as the majority of species prefer variable water regimes. For all species recorded, optimum and tolerance ranges to water regime are indicated using minimum, maximum and quartile values for each index. A simple model of similarity between species and affinity for flooding and exposure is presented, based on a minimum spanning tree diagram.

3.2 Introduction

The primary role of water regime in structuring littoral and floodplain vegetation in semi-arid regions (Mitchell and Rogers, 1985) offers ecologists considerable scope for developing predictive models of vegetation in these ecosystems (Poiani and Johnson, 1993; Stromberg, 1993; Rea and Ganf, 1994b). Our understanding of the effects of flooding on plants is growing rapidly (Furness and Breen, 1980; Rogers and Breen, 1980; Briggs and Maher, 1985; Mitchell and Rogers, 1985; Brock, 1988, 1991; Brock and Casanova, 1991; Wilcox and Meeker, 1991; Froend *et al.*, 1993; Britton and Brock, 1994; Froend and McComb, 1994; Rea and Ganf, 1994a,b,c; Chambers *et al.*, 1995; Nielsen and Chick, 1997; Blanch and Walker, in press), but descriptions of water regime are often subjective (*e.g.* Mountford and Chapman, 1993), making comparisons between wetlands and species difficult.

A potentially useful framework for characterising water regime involves dissecting the hydrograph into quantifiable components known to influence plant growth. These descriptors or *indices* of water regime may pertain to optimal or stressful conditions. For example, shallow water (<10 cm) promotes biomass production in many emergents (Grace, 1989; Squires and van der Vaalk, 1992; Neill, 1993), whilst exposure reduces soil moisture and lowers recruitment (Neill, 1990; Kirkman and Sharitz, 1993). The abundance of a species in the littoral may then be interpreted in terms of the frequency with which such conditions occur. In this thesis 'exposure' refers to the absence of surface water, rather than erosion and damage caused by waves (*e.g.* Day *et al.*, 1988; Shipley *et al.*, 1991).

This chapter develops water regime indices to interpret the distribution and abundance of littoral plants in the Lower Murray. Rather than attempting to determine the range and optimum water regimes of all common littoral species, I characterise water regimes in Pool 5 and examine the utility of this approach in interpreting vegetation patterns. The study extends those of Briggs (1981), Hughes and James (1989), Brownlow *et al.* (1994) and Walker *et al.* (1994, 1995), and complements the correlation of vegetation patterns with distance below weirs (cf. Chapter 2). Briggs developed a simple quantitative description of the water regime requirments of Australian wetland plant communities, using broad depth ranges and flooding frequencies. Walker *et al.* (1995) discuss the 'anatomy' of the stage hydrograph of a dryland river, and attribute ecological significance to components such as the return time of flooding and the slope of the rising limb. Brownlow *et al.* (1994) distinguished water regime groups by clustering sites based on the time inundated within 5 cm depth classes in a seasonally predictable, fluctuating wetland (Bool Lagoon, South Australia). A similar approach was used here, with depth classes chosen to reflect plant growth forms, the processes structuring littoral vegetation, and physiological stresses.

3.3 Methods

3.3.1 Survey methods

The vertical distribution of perennial littoral plants was surveyed at 12 sites (cf. Chapter 2) in Pool 5 from 21-24 January 1994. Vegetation was scored using a semi-quantitative scale incorporating estimates of abundance and cover (Table 3.1) in three 5 m-wide transects per site. Transects were selected randomly within a 100-m wide section of river bank, perpendicular to the river. Within each transect, the vertical distribution of plants was scored within quadrats equivalent to a change in height of 20-100 cm, measured vertically above and below the water level using a dumpy level and staff (Plate 3.1). Twenty-centimetre high quadrats were used below the surface and within the first 150 cm above the surface, and thereafter 50 and 100 cm high quadrats at higher elevations. This reflected the more rapid change in vegetation zonation close to pool level. Heights of quadrats were independent of horizontal distance. Transects extended from 1 m below the surface to the top of the bank, and included 10 m of floodplain adjacent to the littoral. For each site, scores for each species were averaged across the transects within quadrats of the same elevation. River-bend attributes are the same as for the longitudinal study (cf. Chapter 2).

3.3.2 Analyses

Cover/abundance data were analysed using Semi-strong Hybrid multidimensional Scaling with varimax rotation (SHS: Belbin, 1991; 1993). An association measure derived from the standard Bray and Curtis measure was used, one particularly applicable to determining associations between species rather than sites (Two-Step; Belbin, 1993). The Two-Step association corrects for the frequency bias in classification caused by many metrics, whereby species with similar frequency distributions are grouped together regardless of

Table 3.1. Hybrid cover/abundance scale used for surveying littoral and floodplain plants. Full species names are given in Fig. 3.2.

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

their distribution between sites. A high frequency of large associations was corrected using ordinal scaling for association values in the second 'hump' of the frequency histogram of association measures (Belbin, 1993). Flexible UPGMA clustering suggested groupings of sites and species (ß =-0.1) (Belbin, 1993; Belbin and McDonald, 1993). Only quadrats in which two or more species were recorded were used for determining associations between 'sites' (*i.e.* quadrats; *n*=83). Data for all quadrats were used for determining relationships between species (101 quadrats).

Similarity between species was also examined using network analyses, principally bond-strength and Minimum Spanning Tree (MST) techniques (Belbin, 1993). Both determine the similarity between species from association values. Bond-strength analysis determines the degree of 'neighbourliness' between species as follows. Two species which are mutual nearest-neighbours (lowest pair-wise association value for each) are assigned a 'first-first' neighbour bond. A first-second bond reflects lower similarity (higher association): species A is species B's nearest neighbour, but species B is only species A's second-nearest neighbour. A second-second bond indicates lower similarity, and so on. The level of bond-strength is shown by lines of differing thickness connecting species on an ordination plot.

MST analysis provides a complementary approach whereby a 'tree' of species is constructed in which lines connecting species represent the value of pair-wise associations, with the network having the minimum possible length. Line length is proportional to association value, with short lines indicating high similarity.

3.3.3 Water regime indices

For each elevation range (*i.e.* across the three replicate quadrats) per site, the pattern of flooding and drying was described using 6 quantitative indices of water regime (Table 3.2). A Microsoft QBASIC program was constructed to determine values for indices from the stage hydrograph for each site for the two years prior to the survey (Fig. 3.1; 26 January 1992-24 January 1994). Hydrograph data were obtained from SA Water, Adelaide, and daily water levels at intermediate sites determined by linear interpolation. Indices were determined for the base of each quadrat.

Spearman rank correlations, r_s, indicated which indices were significantly correlated with SHS ordination scores for species. Values of α were corrected for multiple comparisons using a Bonferroni adjustment (Day and Quinn, 1989). Sites were grouped using UPGMA clustering based on values of water regime indices for each quadrat.

3.4 Results

3.4.1 Vegetation patterns

Broad patterns of tolerance to flooding and exposure are shown in the species ordination, although species which are common and widespread are not well distinguished (Fig. 3.2). Axes 1 and 3 explained three quarters of the variance, with a further 10% loaded on axis 2. Axis 1 is correlated with distance along the pool, elevation above pool level, position

Table 3.2. Water regime indices.

Quantitative index of water regime	Ecological relevance to vegetation
Days flooded ≥0 cm†	Wetting and drying influences oxygen concentrations and redox potentials in littoral and floodplain sediments, decomposition of organic matter, sediment deposition, and dispersal and germination of regenerative propagules. Conversely, exposure kills desiccation-intolerant species and limits soil moisture availability.
Days flooded 0-20 cm	Growth and recruitment in many emergent macrophytes is highest in shallow water, as the availability of both water and atmospheric gases is optimal (cf. Chapter 5). Light availability is high for mudmat and short submersed species, though wave action may be strong.
Days flooded 20-60 cm	This is an optimal depth for most submersed and semi-emergent species in the turbid Lower Murray. Plants are largely protected from wave action yet receive sufficient light for photosynthesis (cf. Chapters 7-10). However, all except the tallest emergents generally show reduced growth in this depth range (Chapters 5 and 6).
Days flooded ≥200 cm	Most emergents are top-flooded at this depth, preventing access to atmospheric gases. Submersed species can become light-limited, particularly when flooded with highly-turbid floodwaters (Chapter 7).
Days exposed ≥100 cm	Desiccation kills submersed species, and low soil moisture limits stomatal conductance and thus recruitment in emergents (Chapters 5 and 6). Seedlings are particularly prone to water stress. Observations suggest roots do not extend to 1 m in many littoral and floodplain species.
Longest exposure (days)	Germination and establishment of many littoral plants is influenced by the length of exposure and soil moisture stress. In addition, obligate submersed or semi-emergent species tolerate only short periods of exposure.

† Flooded to any depth, including 0-20 cm, 20-60 cm and ≥200 cm.

on bend and bend shape, and a range of water regime indices (Table 3.3). The highest correlations were with distance and elevation (r_s=0.61 and -0.48, respectively). Exposure by ≥100 cm and flooding to 0-20 cm and, to a lesser extent, 20-60 cm were significantly correlated with SHS scores, although values of r_s were <0.48 ($P<0.05$ to $P<0.001$). By incorporating the vertical distribution of species along Pool 5, as opposed to solely longitudinal distribution patterns examined Chapter 2, r_s declined from 0.937 to 0.61 for distance downstream (cf. Tables 2.2 and 3.3). Similar correlations were determined for the longitudinal distribution of species in Pools 2 and 3 in 1988 (surveyed by Walker *et al.*, 1994). The positive correlation between distance and bend shape reflect decreasing channel sinuosity in reaches in the mid and lower pool.

To varying degrees, all six water regime indices were significantly correlated with distance along the pool and/or elevation ($P<0.05$ to $P<0.001$). The biological significance of these correlations must be interpreted with caution due to the linearity of gradients of water regime along the pool (when based on linear interpolation). By way of illustration, the number of days flooded from 73-75 cm, arguably of little biological relevance for most species, was correlated with SHS axes, and found to explain 60% of the variance on axis 1 ($P<0.001$, but $P>0.05$ for axes 2 and 3, data not shown).

Juncus, Typha and *Schoenoplectus* occur within 10 km of Lock 5 (Fig. 2.2), and are found on the left of axis 1. Species with broad tolerances to water regime form a loose group at associations of -0.25 to 0.25 (*e.g. Phragmites*, *Cyperus gymnocaulos* and *Bolboschoenus medianus*), whilst species on the right occurred high on the floodplain 5 km below Lock 6 (*Eleocharis, Pseudoraphis*).

Axis 3 is correlated positively with the frequency of shallow flooding and negatively with exposure to ≥100 cm (r_s=0.42 and -0.39, respectively). *Typha* and *Vallisneria* (high, positive scores) are intolerant of exposure, whilst species at large negative scores occur high on the bank where exposure is common and shallow flooding infrequent. Deep submersion apparently influences vegetation structure less than shallow flooding and exposure, with flooding to ≥200 cm weakly correlated with axis 2 ($r_s = -0.35$, $P<0.05$; Table 3.3). Vegetation patterns were not correlated with the number of days flooded to any depth (≥0 cm), nor the longest period of exposure ($P>0.05$ for all axes).

Cluster analysis suggested five principal species groups (Figs 3.2 and 3.3), corresponding to broad water regime patterns. Species inhabiting infrequently flooded elevations (*Bolboschoenus caldwellii*, *Cyperus bulbosus, Brachycome* and *Phyla*) separated at a high dissimilarity (0.41), followed by eighteen species found from shallow, permanently flooded areas to sites high on the bank (reading downwards: *Centipeda* to *Pseudoraphis*). The eighteen species form three groups. *Eleocharis* and *Pseudoraphis* were recorded infrequently but were locally abundant in high-floodplain areas where flooding was infrequent but where floodwaters appeared to pond after recession. This concurs with observations of these species in more frequently flooded areas in the Lower Murray, and in low-floodplain sites in the mid-Murray (e.g. Barmah-Millewa forest, Echuca). The second group consists of common floodplain species, such as the drought-tolerant shrub

Table 3.3. Spearman rank correlations between scores for vegetation on the first three SHS axes and water regime indices and physical characteristics of the river. Significance levels between SHS scores and correlates are as follows: *P*<0.001, ***; *P*<0.01, **; *P*<0.05, * (following Bonferroni adjustment for multiple comparisons) (*n*=101).

Axis 1	**1.00**												
Axis 2	**0.14**	**1.00**											
Axis 3	**0.07**	**0.12**	**1.00**										
Distance downstream of Lock 6	__0.61***__	**0.25**	**0.07**	1.00									
Elevation above pool level	__-0.48***__	**0.02**	**-0.26**	-0.51	1.00								
Number of days flooded to ≥ 0 cm	**0.07**	**-0.24**	**0.06**	-0.03	-0.75	1.00							
0-20 cm	__0.37**__	**-0.09**	__0.42***__	0.24	-0.47	0.35	1.00						
20-60 cm	__0.32*__	**-0.01**	**0.06**	0.32	-0.66	0.67	0.24	1.00					
≥ 200 cm	**-0.28**	__-0.35*__	**0.26**	-0.58	-0.22	0.56	0.06	0.14	1.00				
Number of days exposed to ≥ 100 cm	__-0.43***__	**0.17**	__-0.39**__	-0.38	0.89	-0.68	-0.46	-0.58	-0.34	1.00			
Longest period exposed	**-0.07**	**0.25**	**-0.07**	0.02	0.76	-0.99	-0.35	-0.67	-0.56	0.69	1.00		
Position on bend	__0.36**__	**0.11**	**0.11**	0.60	-0.19	-0.14	0.19	0.14	-0.37	-0.14	0.14	1.00	
Bend shape	__-0.46***__	**-0.19**	**-0.04**	-0.47	0.11	0.25	-0.10	-0.05	0.43	0.01	-0.24	-0.44	1.00

Muehlenbeckia and prostrate grass *Sporobolus*, whilst the third group includes widespread, abundant species with varying but wide tolerances to flooding and exposure (*e.g. Phragmites*, *Cyperus gymnocaulos* and *Bolboshoenus medianus*). The latter group contained the most species (11).

The remaining group includes aquatic species and those requiring high soil moisture (*Vallisneria*, *Typha*, *Juncus* and *Schoenoplectus*; Plate 3.1). *Juncus* was recorded only once in Pool 5 (indicated by low similarity to the other three), but as it was frequently observed in similar areas in other pools (in stable water levels, close to the river's edge), the datum was included. *Vallisneria* occurred in stable water-level reaches from depths 10-80 cm where exposure was very infrequent and light availability high.

The groups broadly agree with those suggested from ordination (Fig. 3.2, axes 1 and 3), though the latter suggest groupings are less distinct than those determined by clustering (particularly for widespread, abundant species).

Network analysis confirms the importance of water regime and species tolerances to flooding in structuring vegetation. Six first-first neighbour bonds were determined by bond-strength analysis (Fig. 3.3, axes 1 and 2). The six pairs of nearest neighbours fall within the 5 cluster groups (with the neighbours *Paspalum-Cyperus exaltatus* and *Cynodon-Cyperus gymnocaulos* falling within the 'widespread, tolerant' group (cf. Fig. 3.3)). Of the aquatic species, *Vallisneria* and *Typha* are most similar, whilst *Schoenoplectus* is more similar to *Vallisneria* than to *Typha* (first-second and second-second neighbours, respectively). Similarly, *Brachycome* and *Bolboschoenus caldwellii* are most similar amongst the species restricted to infrequently flooded areas, with *Phyla* more similar to *B. caldwellii* than to *Brachycome*. The large number of second-second and first-third bonds between both *Phragmites* and *Cyperus gymnocaulos* and other species reflects their broad tolerances of flooding and drying. This is also shown by MST analysis, in which both have five linkages, one being mutual (Fig. 3.4). Species recorded in at least 25% of sites are placed centrally in the network, with a general gradient of increasing flooding frequency oriented right and downwards. Species occupying infrequently flooded areas occur on the left, and obligate hydrophytes on the lower right. Fig. 3.4 is a summary model of species relationships, and broadly relates species frequencies and water regime tolerances.

3.4.3 Classification of water regime

Clustering of sites based on the six indices of water regime (Table 3.2) suggest seven water regime groups (Table 3.4). Flooding frequency decreases from group A-G: 730 days in A to 22 in G. Conversely, the median longest period of exposure increases from 0 to 660 days from group A-G. The increase or decrease in other indices between groups A and G also reflect longitudinal and vertical water regime gradients along Pool 5. Group A occurred at sites permanently or nearly permanently flooded with relatively stable water-levels, and depths optimal for aquatic species such as *Vallisneria* and *Typha*. The longest exposure was for 62 days in 2 y, and the frequency of flooding to depths 20-60 cm in the range 0-585 days in 2 y. This is demonstrated by mapping the 7 groups across quadrats along the pool (Fig. 3.5). Groups form 'bands' corresponding to the decreasing amplitude of the stage hydrograph down the pool. The significance of the weir at Lock 5 in controlling water regime, and thereby vegetation composition and distribution, is clearly shown. Group A occurs close to or below pool level, and mainly within 30 km of Lock 5. Group B is restricted to 10-40 cm above pool level, and did not occur within 10 km of Lock 5. Bands of sites experiencing regimes groups C and E were 0-120 cm high in the upper pool, declining to c. 10-50 cm in the lower pool. Groups A and E abutt at Lock 5, whereas they are 2 m apart at Lock 6. This reflects the much greater variability in stage in the tailwater of Lock 6, and the much smaller flood amplitude at Lock 5 (Fig. 3.1).

By plotting mean cover/abundance scores for species across water regime groups A-G, a profile of the range and optimum water regimes can be determined (Fig. 3.6). Fifty percent of species occurred in 4 or more of the 7 groups, suggesting adaptations permitting growth under a broad range of water regimes are common in littoral and floodplain plants of the Lower Murray. Species characterised as widespread and broadly tolerant of water regime in the cluster and MST analyses occur across most regime groups. For example, *Cyperus gymnocaulos* had mean scores of 2-3.5 across all groups, confirming the broad tolerances to flooding and exposure indicated by network analyses (Figs 3.1 and 3.5). No regime appears to be particularly favourable or detrimental for this species, and this concurs with its ubiquity throughout the Murray's littoral. *Phragmites* occurred in all regimes, but with an optimum in groups B and C where the median flooding frequency (to ≥ 0cm) was 499 and 351 days in 2 y, respectively. Exposure to ≥ 100 cm was zero or infrequent (maximum of 236 days in B). *Bolboschoenus medianus* occurred in groups A-F, with no obvious

Table 3.4. Seven water regime groups determined from cluster analysis based on water regime indices for each quadrat (*i.e.* from the matrix of site x water regime indices). Groups A-G are in order of decreasing flooding frequency. Values are numbers of days in two years (maximum of 730 days: 26 January 1992-24 January 1994) flooded or exposed to within specified elevation ranges. Minimum, median and maximum values are indicated for each index.

Water regime index	A			B			C			D			E			F			G		
	min	median	max	min	median	max	min	median	max	min	median	max	min	median	max	min	median	max	min	median	max
Days flooded ≥0 cm	513	730	730	491	499	512	259	351	458	209	286	306	88	163	247	62	85	105	0	22	33
Days flooded 0-20 cm	0	163	552	33	52	136	14	48	110	11	45	76	12	29	45	19	25	33	0	14	22
Days flooded 20-60 cm	0	189	585	73	125	163	23	68	142	35	61	75	28	58	66	30	51	57	0	0	19
Days flooded ≥200 cm	0	0	252	0	110	218	0	38	207	0	0	88	0	0	0	0	0	0	0	0	0
Days exposed ≥100 cm	0	0	0	0	0	0	0	0	236	0	234	312	0	289	448	195	446	519	47	567	592
Longest exposure (days)	0	0	62	122	125	125	220	236	246	238	245	269	260	290	314	311	313	319	657	660	730

optimum. Conversely, *Paspalum* was most abundant in frequently flooded sites (group A: flooded 0-20 cm for a median of 163 days in 2 y), but did occur in areas shallowly flooded only 11-45 days in 2 y (groups D and E). The four species occupying essentially permanently flooded areas (cf. Fig. 3.3) occurred only in regime group A. Although the maximum period of continuous exposure in A was 62 days, the zero median value indicates a highly right-skewed frequency distribution of data which indicates the site exposed for 62 days is atypical of the group. Species at 'infrequently flooded' sites (Fig. 3.3) had optimum cover/abundance in regime group F.

Differences between the distribution of submersed macrophytes in Pool 5 and in Pools 2 and 3 in February 1988 (Walker *et al.*, 1994) indicate that regular deep flooding significantly restricts colonisation of mid and upper reaches in these species. Flood amplitudes were considerably lower in the 3 y prior to the 1988 survey (1-2.5 m downstream and <0.2 m upstream of Lock 3) than in the 2 y preceding the present study (3.8-4.2 m below Lock 6 and 0.9-1.2 m above Lock 5; Fig. 3.1). Hence, in 1988 *Vallisneria americana* (named *V. spiralis* in the earlier study), *Potamogeton crispus* and *P. tricarinatus* extended along most of Pools 2 and 3. Prolonged, deep flooding prior to the Pool 5 survey limited the distribution of *Vallisneria* considerably, and no other submersed species were recorded. Distribution patterns for *Cyperus gymnocaulos* and *Phragmites* were similar for both studies, however, confirming their broad tolerances to water regime.

The apparent water regime 'preferences' in Fig. 3.6 are based solely upon cover/abundance scores, and do not convey any information regarding the frequency of species *within* regime groups. Hence, *Eleocharis* was locally abundant in regime group E, but was recorded in only two quadrats (mean cover/abundance of 2.3). *Bolboschoenus medianus* was widespread, occurring in 6 of the 7 groups, but was less abundant (mean; 1-1.5). As the water regime indices were determined for the base of the vertically-oriented quadrats (*i.e.* flooding patterns determined at 0 cm in quadrats 20, 50 and 100 cm high), water regime preferences are 'drier' than indicated by Fig. 3.6, though the extent of the right-shift is probably small.

Details of the range and optimum values for the six water regime indices are presented for each species in Table 3.5. The data can be used to estimate the relative performance of a

Table 3.5. A characterisation of the water regimes supporting common macrophytes of the Lower Murray. Species recorded at four or more sites in Pool 5 are shown. Numbers refer to the number of days in two years (730 days: 26 January 1992-24 January 1994) in which the water level was within (or above or below) a specified elevation range. The range and distribution of values are indicated by minimum and maximum values, and quartiles. Reliability is proportional to the number of records per species (indicated in brackets)

Species		Quartile			
	min	25%	50%	75%	max
Bolboschoenus caldwellii (4)					
Days flooded ≥ 0 cm	85	87	110	140	163
Days flooded 0-20 cm	22	23	23	27	40
Days flooded 20-60 cm	51	56	58	60	66
Days flooded ≥ 200 cm	0	0	0	0	0
Days exposed ≥ 100 cm	436	442	457	481	515
Longest exposure (days)	290	302	310	313	313
Bolboschoenus medianus (27)					
Days flooded ≥ 0 cm	79	163	304	432	730
Days flooded 0-20 cm	12	23	37	54	228
Days flooded 20-60 cm	26	56	64	87	189
Days flooded ≥ 200 cm	0	0	0	72	194
Days exposed ≥ 100 cm	0	0	0	406	515
Longest exposure (days)	0	226	238	290	315
Centipeda cunninghamii (30)					
Days flooded ≥ 0 cm	62	175	304	365	496
Days flooded 0-20 cm	11	20	29	44	95
Days flooded 20-60 cm	23	40	58	67	101
Days flooded ≥ 200 cm	0	0	13	116	207
Days exposed ≥ 100 cm	0	0	87	262	519
Longest exposure (days)	125	235	238	280	319
Cynodon dactylon (35)					
Days flooded ≥ 0 cm	62	171	240	304	535
Days flooded 0-20 cm	10	21	31	49	276
Days flooded 20-60 cm	26	52	61	67	136
Days flooded ≥ 200 cm	0	0	0	7	88
Days exposed ≥ 100 cm	0	0	219	327	519
Longest exposure (days)	41	238	260	285	319
Cyperus exaltatus (20)					
Days flooded ≥ 0 cm	22	273	332	399	700
Days flooded 0-20 cm	10	20	30	53	552
Days flooded 20-60 cm	0	37	51	64	171
Days flooded ≥ 200 cm	0	0	62	105	197
Days exposed ≥ 100 cm	0	0	81	245	567
Longest exposure (days)	9	232	236	250	660
Cyperus gymnocaulos (61)					
Days flooded ≥ 0 cm	0	162	297	392	691
Days flooded 0-20 cm	0	24	35	55	276
Days flooded 20-60 cm	0	51	61	75	171
Days flooded ≥ 200 cm	0	0	0	71	252
Days exposed ≥ 100 cm	0	0	20	286	592
Longest exposure (days)	14	233	239	290	730

Table 3.5 continued

Species			Quartile		
	min	25%	50%	75%	max
Glycyrrhiza acanthocarpa (10)					
Days flooded ≥ 0 cm	202	252	318	435	512
Days flooded 0-20 cm	10	28	39	53	136
Days flooded 20-60 cm	29	49	63	81	163
Days flooded ≥ 200 cm	0	0	10	62	132
Days exposed ≥ 100 cm	0	0	32	267	401
Longest exposure (days)	122	225	237	259	272
Muehlenbeckia florulenta (8)					
Days flooded ≥ 0 cm	22	92	148	228	331
Days flooded 0-20 cm	12	18	23	27	40
Days flooded 20-60 cm	0	49	55	64	71
Days flooded ≥ 200 cm	0	0	0	7	34
Days exposed ≥ 100 cm	0	334	429	454	567
Longest exposure (days)	236	264	298	312	660
Paspalidium jubiflorum (30)					
Days flooded ≥ 0 cm	0	140	207	275	354
Days flooded 0-20 cm	0	18	24	33	70
Days flooded 20-60 cm	0	45	55	64	78
Days flooded ≥ 200 cm	0	0	0	0	156
Days exposed ≥ 100 cm	1	242	347	442	592
Longest exposure (days)	235	246	270	306	730
Paspalum distichum (32)					
Days flooded ≥ 0 cm	163	299	343	440	513
Days flooded 0-20 cm	11	21	35	58	189
Days flooded 20-60 cm	23	50	65	83	171
Days flooded ≥ 200 cm	0	0	40	105	218
Days exposed ≥ 100 cm	0	0	0	235	448
Longest exposure (days)	62	227	236	244	290
Phragmites australis (68)					
Days flooded ≥ 0 cm	33	163	301	452	730
Days flooded 0-20 cm	0	23	44	74	552
Days flooded 20-60 cm	19	55	66	105	471
Days flooded ≥ 200 cm	0	0	0	31	163
Days exposed ≥ 100 cm	0	0	0	221	519
Longest exposure (days)	0	222	239	290	657
Phyla canescens (5)					
Days flooded ≥ 0 cm	87	132	142	162	164
Days flooded 0-20 cm	19	22	23	37	40
Days flooded 20-60 cm	51	51	58	63	66
Days flooded ≥ 200 cm	0	0	0	0	0
Days exposed ≥ 100 cm	228	312	398	444	470
Longest exposure (days)	283	290	304	306	313
Pratia concolor (4)					
Days flooded ≥ 0 cm	0	47	75	106	162
Days flooded 0-20 cm	0	14	21	25	31
Days flooded 20-60 cm	0	23	41	55	66
Days flooded ≥ 200 cm	0	0	0	0	0
Days exposed ≥ 100 cm	398	452	495	537	592
Longest exposure (days)	290	307	316	422	730

Table 3.5 continued

Species		Quartile			
	min	25%	50%	75%	max
Rumex bidens (10)					
Days flooded $\geq$ 0 cm	94	128	204	481	700
Days flooded 0-20 cm	19	28	61	109	552
Days flooded 20-60 cm	51	54	59	94	136
Days flooded $\geq$ 200 cm	0	0	0	0	26
Days exposed $\geq$ 100 cm	0	0	0	234	417
Longest exposure (days)	9	151	270	308	312
Schoenoplectus validus (10)					
Days flooded $\geq$ 0 cm	513	707	730	730	730
Days flooded 0-20 cm	0	0	176	212	552
Days flooded 20-60 cm	62	166	335	442	585
Days flooded $\geq$ 200 cm	0	0	0	0	22
Days exposed $\geq$ 100 cm	0	0	0	0	0
Longest exposure (days)	0	0	0	7	62
Senecio cunninghamii (10)					
Days flooded $\geq$ 0 cm	22	97	135	150	513
Days flooded 0-20 cm	17	21	25	39	189
Days flooded 20-60 cm	0	51	55	62	171
Days flooded $\geq$ 200 cm	0	0	0	0	0
Days exposed $\geq$ 100 cm	0	55	333	437	567
Longest exposure (days)	62	300	307	312	660
Sporobolus mitchellii (14)					
Days flooded $\geq$ 0 cm	62	90	205	299	370
Days flooded 0-20 cm	11	19	23	32	55
Days flooded 20-60 cm	28	38	51	65	73
Days flooded $\geq$ 200 cm	0	0	0	24	156
Days exposed $\geq$ 100 cm	0	167	299	369	519
Longest exposure (days)	234	244	271	313	319
Stemodia florulenta (11)					
Days flooded $\geq$ 0 cm	0	75	162	280	370
Days flooded 0-20 cm	0	21	23	39	55
Days flooded 20-60 cm	0	40	55	66	85
Days flooded $\geq$ 200 cm	0	0	0	0	32
Days exposed $\geq$ 100 cm	0	132	398	495	592
Longest exposure (days)	234	246	290	316	730
Typha domingensis (4)					
Days flooded $\geq$ 0 cm	700	723	730	730	730
Days flooded 0-20 cm	0	0	98	284	552
Days flooded 20-60 cm	62	162	291	407	471
Days flooded $\geq$ 200 cm	0	0	0	5	19
Days exposed $\geq$ 100 cm	0	0	0	0	0
Longest exposure (days)	0	0	0	2	9
Vallisneria americana (6)					
Days flooded $\geq$ 0 cm	730	730	730	730	730
Days flooded 0-20 cm	0	0	0	1	195
Days flooded 20-60 cm	0	172	291	450	585
Days flooded $\geq$ 200 cm	0	0	0	14	33
Days exposed $\geq$ 100 cm	0	0	0	0	0
Longest exposure (days)	0	0	0	0	0

species given a water regime defined using the indices. For example, *Paspalidium* is unlikely to survive in areas flooded for more than 354 days in a 2 y period (*i.e.* 50% of the time), and seems to require a continuous period of exposure of at least 235 days. In contrast to Fig. 3.6, Table 3.5 is based on presence/absence data, with the distribution of plants along gradients of flooding and exposure indicated by quartiles. Thus, *Schoenoplectus* plants appear able to tolerate exposure for up to 217 days in 2 y (730-513 days), but values of 730 days for both the 50% quartile and maximum indicate that it occurs more frequently in permanently flooded areas. For most species, however, there appears to be little skew. *Phragmites* appears to require at least 33 days flooding (to any depth) in 2 y. The 50% quartile value of 301 days is lower than that experienced in regime groups B and C, in which mean cover/abundance is greatest (491 and 351 days, Fig. 3.6 and Table 3.5). *Vallisneria* only occurred in permanently flooded areas and where submersion to 2 m or more was infrequent (33 days in 2 y), and had an optimum depth of 20-60 cm (cf. Chapter 10).

3.5 Discussion

Plants inhabiting the margins of rivers and wetlands in semi-arid regions must tolerate cycles of flooding and exposure/low soil moisture that often operate on aseasonal and often unpredictable spatial and temporal scales (Braune, 1985; Mitchell and Rogers, 1985; Brock, 1991; Walker *et al.*, 1995, 1997). These influences have selected for phenotypes exhibiting a range of ruderal and stress-tolerant traits (Grime, 1979; van der Vaalk, 1981; Rørslett, 1989; Blanch and Walker, in press), which permit many species to occupy positions across most or all of the aquatic-terrestrial ecotone. This represents the species' fundamental niche (Palmer and Dixon, 1990), with the realised niche being a part of this, determined by the presence of favourable water depths/soil moisture. Growth and recruitment are rapid at such times, but much slower in unfavourable water regimes (Furness and Breen, 1980).

This chapter uses quantitative indices of water regime to estimate the flooding and exposure conditions conducive to growth in a range of littoral species. Clustering of sites based on six water regime indices suggested seven water regime groups (Fig. 3.3), forming 'bands' along the weir pool (Fig. 3.5). Multivariate techniques suggested five principal species groups (Figs 3.2 and 3.3), corresponding to broad water regimes at different distances downstream of Lock 6 and elevations above pool level.

Approximately half of the 26 perennial species formed more or less distinct groups in ordination space (Fig. 3.2). These include those restricted to reaches with stable water levels (*e.g. Vallisneria*, *Typha*; Chapter 2), common and uncommon floodplain species (*e.g. Paspalidium*, *Muehlenbeckia* and *Eleocharis*), and species occurring in infrequently flooded areas of the littoral zone and floodplain (*e.g. Brachycome, Phyla*). The remainder are widespread and mostly abundant, appearing to tolerate a broad range of water regimes (Fig. 3.6). These were found in at least 4 of the 7 water regime groups determined from clustering of sites based on the indices of water regime. They exhibit an array of adaptations to variable hydrological conditions, including desiccation-tolerant tubers (*e.g. Bolboschoenus medianus*), rapid clonal growth (*Cynodon*), colonisation by fragments (*Paspalum*), long stems (*Phragmites*), and high seed production (*Centipeda*).

Phragmites and *Cyperus gymnocaulos* were the most widespread and abundant species, occurring from the permanently flooded littoral to high on the floodplain (groups A-G; Fig. 3.6). *Phragmites* appears able to survive with only 33 days of flooding in 2 y, whilst *C. gymnocaulos* survived without flooding over this period (Table 3.5). However, these plants, as indeed may have all species in the survey to some extent, may have accessed soil moisture derived from seepage from the river.

Whereas sites are assumed independent in multivariate analyses (Ludwig and Reynolds, 1988), the water regimes at all sites within a pool are to some extent related. This is implicit in Fig. 3.5, which shows that water regime is a function of river distance and elevation (see correlations in Table 3.3). This reflects the continuum in flooding patterns along longitudinal and vertical axes in the pool. Where change is gradual rather than stepped, ordination is a more appropriate technique for investigating similarities between objects (Austin, 1985). However, groups may then be difficult to distinguish (Brownlow *et al.*, 1994). Clustering provides an alternative approach, though the 'naturalness' of groups is uncertain (Belbin, 1991).

The minimum spanning tree diagram is a useful model for examining species relationships and broad trends in tolerance to water regime (Fig. 3.4). Together with bond-strength analysis, clustering and ordination, it indicates which species are likely to have similar distribution and abundance patterns with respect to water regime. Such similarities and groupings may prove useful in selecting species for wetland management programs.

Several water regime indices were significantly correlated with SHS axes, but explained less than half the variance in vegetation patterns. Biotic factors such as shading by riparian trees and *Phragmites*, and grazing, as well as soil moisture and sediment characteristics are also important. Ordination scores were not significantly correlated with the number of days flooded to ≥ 0 cm (P>0.05) (Table 3.3), but only with biologically more meaningful indices such as 0-20 cm and 20-60 cm. However, significant correlations between vegetation patterns and aspects of water regime of little importance (*e.g.* flooding to 73-75 cm, P<0.0001) indicates that these must be viewed with caution.

The data presented in Table 3.5 may be useful in floodplain and wetland management which incorporates water-level manipulations to stimulate vegetation development. Optimum water regimes should be determined from the 25%, 50% and 75% quartiles for each index.

Caution is required in applying data presented here, however, as they reflect specific environmental factors. For example, growth of *Bolboschoenus medianus* during and after one month's shallow flooding in late spring (median number of days flooded 0-20 cm equals 37, Table 3.5) will be much greater than during one month's flooding in winter (cf. Chapter 6). Other species surveyed show similar seasonal growth patterns (e.g. *Typha domingensis*, Dickerman and Wetzel, 1985; *Phragmites australis*, Hocking, 1989a,b; *Vallisneria americana*, Chapter 10).

Flow regulation in the Lower Murray has reduced the frequency of medium flows by 70% (30-80 GL/day; Jacobs, 1989; Walker and Thoms, 1993), causing a contraction in the area of vigorous floodplain vegetation (*e.g.* Bren, 1988). Species found in largely permanent backwaters and wetlands on the floodplain prior to regulation have colonised the main channel where the maintenance of a year-round base flow has provided ideal conditions (Walker *et al.*, 1994). Before locking, continually rising and falling river levels in the channel greatly restricted growth in such species. Vegetation changes since regulation reveal a spatial shift in plant diversity from the floodplain to the channel. For example, most species recorded in Pool 5 in the survey are broadly tolerant of flooding and drying, whereas only 4 occurred solely in areas with permanent water and a stable hydrologic regime (*Vallisneria*, *Typha*, *Juncus* and *Schoenoplectus*; Figs 3.5 and 3.6). On a broader scale, the estimated number of species requiring mostly continuous flooding or very frequent inundation in the Lower Murray is approximately 35-45 (Blanch, unpub. data). The number of exposure-tolerant species is roughly three times that. This ratio reflects selection for morphological and physiological adaptations and resource allocation strategies that permit tolerance to flooding and exposure (Mitchell and Rogers, 1985; Brock, 1991; Casanova, 1994). The implication is that manipulations of the rate, duration and timing of flooding and drying of the floodplain could be used to promote vegetation diversity by restoring a greater range of water regimes, thereby producing the hydrologic conditions amenable to the greatest number of species (Walker and Thoms, 1993; Stanford *et al.*, 1996; Nilsson and Brittain, 1996).

As plants respond rapidly to changing water levels, the timing of surveying may greatly influence vegetation-water regime relationships. The distribution of some species across water regimes are likely to become narrower with an increasing interval between flooding and surveying. A left-shift in species distributions in Fig. 3.6 is predicted as recruitment slows high on the littoral. The occurrence of submersed and semi-emergent species on the floodplain during and immediately after flooding is an extreme example. *Vallisneria*, *Potamogeton crispus* and *Myriophyllum papillosum* have been observed growing amongst floodplain species such as *Sporobolus mitchellii* and *Paspalidium jubiflorum* at such times. This contrasts with Fig. 3.6, which shows that one month after flooding, *Vallisneria* occurred only in the channel. The mode of reproduction in such instances my be by sexual or asexual propagules transported by floodwaters from channel populations or from floodplain seedbanks. The time scale for establishment, growth and flowering in such individuals is highly constrained by the duration and depth of floodplain inundation.

This chapter describes an initial investigation of the application of indices of water regime to explaining littoral vegetation patterns in the Lower Murray. Data were analysed for a single survey only using a small subset of the potential descriptors of water regime which may explain vegetation patterns. Nevertheless, it provides a simple method for rapidly estimating the water regime preferences of diverse littoral and floodplain species. It requires semi-quantitative survey data from a broad range of water regimes, and stage data for each survey site. Variability in water levels should determine the minimum temporal density of stage data.

The approach appears most appropriate for hydrologically variable lentic and lotic systems in which gross descriptors of water regime, such as mean growing season water depth, are too simplistic. Reliability is proportional to the number of records per species and to the height of quadrats relative to water-level fluctuations (cf. Palmer and Dixon, 1990). Future investigations for Lower Murray species should examine other weir pools and a wider range of species. Other ecologically important water regime indices may include the number of times flooded and exposed, rates of change in water level, spring *v.* autumn flooding and the number of times (as opposed to the total days) flooded to particular depths.

Flooding patterns were similar and largely seasonal in the 2 y prior to the survey (Fig. 3.1). In contrast, the hydrograph shows distinctly aseasonal and variable patterns at other times (*e.g.* 1980's; Walker and Thoms, 1993), as is common in semi-arid rivers (Finlayson and McMahon, 1988; Walker *et al.*, 1995), and indices need to be developed to accommodate these influences. The influence of previous water regimes on community resilience may be investigated by comparing correlations determined for indices calculated over 1, 2, 4 and 6 y prior to surveying. This may be most insightful when flows are more variable than from 1988-1994 (cf. Fig. 2.2).

The following chapters consider hypotheses regarding growth, resource allocation, recruitment and carbon assimilation in *Bolboschoenus medianus* and *Vallisneria americana* under a range of water regimes. These species were chosen as broadly representative of two dominant plant groups in the Lower Murray: sedges with subterranean tubers and rhizomes which act as carbohydrate sources for growth and sinks for over-wintering, and submersed species restricted to a narrow elevation range by exposure from above and by sub-saturating irradiances below depths of 0.5-1 m. Plant responses in field, pond and laboratory experiments were examined to determine how different aspects of water regime, particularly depth and rate of exposure, influence these species. Both are widespread and exhibit morphological and physiological adaptations to variable hydrological conditions. Neither has received significant ecological study in semi-arid southern Australia.

Plate 3.1 Upper panel: Survey quadrats equivalent to changes in elevation of 20-100 cm. Establishment and growth of littoral vegetation at this site (upper pool) is constrained by erratic changes in water levels and strong currents. Elevations were determined relative to the water level with a dumpy level (right panel). *Vallisneria americana* and other aquatic species mainly occur in the hydrologically stable lower pool (lower panel).


SITE
JAN '94


SITE
FEB '94

Figure 3.1. Stage hydrographs for 2 y prior to the survey; immediately downstream of Lock 6 (upper line) and immediately upstream of Lock 5. Zero indicates pool level upstream of Lock 5 (elevation 16.30 m AHD).

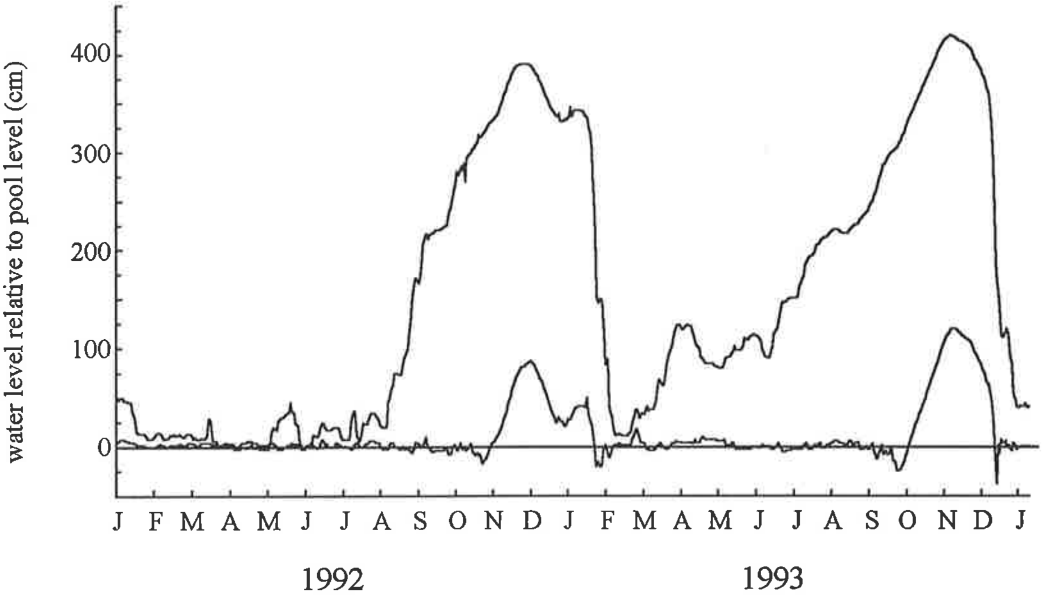
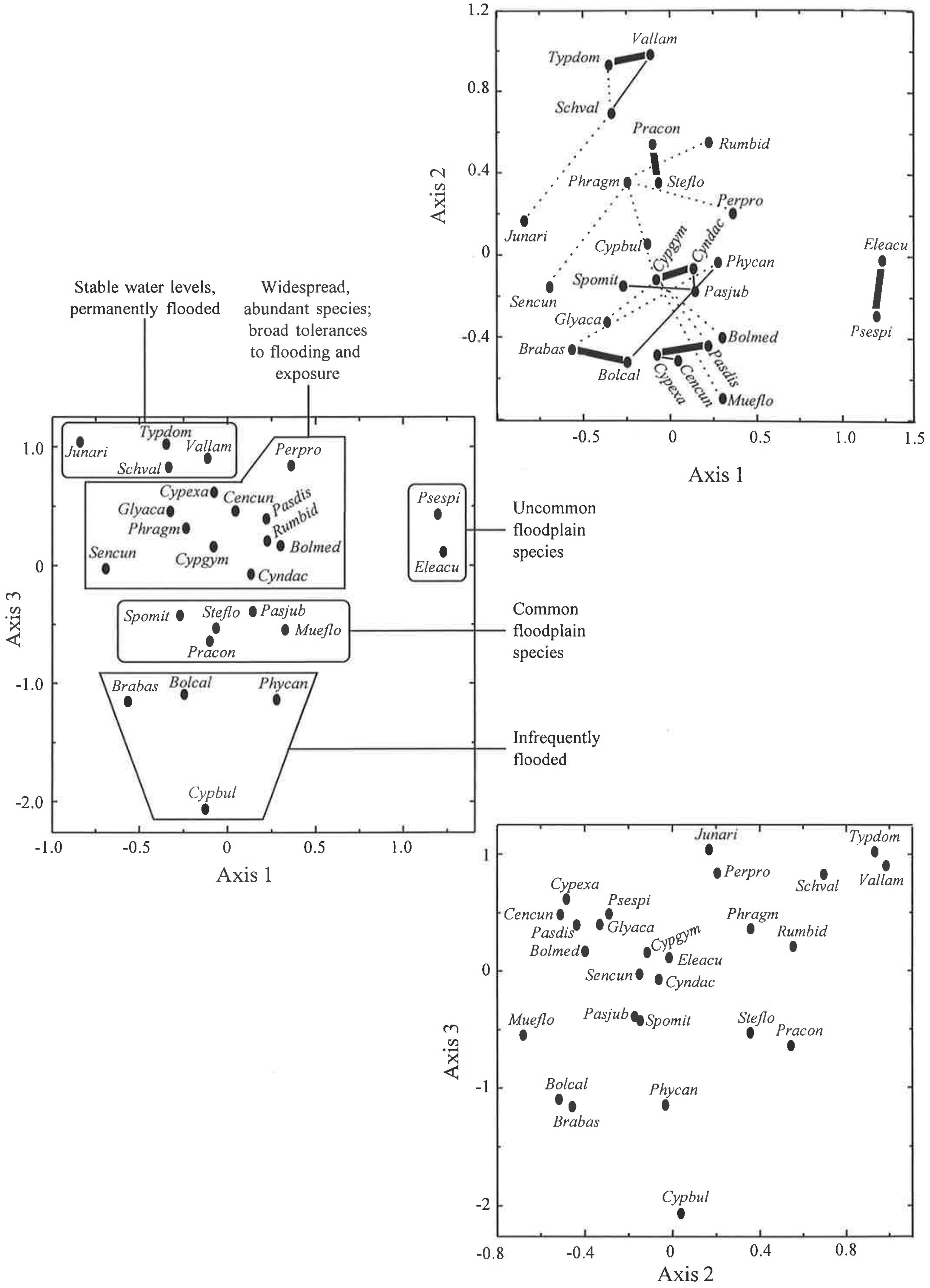

water level relative to pool level (cm)
400
300
200
100
0
J F M A M J J A S O N D J F M A M J J A S O N D J
1992
1993

Figure 3.2. SHS ordination of species based on cover/abundance data across sites. Species are indicated by abbreviations, with full names given below. Thus *Bolmed* indicates *Bolboschoenus medianus.* Similarities between neighbours determined from bond-strength analysis are indicated (axes 1 and 2): thick, first-first neighbours; thin, first-second neighbours; dashed, second-second or second-third neighbours. Relationships are independent of axis orientation. Species groups indicated by clustering are shown for axes 1 and 3 (cf. Fig. 3.3). Varimax rotation loaded half of the variance (49%) on axis 1, 23% on axis 3 and 10% on axis 2 (Stress = 0.06).

Bolboschoenus caldwellii (V. Cook)Sojak (Cyperaceae)
Bolboschoenus medianus (V. Cook)Sojak (Cyperaceae)
Brachycome basaltica F. Muell. var. *gracilis* Benth (Asteraceae)
Centipeda cunninghamii (DC.)A. Braun & Asch. (Asteraceae)
Cynodon dactylon (L.)Pers. (Poaceae)
Cyperus bulbosus Vahl. (Cyperaceae)
Cyperus exaltatus Retz. (Cyperaceae)
Cyperus gymnocaulos Steudel. (Cyperaceae)
Eleocharis acuta R.Br. (Cyperaceae)
Glycyrrhiza acanthocarpa (Lindley)J. Black (Fabaceae)
Juncus aridicola L. Johnson (Juncaceae)
Muehlenbeckia florulenta Meissner (Polygonaceae)
Paspalidium jubiflorum (Trin.) Hughes (Poaceae)
Paspalum distichum L. (Poaceae)
Persicaria prostrata (R. Br.) Sojak (Polygonaceae)
Phragmites australis (Cav.) Trin. ex Steudel (Poaceae)
Phyla canescens (Kunth.)E. Greene (Verbenaceae)
Pratia concolor (R.Br.)Druce (Campanulaceae)
Pseudoraphis spinescens (R.Br.) Vick. (Poaceae)
Rumex bidens R. Br. (Polygonaceae)
Schoenoplectus validus (Vahl.) A. Love & D. Love (Cyperaceae)
Senecio cunninghamii DC. (Asteraceae)
Sporobolus mitchellii (Trin.) C.E. Hubb. ex S.T. Blake (Poaceae)
Stemodia florulenta W.R. Barker (Scrophulariaceae)
Typha domingensis (Pers.) Steudel (Typhaceae)
Vallisneria americana Michx. var. *americana* (Hydrocharitaceae)

Nomenclature follows Black (1980) for all species except *Persicaria prostrata* (Harden, 1993), *Phyla canescens* (Munir, 1993), *Stemodia florulenta* (Jessop, 1993), and *Vallisneria americana* (Jacobs and Frank, in press).



Stable water levels, permanently flooded

Widespread, abundant species; broad tolerances to flooding and exposure

Uncommon floodplain species

Common floodplain species

Infrequently flooded

Figure 3.3. Flexible UPGMA cluster of species based on cover/abundance data across sites. Five groups were determined at a dissimilarity of 0.22.

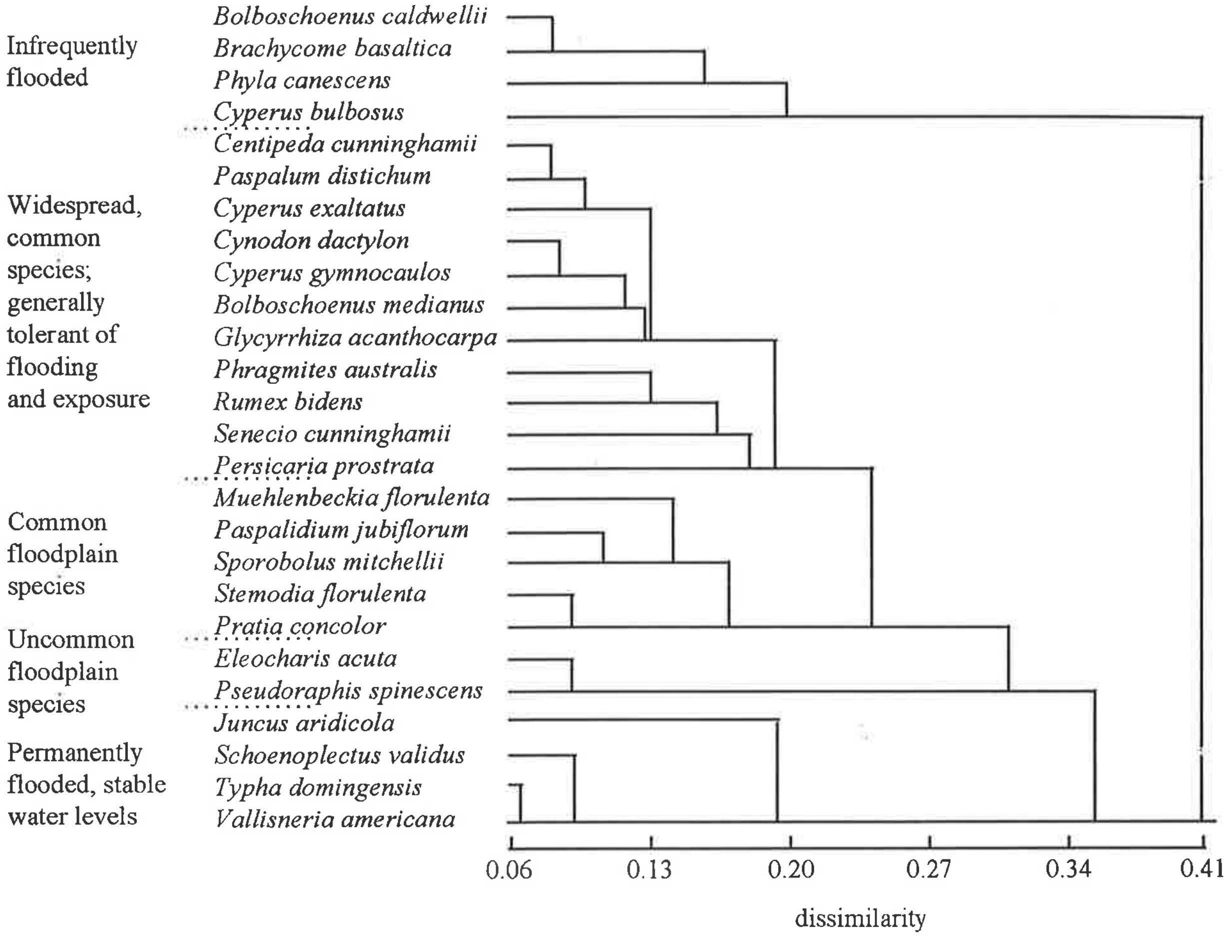

Infrequently flooded
Widespread, common species; generally tolerant of flooding and exposure
Common floodplain species
Uncommon floodplain species
Permanently flooded, stable water levels
Bolboschoenus caldwellii
Brachycome basaltica
Phyla canescens
Cyperus bulbosus
Centipeda cunninghamii
Paspalum distichum
Cyperus exaltatus
Cynodon dactylon
Cyperus gymnocaulos
Bolboschoenus medianus
Glycyrrhiza acanthocarpa
Phragmites australis
Rumex bidens
Senecio cunninghamii
Persicaria prostrata
Muehlenbeckia florulenta
Paspalidium jubiflorum
Sporobolus mitchellii
Stemodia florulenta
Pratia concolor
Eleocharis acuta
Pseudoraphis spinescens
Juncus aridicola
Schoenoplectus validus
Typha domingensis
Vallisneria americana
0.06
0.13
0.20
0.27
0.34
0.41
dissimilarity

Figure 3.4. Minimum spanning tree analysis showing relationships between species based on pair-wise association values. Line length is proportional to association (see scale), but the orientation of main and side 'branches' was determined from ordination, cluster and bond analyses. Species are aligned diagonally along a gradient of flooding frequency. Species within the ellipse are widespread and abundant, occurring in 25% of sites or more, indicating broad tolerance to flooding and exposure. *Cyperus gymnocaulos* and *Phragmites* occurred in 60% of sites or more.

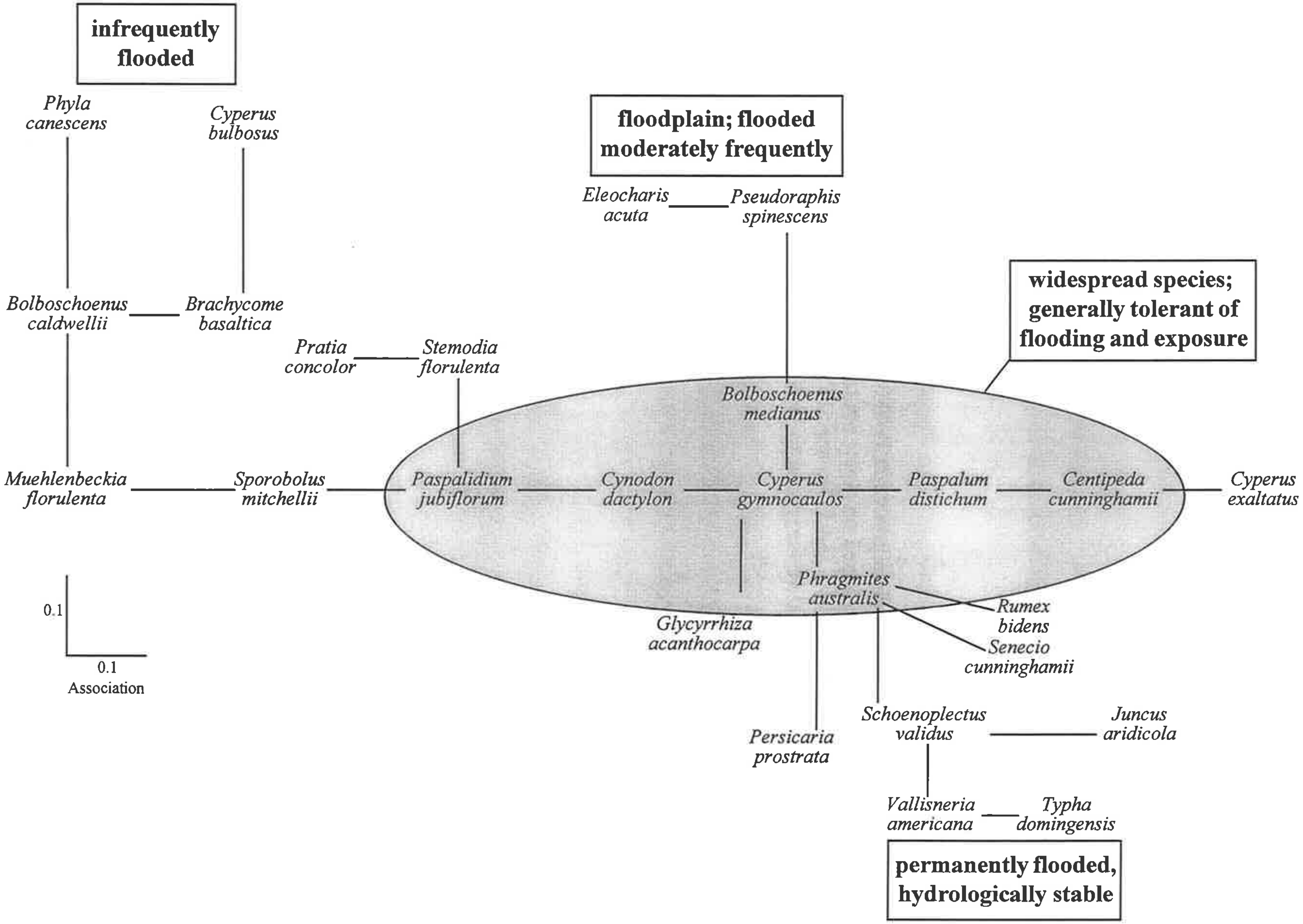
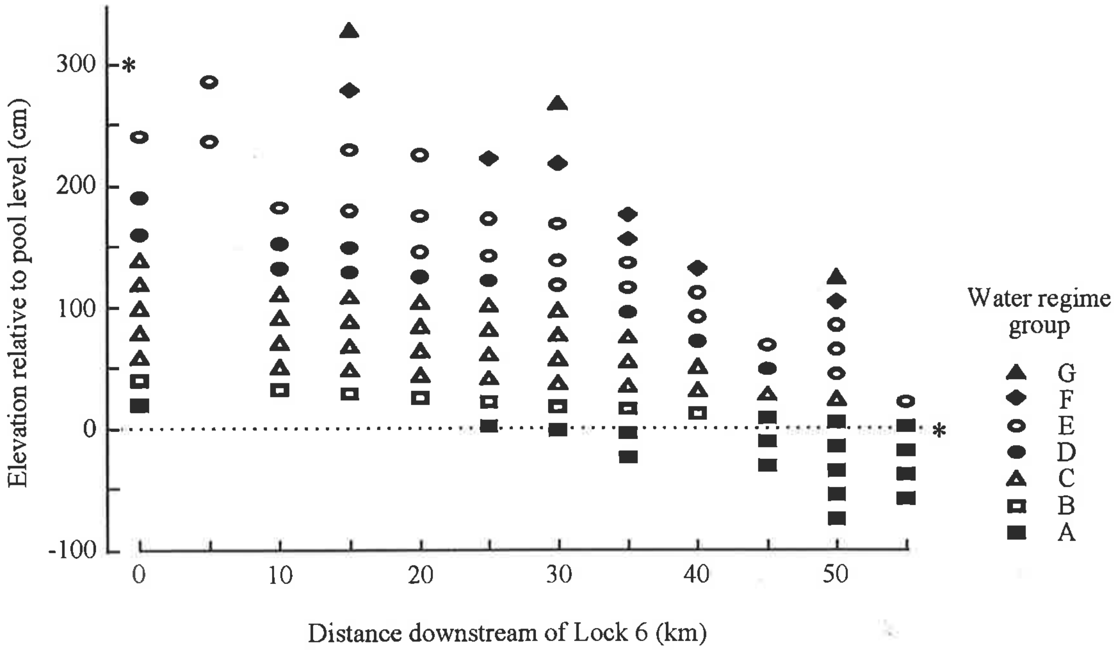
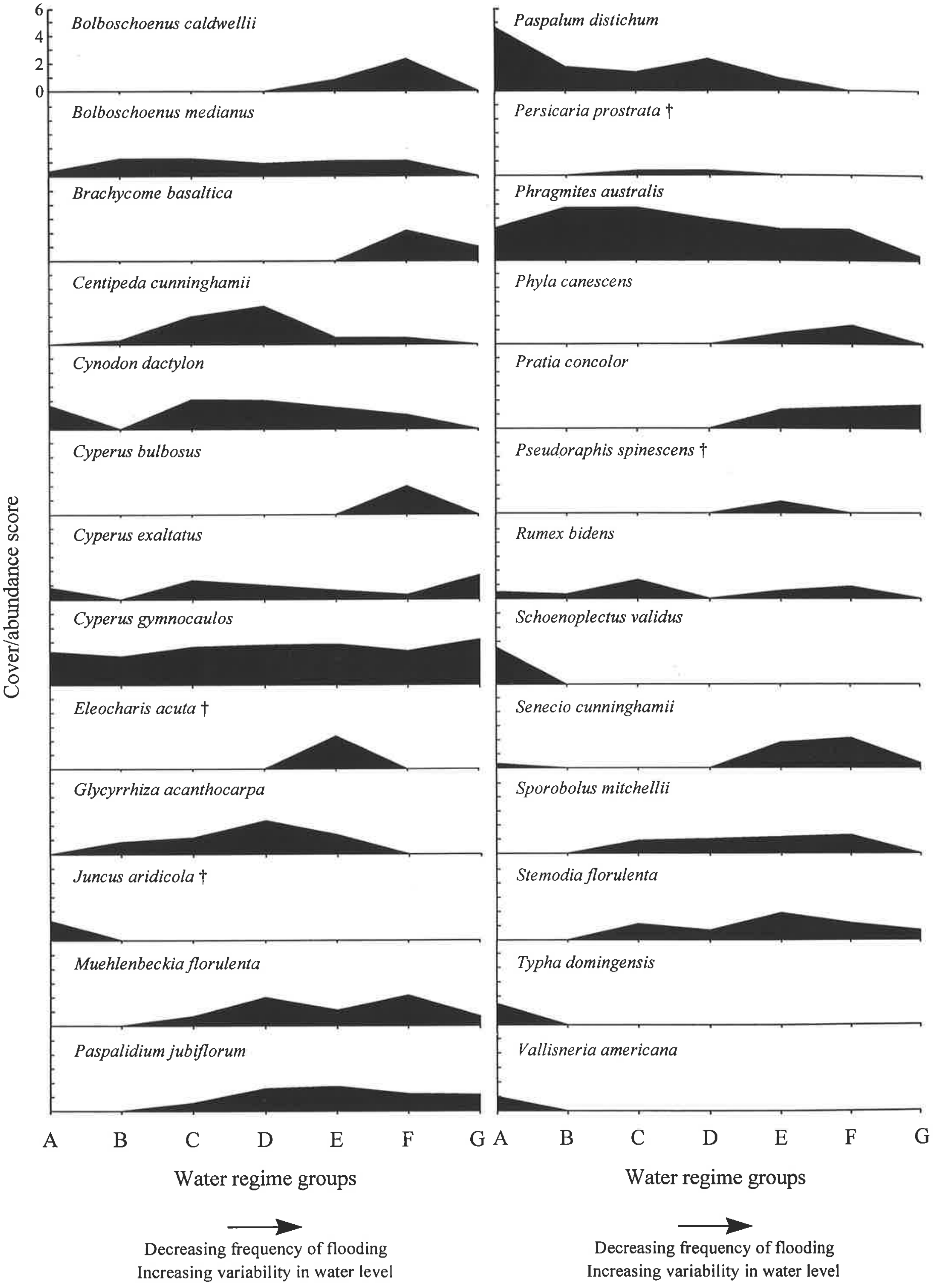

infrequently flooded
Phyla canescens
Cyperus bulbosus
Bolboschoenus caldwellii
Brachycome basaltica
Muehlenbeckia florulenta
Sporobolus mitchellii
Pratia concolor
Stemodia florulenta
floodplain; flooded moderately frequently
Eleocharis acuta
Pseudoraphis spinescens
widespread species; generally tolerant of flooding and exposure
Bolboschoenus medianus
Paspalidium jubiflorum
Cynodon dactylon
Cyperus gymnocaulos
Paspalum distichum
Centipeda cunninghamii
Cyperus exaltatus
Phragmites australis
Glycyrrhiza acanthocarpa
Rumex bidens
Senecio cunninghamii
Persicaria prostrata
Schoenoplectus validus
Juncus aridicola
Vallisneria americana
Typha domingensis
permanently flooded, hydrologically stable
0.1
0.1
Association

Figure 3.5. Distribution of water regime groups in Pool 5. Groups were determined from flexible UPGMA clustering of sites based on water regime indices (Tables 3.2 and 3.4). * indicates weir pool levels for Locks 6 and 5. No species were recorded in some quadrats *e.g.* mid and lower quadrats at 5 km were exposed to high currents and erosion. Note that scales differ between axes.



Elevation relative to pool level (cm)
300
200
100
0
-100
*
*
0
10
20
30
40
50
Distance downstream of Lock 6 (km)
Water regime group
G
F
E
D
C
B
A

Figure 3.6. Mean cover/abundance scores for perennial littoral plants in Pool 5 across 7 water regime groups (Table 3.4). Water regime groups were determined from cluster analysis of sites based on 6 indices of water regime (Table 3.2). † indicates species for which few data exist (recorded in only 1 or 2 quadrats), thereby obviating firm conclusions.


Cover/abundance score
6
4
2
0
Bolboschoenus caldwellii
Bolboschoenus medianus
Brachycome basaltica
Centipeda cunninghamii
Cynodon dactylon
Cyperus bulbosus
Cyperus exaltatus
Cyperus gymnocaulos
Eleocharis acuta †
Glycyrrhiza acanthocarpa
Juncus aridicola †
Muehlenbeckia florulenta
Paspalidium jubiflorum
A B C D E F G
Water regime groups
Decreasing frequency of flooding
Increasing variability in water level
Paspalum distichum
Persicaria prostrata †
Phragmites australis
Phyla canescens
Pratia concolor
Pseudoraphis spinescens †
Rumex bidens
Schoenoplectus validus
Senecio cunninghamii
Sporobolus mitchellii
Stemodia florulenta
Typha domingensis
Vallisneria americana
A B C D E F G
Water regime groups
Decreasing frequency of flooding
Increasing variability in water level

Chapter 4

An evaluation of the *River Murray Hydraulic Model* with regard for ecological research and environmental flow management*

4.1 Abstract

The *River Murray Hydraulic Model* (RMHM) is a PC-based computer simulation model developed by consultants for South Australia's water resource agency, SA Water, to predict flood heights (stage) and discharge based on discharge at Lock 10. However, it may be of use to ecologists researching the effects of flooding on riverine and floodplain biota, and to water resource managers for determining appropriate methods for delivering environmental flows. To be of use, model predictions must be of sufficient accuracy compared to the sensitivity of the biota in question. Prediction accuracy, as measured by the average absolute difference D_a between observed and predicted stage, was high for water levels (0.06-0.39 m) and low for discharges (to over 6 000 ML/day, or 16% of mean discharge). Improving the quality of inputs to run the model improved prediction accuracy by as much as 80%, but it is a time consuming process due to the complex structure of the input files. Model predictions underestimate the transmission time of flow changes down the River, with output 16 days 'ahead' of observed levels at Lock 3. Linear interpolation between observed data for each Lock is generally more accurate and less time consuming for predicting stage, and was considered the most appropriate method for predicting stage in the investigation of the influence of water regime on the ecology of littoral macrophytes (Chapters 2 and 3). Nevertheless, the RMHM is potentially very useful in researching the effects of flooding on aquatic plants and animals, the effects of altered discharge on

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* Some of the analyses and information presented in this chapter follow those of an earlier and less detailed study which examined performance of the RMHM from an hydrological rather than an ecological perspective (Maheshwari *et al.*, 1993). These are included to allow a more general appraisal of the RMHM's accuracy than would otherwise be possible, and are acknowledged where used. Analyses presented in this chapter were conducted for a greater number of weir pools and over a longer period of flows than in Maheshwari *et al.* (1993). The majority of the analyses are original however, as is the discussion of the RMHM's value in ecological research and environmental flow management, and recommendations for improving it, or similar models, for these purposes. Information from both investigations have been incorporated into Blanch, Maheshwari *et al.* (in review).

cyanobacterial blooms via increased velocity, and determining the necessary discharge from Lake Victoria and weir operations to flood particular wetlands or floodplain for environmental purposes.

4.1 Introduction

The Lower Murray is a complex hydraulic system with 10 low-level weirs, earthen levees, barrages and instream and offstream storages (Fig. 4.1, and Figs 1.1 and 1.4). Discharge, salinity and water level at any point in the system may be estimated using the *River Murray Hydraulic Model* (RMHM), a PC-based computer model developed by consultants to SA Water (formerly the Engineering and Water Supply Department of South Australia) (Water Studies, 1992; Maheshwari *et al.*, 1993). The model indicates the effects of changes in operating strategies, and is potentially useful for investigating the flooding requirements of riverine and floodplain biota and environmental flow management (Blanch *et al.*, 1994, 1996).

Accordingly the accuracy and ease of use of the RMHM was evaluated for predicting stage at the survey sites used in studying the influence of water regime on macropophyte communities of the Lower Murray (Chapters 2 and 3). In that investigation it was necessary to determine the patterns of flooding and drying at each site for comparison with the distribution of species across the elevation gradient. The level of prediction accuracy required was to within ±20 cm in general, and to within ±10 cm during low flow periods (discharge <30 000 ML/day) which occur for approximately 8-10 months per year.

The generally low relief of the Murray floodplain means that differences of as little as 0.10 m in water level may represent large differences in areas inundated by a given flood. In addition, a 0.10 m margin of uncertainty could vitally affect some plants and animals, depending on their size, mobility and tolerance to drying and wetting. For example, an increase in flooding depth from 0 to 0.15 m for 6 weeks caused 100% mortality in seedlings of the wetland tree *Melaleuca halmaturorum* in Bool Lagoon, south-east South Australia (Denton and Ganf, 1994). A 0.15 m increase in flooding depth reduced above-ground biomass by 50% in the emergent herb *Myriophyllum variifolium* and shoot production by 80% in the emergent sedge *Eleocharis acuta* (Blanch and Brock, 1994). Small changes in water level affect the growth of plants growing at the extremes of their depth distribution more so than at their optimum depth. Thus the emergent sedge *Bolboschoenus medianus* showed little difference in shoot production at 0 and -0.20 m depths (its optimum range for growth as an adult), but plants at -0.60 m (lower end of depth distribution) produced 72% fewer shoots than those at -0.40 m (Chapter 5).

High temperatures, low velocities and turbulence induce thermal stratification in weir pools in the Lower Murray, creating 'dead zones' (Reynolds *et al.*, 1990) or areas of slow moving water conducive to rapid increases in cell density in the cyanobacterium *Anabaena* spp (M. Burch, SA Water, Adelaide, pers. comm.). Field observations suggest that minor flow increases (of several thousand megalitres per day) above the optimum flow range of 2 500 - 6 000 ML/day for the formation of blooms, may reduce the incidence of surface scum formation and hence be a useful management tool (Burch *et al.*, 1994). Hence to be of use to ecologists and managers, the RMHM must be sufficiently accurate so that the error in stage and flow prediction is not greater than the changes in level/discharge that significantly affect the growth of the study organism.

In this chapter the RMHM is subjected to tests designed to assess its accuracy. The model's performance is tested by examining discharge, the primary currency for hydrologists, managers and algologists, and water levels, arguably the parameter most relevant for ecological research and environmental flow management.

4.2 Operational rules

Regulation of the Lower Murray accounts for flows to and from Lake Victoria, flows and water levels in the weir pools and operation of barrages at the river mouth. The operational rules, outlined below, are incorporated into the RMHM with some simplifications (Water Studies, 1992). More general information for the Murray-Darling system is provided by Jacobs (1989).

4.1.1 Lake Victoria

South Australia has an annual water entitlement of 1850 GL (Murray-Darling Basin Act, 1993), guaranteed by interstate agreement, although it frequently receives more. At Lake Victoria operations maintain daily and monthly entitlement flows (Table 4.1)

Table 4.1. Daily and monthly entitlement flows to South Australia. Note that the February daily entitlement is 6700 ML in leap years (from Maheshwari *et al.*, 1993).

	Entitlement Flows											
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Daily (ML)	7000	6900	6000	4500	3000	3000	3500	4000	4500	5500	6000	7000
Monthly (GL)	217	194	186	135	93	90	109	124	135	170	180	217

during periods of low flow, and store as much surplus water as possible during above-entitlement flows. A secondary objective is to limit increases in lake salinity caused by evaporation, although water conservation requirements may override this concern. The rules incorporated into the RMHM assume the provision of daily (hence monthly) entitlement flows. Above-entitlement flows are stored in the lake provided that (a) the discharge at Lock 9 is >900 ML d^{-1}, (b) the lake water level is <27.0 m AHD and (c) the lake salinity is within acceptable limits.

4.1.2 Locks and weirs

The 10 low-level (3 m) weirs maintain stable pools mainly to facilitate water abstraction for irrigation and other uses (Fig. 4.1). Each lockmaster makes adjustments to bays of stoplogs (*sluice section*) and Boulé panels (*navigable pass*) to accommodate upstream flows. The lockmaster passes information to colleagues downstream, so that the necessary changes to weir configurations can be made at appropriate times.

Many possible combinations of stoplogs and panels could produce a given flow at a given pool level. In the RMHM the weir configurations are represented simply as one bay each for both sluice and navigable pass sections. The rules for manipulating stoplogs and panels concern (a) the distribution of flows between the sluice and pass sections, (b) the alteration of flows to maintain the pool level and (c) the times for removal (or re-instatement) of the navigable pass during the rising (or falling) limbs of the flood hydrograph.

4.1.3 Barrages

Five barrages near the Murray mouth (Tauwitchere, Goolwa, Mundoo, Ewe Island and Boundary Creek) control water levels in Lakes Albert and Alexandrina and prevent seawater entering the river. Stoplogs are installed during low flows and removed as necessary during higher flows. The change in water level across each barrage is typically about 0.75 m.

In the RMHM, the configuration and operation of the barrages are simplified: the small overflow from the Boundary Creek barrage is ignored and overflows from the remaining barrages are represented as if from one barrage. The decision rules concern (a) the magnitude of the combined overflow and (b) maintenance of lake water levels.

4.3 Description of the model

The RMHM simulates daily water levels and flows at 5 to 7 locations along each weir pool, corresponding to cross-sections measured by SA Water, and estimates conditions at other locations by interpolation. The model components include the weirs (Locks 1 to 10) and barrages, offstream storages (Lakes Victoria, Bonney and Albert), instream storages (Lake Alexandrina) and water allocations for irrigation and other purposes.

The model employs an unsteady form of the continuity equation and the steady form of the momentum equation. It is written in Borland Turbo Pascal 6.0 and is menu-driven. The user specifies a known or estimated flow hydrograph at Lock 10 for the duration of simulation, and temporal changes in water levels and flow rates at downstream stations are estimated by routing the hydrograph downstream. The maximum simulation period is one year.

Model inputs are of two kinds: *default data* and *user-specified data. Default data* are used without modification for routine simulations, and specify the configuration of the river system, weirs and barrages, and the relevant operating rules. *User-specified* data are input at the beginning of each simulation. They include the start and finish dates of the simulation period, the observed or estimated flow hydrograph at Lock 10 for the duration of the simulation ("upstream boundary condition data") and the actual (or estimated) water levels and flows on the first day of the simulation period at stations upstream and downstream of Locks 1 to 9 ("initial condition data"). Simulations generated using these basic user-specified inputs will be referred to as output from *minimal inputs*. Extra user-specified inputs, here called *improved inputs*, include inflows and outflows to Lake Victoria and the estimated stage hydrograph at any Lock downstream of Lock 10, which overrides that for Lock 10. Data for Lock 7 were used in this study. The Lock 7 hydrograph was estimated by subtracting flows recorded at the Lake Victoria outlet regulator at Rufus River from those recorded at gauging station GS 426 200, about 400 m downstream of Lock 7, thus giving the flow in the main channel.

The output includes daily water levels and flows at stations upstream and downstream of Locks 1 to 9, and at the barrages, and daily inflow, outflow and storage in Lake Victoria. Results may be viewed in graphical or tabular form.

4.4 Methods

A sequence of 5.5 consecutive years (1 July 1988 to 22 February 1994, thus six model runs) was selected for simulating water level elevations (WLE's). Data for the two years 1 April 1989 to 31 March 1991 were used to predict discharge (flow). Gauged records were obtained from SA Water, Adelaide, and the Department of Environment and Natural Resources, Berri.

The model's performance is evaluated with regard for the average accuracy and trend in the prediction for (a) the entire range of WLE's and flow rates and (b) specific ranges of WLE and flow rate.

The degree to which improved inputs increased prediction accuracy compared with minimal inputs was examined at two sites between Locks 3 and 4, by comparing both simulations with observed WLE's. Simple *post hoc* adjustments to the output of minimal input-based predictions was then determined for low flows by simple subtraction from observed WLE's. Model predictions based on both levels of input were then compared with estimates obtained by simple linear interpolation between the observed daily WLE data for Locks 3 and 4. This comparison was used to determine which method of prediction was most appropriate for generating hydrographs for studying vegetation-hydrology relationships in Chapters 2 and 3.

Finally, temporal accuracy for various weirs is indicated by comparing observed and predicted WLE (based on minimal inputs) using least-squares regression.

4.4.1 *Accuracy and trends*

Qualitatively, the accuracy and trends of predictions may be assessed simply by comparing simulated and actual data. Quantitatively, the data may be compared and analysed using a variety of indices:

Regression

A regression relates predicted (X_p) and observed values (X_o). The equation for a line forced through the origin is:

$$X_p = \lambda . X_o \qquad (1)$$

where λ is the regression coefficient (slope).

Goodness of fit is indicated by the coefficient of determination (r^2) and standard error of the estimate (SE). Values of $\lambda < 1.0$ indicate under-prediction and values > 1.0 indicate over-prediction. The absolute value of the average prediction error (E_r %) is:

$$E_r = |\lambda - 1)| \, . \, 100 \qquad (2)$$

This is of little value if r^2 and SE indicate a poor fit.

Coefficient of Efficiency

The Coefficient of Efficiency (C_e) (Nash and Sutcliffe, 1970) indicates bias in prediction:

$$C_e = \frac{\sum_{i=1}^{n}\left(X_{oi} - \overline{X}_o\right)^2 - \sum_{i=1}^{n}\left(X_{oi} - X_{pi}\right)^2}{\sum_{i=1}^{n}\left(X_{oi} - \overline{X}_o\right)^2} \qquad (3)$$

where n =number of observations,

X_{oi} =ith value of observed measurements,

X_{pi} =ith value of predicted measurements, and

$\overline{X}_o$ =average of observed values.

If r^2 and C_e are similar, the model is free of bias for part or all of the data (depending on the value of r^2). A good fit is indicated by a value of λ close to unity and high values of r^2 and C_e. Otherwise, C_e has little meaning.

Average absolute error (E_a) is the average of the sum of (observed - predicted)/observed data, as a percentage.

$$E_a = \frac{100}{n}\sum_{i=1}^{n}\frac{|X_{oi} - X_{pi}|}{X_{oi}} \tag{4}$$

Average absolute difference (D_a) is simply the average of all (observed - predicted) data and has units of metres for stage and ML/day for discharge. Hence it is of interest to ecologists and for environmental flow purposes as it allows direct comparison with the flooding requirements of biota.

$$D_a = \frac{1}{n}\sum_{i=1}^{n}|X_{oi} - X_{pi}| \tag{5}$$

Average absolute difference from the mean (D_{am}) is D_a divided by the mean, expressed as a percentage.

$$D_{am} = \frac{100}{n\overline{X}_o}\sum_{i=1}^{n}|X_{oi} - X_{pi}| \qquad 6)$$

Average of ratios of predicted to observed values (ρ) is the average of all (predicted/observed) data.

$$\rho = \frac{1}{n}\sum_{i=1}^{n}\frac{X_{pi}}{X_{oi}} \tag{7}$$

4.4.2 Accuracy and trends for specific WLE and discharge

The WLEs at Locks 3, 5, 7, 9 and 10 and flows at Locks 1 and 9 are divided into stage classes of equal size. A difference between simulated and observed daily data (a positive difference indicates over-prediction; a negative difference indicates under-prediction) is assigned to a category based on observed WLE or flow. The mean and standard deviation of the difference between observed and simulated WLE and flow in each category are then plotted for each weir.

4.5 Results and Discussion

4.5.1 Average model accuracy and trends

Plots of observed and predicted water levels (using minimal and improved inputs), and flows are shown in Figs 4.2-4.4, and corresponding indices are shown in Tables 4.2 and 4.3.

Figs 4.2-4.4 show that predicted water levels and flows generally are near the observed data, and indicate the RMHM faithfully predicts stage for the purposes of flood forecasting and general river management. However, sudden changes in flow are not as well modelled, such as rapid flooding and drawdown. Flood recession is predicted ahead-of-time in the more downstream Locks, probably due to underestimates in Manning's *n* (see below).

Predictions were generally more accurate using improved inputs, especially for Locks downstream of Lock 7 due to the overriding of errors in the Lock 10 hydrograph inputs by those for Lock 7, and the inclusion of bypass flows *via* Lake Victoria. Improved inputs significantly out-performed minimal inputs in many instances across a range of flows. An interesting example is for downstream of Locks 7 and 5 in mid-1989 for which minimal inputs overestimate stage by 1-2.5 m. The opposite is true for Lock 3 over this period, when values of up to 1.5 m below pool level are predicted using improved inputs.

Minor underprediction using both levels of inputs occurred for flows close to pool level, *e.g.* upstream and downstream for most Locks in mid-1988 and mid-late 1992. When flow is wholly within the channel, only minor changes in flow are necessary to alter stage significantly (< c. 35 000 ML/day).

For water levels and flows, values of r^2 and C_e indicate low bias (Table 4.2) except for sites upstream of Locks 1, 3 and 5 where r^2 values were 0.77–0.68 (minimal inputs). Values of λ indicate little bias across all flows. However, Fig. 4.3 and D_a values up to 0.23 m at upstream sites and 0.49 m at downstream sites (Table 4.2) indicate bias for some classes. Greater prediction accuracy at high WLEs may have masked lower accuracy at low and medium elevations in calculations of D_a (see Fig. 4.5).

Table 4.2. Performance indices of the Model for water level elevations (WLE) upstream and downstream of Locks. Predictions are based on 5 years data, 1 January 1988 - 22 February 1994. Model output was generated using minimal and improved inputs (see text).

Parameter	λ	SE/X^2	r^2	E_r (%)	C_e	E_a (%)	D_a (m)	D_{am} (%)	ρ
Lock No.									
				MINIMAL INPUTS					
Upstream									
1	0.99	5.6	0.77	0.89	0.76	3.41	0.13	3.80	1.00
2	0.99	11.9	0.82	0.61	0.82	2.67	0.18	2.74	1.00
3	1.00	4.9	0.74	0.23	0.73	1.07	0.11	1.11	1.00
4	1.00	4.0	0.83	0.01	0.83	0.86	0.18	0.87	1.00
5	1.00	1.4	0.68	0.01	0.68	0.68	0.07	0.42	1.00
6	1.00	1.2	0.83	0.16	0.82	0.38	0.07	0.38	1.00
7	1.00	13.2	0.87	0.27	0.87	1.01	0.23	1.01	1.00
8	1.00	6.8	0.87	0.18	0.87	0.68	0.17	0.69	1.00
9	1.00	4.2	0.82	0.21	0.81	0.48	0.13	0.48	1.00
Downstream									
3	1.01	57.50	0.81	0.16	0.79	6.04	0.45	5.61	1.02
4	1.00	48.50	0.81	0.25	0.76	4.21	0.49	4.01	1.00
5	1.00	27.60	0.84	0.31	0.83	2.52	0.36	2.48	1.00
6	0.99	25.34	0.85	1.18	0.83	2.35	0.42	2.37	0.99
7	1.00	40.72	0.86	0.02	0.99	1.94	0.42	1.88	1.00
9	1.00	29.38	0.87	0.09	0.87	1.19	0.31	1.18	1.00
10	1.00	23.22	0.93	0.25	0.91	0.93	0.27	0.93	1.00
				IMPROVED INPUTS					
Upstream									
1	1.01	2.42	0.90	0.53	0.90	2.40	0.09	2.56	0.99
2	1.00	5.8	0.91	0.27	0.91	1.76	0.12	1.76	1.00
3	1.00	1.2	0.92	0.14	0.92	0.61	0.06	0.62	1.00
4	1.00	1.5	0.94	0.23	0.93	0.53	0.07	0.53	1.00
5	1.00	0.5	0.88	0.11	0.87	0.28	0.05	0.28	1.00
6	1.00	0.6	0.91	0.22	0.89	0.32	0.06	0.32	1.00
7	1.00	11.2	0.89	0.07	0.89	0.89	0.20	0.88	1.00
8	1.00	9.6	0.82	0.23	0.81	0.76	0.19	0.75	1.00
9	1.00	3.5	0.85	0.20	0.84	0.44	0.12	0.44	1.00
Downstream									
3	0.99	42.44	0.93	1.19	0.84	4.88	0.36	4.59	0.99
4	0.99	19.3	0.93	1.21	0.90	2.73	0.32	2.64	0.99
5	0.99	9.87	0.94	0.96	0.93	1.68	0.24	1.69	0.99
6	0.98	10.77	0.93	1.64	0.89	1.93	0.35	1.98	0.98
7	1.00	7.02	0.98	0.28	1.00	0.86	0.19	0.87	1.00
9	1.00	54.17	0.79	0.18	0.77	1.41	0.36	1.40	1.00
10	1.00	51.03	0.86	0.27	0.82	1.34	0.39	1.32	1.00

For water levels, values of *SE*/mean, E_r, E_a, D_a, D_{am} and ρ indicate the predictive error is lower on the upstream than on the downstream side. Values of λ, E_r and r^2(see also Figs

Table 4.3. Performance indices of the RMHM for flows at Locks 1 and 9. Predictions are based on 2 years data, 1 April 1989 - 31 March 1991. Model output was generated using minimal inputs (from Maheshwari *et al.*, 1993).

Parameter	λ	SE/X^2	r^2	E_r (%)	C_e	E_a (%)	D_a (ML/d)	D_{am} (%)	ρ
Lock No.									
9	1.12	12.7	0.98	12.0	0.96	24.3	4982	14.7	1.08
1	1.00	24.3	0.92	0.0	0.92	35.2	6122	16.0	1.06

4.2 and 4.3) indicate a greater tendency to over-predict water levels on the upstream side than on the downstream side for all weirs. It appears that relatively stable levels are more accurately predicted. Similarly, values of λ, E_r and r^2 (Table 4.3, see also Fig. 4.4) indicate that the model generally over-predicts flows at Locks 9 and 1.

For all weirs D_a was higher on the downstream side than on the upstream side. Greater prediction accuracy upstream of weirs was due to the lower variation in stage than observed downstream. For environmental flow management, D_a is perhaps the most relevant statistic as it indicates prediction accuracy in metres, and can be compared to the flooding requirements of aquatic plants and animals. Even the largest values for D_a upstream of weirs (0.23 m at Lock 7) were smaller than the smallest values for the downstream sides of weirs (0.27 m at Lock 10). Whilst no pattern in D_a occurred at upstream stations, values generally increased with distance downstream, with a maximum of 0.49 m at Lock 4. This error is large compared to water-level changes that are biologically significant for aquatic and terrestrial biota, which may respond to changes in water level of only a few centimetres.

In terms of D_{am}, but not D_a, the errors in predicting upstream and downstream WLE are low at all weirs, whilst errors in predicting flows are high. Tables 4.2 and 4.3 show that the error for water levels is less than 6%, whereas the error for flow may approach 16%.

4.5.2 Comparison of prediction accuracy using minimal and improved inputs

Predictions based on improved inputs were generally more accurate than those based on minimal inputs (Figs 4.2 and 4.3, Table 4.2). Exceptions are for flood peaks, where greater accuracy generally occurred using minimal inputs. For example, improved inputs underestimated peak stage by c. 0.5 m downstream of Lock 3 for 1990 and 1993 floods (Note that minimal inputs overestimated these peaks by c. 0.3 m).

For the upstream side of Lock 4 SE/X^2 was reduced by 63% and D_a from 0.18 m to 0.07 m. On the downstream side of Lock 7 SE/X^2 was reduced by 80% and D_a fell from 0.42 m to 0.19 m. Accuracy did not increase using improved inputs-based predictions for locks upstream of Lock 7, perhaps due to the offtake for Lake Victoria at Frenchmans Creek upstream of Lock 9. Bias was little affected.

4.5.3 Model accuracy and trends for specific WLEs

No consistent pattern in prediction accuracy occurred for all Locks and WLEs (Figs 4.5 a and b). Predictions are based on minimum inputs. Small standard deviations indicate a consistent error for that category; long bars usually mean a high variability in difference between predicted and observed values at that stage, although they could indicate a change in trend (e.g. from over- to under-prediction). The choice of categories is arbitrary and aggregations of data may obscure minor trends.

The model is slow to respond to changes in flow associated with operation of the weirs. This may be due to inaccuracies in the channel cross-sections (and hence the stage-discharge relationships). Some sites have not been surveyed for 80 years and geomorphological changes are known to have occurred (Thoms and Walker, 1992).

Upstream

Mean predicted WLEs were generally within 20 cm of observed values for upstream sites (Fig. 4.5a). Mean accuracy was greatest for Lock 7 and poorest for Lock 9, where mean overprediction was c. 0.4 m for medium classes. Precision varied considerably between Locks and across stage classes within Locks. Overprediction in the lowest stage classes at Locks 9, 5 and 3 reflect infrequent instances in which water levels fell below pool level, due either to weir operations to prepare for imminent flooding or difficulties in maintaining pool level immediately after flooding. Poor precision at low flows for Lock 7 is due to a significant overprediction in mid-1989 (see Fig. 4.2). The standard deviation of the mean is generally greatest for low-intermediate stages, presumably corresponding to the initial stages of over-bank flooding, where the effects of vegetation and floodplain topography would be maximal.

Downstream

Precision was much poorer on the downstream side of weirs due to the greater variation in stage. Interestingly, this is particularly so when the river is regulated (discharge <50 000 ML/day). Above this flow, weirs are dismantled and do not affect stage. Mean prediction error was <0.4 m on the downstream side for all Locks, and <0.25 m for Locks 7 and 3. Similar patterns occurred for Locks 10 and 7, and for Locks 5 and 3, suggesting accuracy is related to distance below Lock 10 (see Fig. 4.8).

The range of water levels observed downstream of any weir is about 5 m, twice the range upstream. Downstream levels fluctuate much more rapidly than those upstream, and large fluctuations are more common. Stage frequently changes by up to 0.40 m and occasionally by as much 1.5 m over a 3 day period downstream of locks, whilst generally by 0-0.10 m upstream of locks. Hence the downstream predictions would be expected to be less accurate than those upstream. However, the accuracy of means is comparable to upstream predictions. Mean predictions for some stage classes are within 10 cm of observed values for both upstream and downstream sites. The inaccuracies are indicated instead by the larger error bars.

4.5.4 Output adjustment

The decline in prediction accuracy with increasing distance upstream of a weir was examined between Locks 3 and 4. Mean prediction error for flows below 14 000 ML/day was 0.32 m, 0.13 m, 0.06 m and 0.01 m on the downstream side of Lock 4, at Loxton and Cobdogla, and upstream of Lock 3 respectively (Fig. 4.6). Seventy six percent of the variance in prediction error at these stations was explained by distance downstream of Lock 4 using a quadratic polynomial curve. Output adjustment factors may be determined from the regression for any point along the pool, allowing *post hoc* adjustments to the predictions. Observed WLE data for two intermediate stations (Loxton and Cobdogla) are available only for this reach. Hence the relationship between prediction error and distance may only be ascertained for this pool. No significant relationship between error and distance for higher flows was determined.

4.5.5 Comparison of RMHM accuracy with linear interpolation between Locks 3 and 4

Linear interpolation between WLEs observed for downstream of Lock 4 and upstream of Lock 3 compare favourably with model predictions at Loxton and Cobdogla (Fig. 4.7). Linear interpolation produced significantly greater accuracy of prediction at Cobdogla for all except the lowest WLEs. Prediction accuracy was greater using improved inputs rather than minimal inputs for higher stage categories at Cobdogla, but similar for lower classes. Model predictions were most accurate for lower WLE at Loxton, with prediction using improved inputs data generally showing the greater accuracy. Linear interpolations proved more accurate at higher WLEs. Standard errors of prediction were at least as good and generally much smaller for linear interpolations than RMHM predictions. The generally greater accuracy and precision of the interpolations, combined with their much simpler calculation, indicates it is the preferable method for predicting WLE's from recorded data (cf. Chapters 2 and 3; Walker *et al.*, 1994).

4.5.6 Temporal prediction accuracy

Fig. 4.8 shows for various locks the temporal difference in days between observed and predicted downstream WLE (using minimal inputs) against distance downstream of Lock 10. The temporal difference, or lead-time, is the number of days corresponding to the minimal deviation between observed and predicted WLE.

A lead-time of 2 days at Lock 10 indicates that predicted stage data are two days ‘ahead’ of observed data, and 16 days ahead at Lock 3. Lead-time increases with distance downstream of Lock 10. A linear regression of temporal difference against distance (r^2=0.97, P<0.0001) suggests considerable error in prediction is introduced by incorrect Manning’s n values and/or cross-sectional data, as the trend to predict changes in WLE’s ahead of observed changes increases with travel distance. Manning’s n is a calibration factor in the equation

$$Q = \frac{1}{n} A R^{2/3} S^{1/2}$$

where Q is discharge (m^3/s), A is the cross-sectional area of flow (m^2), R is the hydraulic radius (m) and S is the slope (m/m) of the water over a uniform reach (Gordon *et al.*, 1992, p 171). Manning's n represents the combined effects of vegetation, substrate and channel form on resistance to flow. Values for n range from 0.025 for non-vegetated, straight channels without pools to 0.15 for heavily vegetated reaches with an uneven bottom and woody debris (Gordon *et al.*, 1992, p173). Fig. 4.8 suggests values of n in the RMHM need to be revised upward to correct for underprediction of flow travel time.

4.5.7 Discharge

Whilst mean prediction error is <5% for all discharges at Lock 1, precision is poor (Fig. 4.9). The opposite is true for Lock 9, where flows are overpredicted but with greater precision. Overprediction was in the order of 12-14% for medium-high flows (*e.g.* 14 000 ML/day in the range 100 000-119 000 ML/day). All flows are generally predicted to within 10% of observed values for both Locks. Poor precision at Lock 1 is unexpected as little variability in stage exists in the lower section of the river, suggesting precision should be high. In addition the floodplain upstream of Lock 1 is restricted - thus error is unlikely to be due to floodplain topography or vegetation. It is suggested that the poor precision at Lock 1 is rather due to underestimation of the travel time of flows due to low Manning's n values. Higher precision at Lock 9, which is immediately downstream of Lock 10, corroborates this conclusion.

4.6 Application to ecological research and environmental flow allocations

When operated using minimal inputs, the RMHM generally predicts WLE's to within 0.2 m upstream and 0.45 m downstream of Locks (D_a in Table 4.2), and often much better (Fig. 4.5). The incorporation of improved inputs can reduce mean prediction error to as little as 0.05 m upstream (Lock 5) and 0.19 m downstream (Lock 7) (D_a in Table 4.2). These values are of acceptable accuracy relative to the water-level fluctuations that influence growth and reproduction of many floodplain and aquatic species. Hence there is considerable potential for the application of the RMHM to studying the effects of flooding at various rates and to different depths on the aquatic and floodplain flora and fauna of the River Murray. For example, the optimum water regime and tolerance ranges to flooding and exposure of four aquatic plants was determined by comparing their distribution between Locks 3 and 4 with flooding histories generated using the RMHM (Blanch *et al.*, 1994, cf. Appendix 2). However, the *post hoc* output adjustment (see above) employed in this study may only be used in this pool, and only for flows below 14 000 ML/day. In addition, data for these and other non-essential gauging stations may only be available on a user-pays basis in the future. This will seriously limit the scope for evaluating the performance of the RMHM and future models.

Improved inputs can reduce prediction error greatly (for example, from 0.18 m to 0.07 m upstream of Lock 4, D_a in Tables 4.2 and 4.3), however generating the improved inputs is time consuming and, due to the 'patchy' discharge data for Lake Victoria, inputs often need to be estimated from the prevailing flow pattern.

Predictions generated with linear interpolation were generally as accurate or considerably more so than those of the RMHM (Fig. 4.7). In addition, the proceedure for generating predictions with the former is much simpler than that necessary for accurate predictions in the latter. The structure of the input files for the RMHM necessitate a high degree of accuracy for the model to run, and the reasons for spurious output, assuming spurious predictions are recognised as such, may therefore be numerous. Files which are necessary for generating accurate prediction, *e.g.* inflow/outflow file for Lake Victoria, are very time consuming to construct due to the exact requirements of the programming language. For these reasons linear interpolation was considered the more appropriate method for generating flooding histories at vegetation survey sites (Chapters 2 and 3). However, this proceedure is only feasible if stage data are known for each Lock, and not for real-time forecasting.

Other applications for which the RMHM may be most appropriate include investigating the effects of weir manipulations and releases from Lake Victoria on water levels in creeks, backwaters and low floodplain. Fluctuating water levels in these areas can be a simple and inexpensive method of stimulating seed germination, carbon release from organic material and invertebrate hatching from eggs in the soil (Boulton and Lloyd, 1992; Blanch *et al.*, 1996). The RMHM could be used to determine quantities required from Lake Victoria and weir levels necessary to flood or dry particular wetlands or creeks. This could be done in advance of water allocations, and predicted and observed effects used to test model accuracy. This will only be meaningful for low flows when weirs can be safely operated and flows are affected.

To be of most use for researching cyanobacterial blooms, future models need to predict velocity and fluid exchange rates. The general perception of algal populations as downstream-moving phenomenon and the influence velocity has on population density can be illustrated *via* a simple calculation. At uniform velocities of 1.0 and 0.1 ms^{-1} the travel time between Locks 1 and 2 (river distance of 88 km) would be 1.02 and 10.2 days, respectively. This increase in the reach retentivity, due to a slower travel time, has a marked influence on population density at Lock 1. If the density of *Anabaena* sp was 1 000 cells mL^{-1} at Lock 2, with a net specific autotrophic growth rate of 0.01 h^{-1}, the faster moving population would reach a density of 1 276 cells mL^{-1} at Lock 1, whereas the slower moving population would attain a density of 11 510 cells mL^{-1}. The latter algal density could generate a potential health risk.

However this general perception of invariable downstream-moving populations was questioned by Reynolds and his coworkers (Reynolds *et al.*, 1991; Reynolds and Glaciter, 1993). Uniform velocities are unlikely across river cross-sectional areas, as rivers are known to contain dead or storage zones of slow moving water. These zones significantly alter downstream algae concentrations as water and particles from these zones mix with the main channel. The model proposed by Reynolds *et al.* (1991) examined the influence of dead zone algal growth on mean main channel algal concentration when the two water sources mixed. The effect was a function of the relative dead zone concentration, the fluid exchange rate between the two and current velocity. For the reach between Locks 1 and 2, assuming a velocity of 0.1 ms^{-1} and an aggregate dead zone of 30% of the reach volume with a fluid exchange of 0.01 h^{-1} the enhancement factor was 0.12 km^{-1} or c. 11 over the 88 km.

Both these calculations serve to demonstrate that any development of the RMHM or future models should endeavour to include predictions of velocity distribution and fluid exchange rates which would assist identification of ideal habitats for algal growth. The enhancement factors predicted from the models of algal growth show how potentially important these predictions are for river management with respect to algal populations.

4.7 Improving the RMHM for ecological research and environmental flow management

The RMHM, or similar models, are valuable tools for ecological studies and environmental flow management in the Lower Murray. The RMHM's accuracy and utility however can be improved to be of maximum benefit. Recommendations for improving the accuracy and usefulness of the RMHM, or that of future models, are given below. The first points detail the necessary improvements in accuracy of the inputs, and the latter the requirements particular to further research and flow management.

- Greater accuracy of the stage *v.* discharge relationships at Lock 10 and the SA border would greatly improve prediction accuracy. Different relationships between discharge, stage, cross-section and velocity at Lock 10 have been calculated by New South Wales, Victorian and South Australian water resource agencies (P. Pfeiffer, SA Water, pers. comm.). This suggests that the stage *v.* discharge relationship used in the RMHM may introduce some degree of error into predictions. The significant improvement in the prediction accuracy for WLE's using Lock 7 hydrograph data to override that of Lock 10 supports this observation.

- A better understanding of bypass flows around Locks is essential for improving prediction accuracy, particularly in Chowilla, Katarapko Creek and Lindsay Island floodplains where minor changes in stage relative to the low relief can significantly alter flooding patterns.

- Improved bathymetric data is essential. Some cross-sections were last surveyed in 1916, prior to construction of the weirs and resulting channel alterations.

- In general, the assumptions, objectives and operating procedures of the RMHM are designed for flood prediction, to assist in managing flows (for minimising damage to infrastructure), to predict 'surplus' flows, and to assist navigation at low flows. Ecological research and environmental flow management have different objectives, emphases and requirements for prediction accuracy. These need to be considered in the development of future models.

- Investigations into the effects of current velocity on cyanobacterial bloom formation in the Lower Murray would benefit greatly from inclusion of accurate predictions of cross-sectional velocities and retention times in flow models. This may necessitate the development of two dimensional models. These are contingent upon accurate bathymetric data and an understanding of fluid exchange between dead zones and the main channel.

- The complex structure of user-defined input files precludes the rapid inclusion of data essential for maximising prediction accuracy, *e.g.* inflows and outflows from Lake Victoria. Similarly, output files are difficult to organise into a form ready for interrogation in a spreadsheet. A standard column-format structure for easy import/export to a spreadsheet is recommended.

- Predictions for points not corresponding to cross-sections can only easily be made for periods up to 14 days. A simple procedure for predicting stage at any point along the Lower Murray for periods up to a year is required.

- The usefulness of the RMHM in predicting the extent of inundation following weir manipulations and releases from Lake Victoria is limited also by uncertainties in floodplain topography mapping. Errors of as little as 0.10 m in either RMHM predictions or in floodplain topography survey data could translate into many hectares when simulating the effects of engineered flooding. Changes in floodplain topography following flooding and errors introduced during surveying are probably greater than RMHM predictions in many cases. Improvements in the quality of input data to the RMHM must be accompanied by continued floodplain surveying to be of greatest use.

4.8 Conclusions

The model faithfully reproduces the trends of observed water levels and flows, and its predictions generally are satisfactory for the range of flow conditions that prevailed during the five and a half years of simulation. Prediction accuracy is generally greater upstream of weirs, with underprediction at low stages and overprediction at intermediate stages. Overall, the error for water levels is <6%, and that for flows is <16%. By also including Lake Victoria inflows and outflows and the stage hydrograph for Locks as inputs, prediction accuracy can be improved by up to 1.4%, or 0.17 m. The generation of these improved inputs is time consuming and requires guessing the stage when data points are missing, and may not be warranted due to the comparatively small improvement in accuracy.

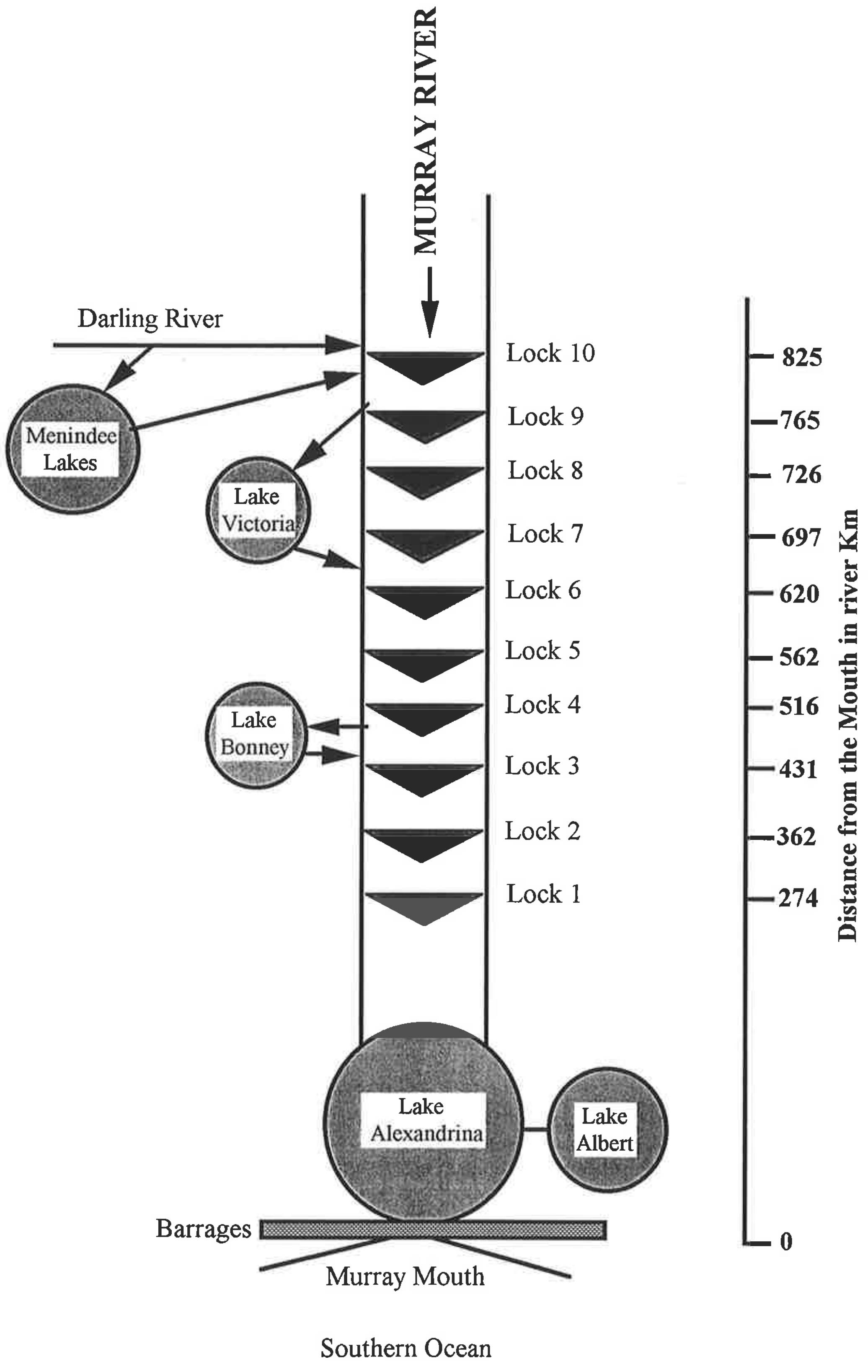
Linear interpolation is generally more accurate and precise in simulating WLE's, than the RMHM for both minimal and improved inputs, at Cobdogla and for flows above 30 000 ML/day at Loxton (Pool 3). By extension it may be assumed to better predict stage between other Locks. It is a simple and rapid procedure, but cannot be used for real time forecasting.

The RMHM predicts changes in WLE's ahead of observed changes, with the lead-time increasing in a linear fashion from 2 days at Lock 10 to 16 days at Lock 3. A least-squares regression of the distance downstream of Lock 10 and the temporal difference in days between predicted (using minimal inputs) and observed WLE's explained 97.1% of the variance. This suggests that values for Manning's n may need to be altered and cross-sectional data revised.

For the RMHM or future models to be of most use in ecological research or environmental flow management, accuracy of the input data needs to be improved. The objectives and assumptions of such models need to reflect the requirements of research and management and level of accuracy defined by aquatic and floodplain biota. File structures need to be simplified and estimates of current velocity should be incorporated.

Nevertheless, there remains significant opportunity for the incorporation of the RMHM into research and management on the lower River Murray. Blanch *et al.* (1994) compared flooding histories generated by the RMHM with the distribution and abundance of four aquatic plants to broadly determine their water regime preferences. Research into flooding effects in other species, and turbulence effects on cyanobacterial/phytoplankton growth may also employ the RMHM. The feasibility of altered weir operation rules and releases from Lake Victoria could be examined as a method of delivering water to floodplains and wetlands.

Figure 4.1. Schematic representation of the Lower Murray showing its major tributary and regulatory structures (not to scale) (from Maheshwari *et al.*, 1993) (see also Figs 1.1 and 1.4).


MURRAY RIVER
Darling River
Menindee Lakes
Lake Victoria
Lake Bonney
Lock 10
Lock 9
Lock 8
Lock 7
Lock 6
Lock 5
Lock 4
Lock 3
Lock 2
Lock 1
Lake Alexandrina
Lake Albert
Barrages
Murray Mouth
Southern Ocean
825
765
726
697
620
562
516
431
362
274
0
Distance from the Mouth in river Km

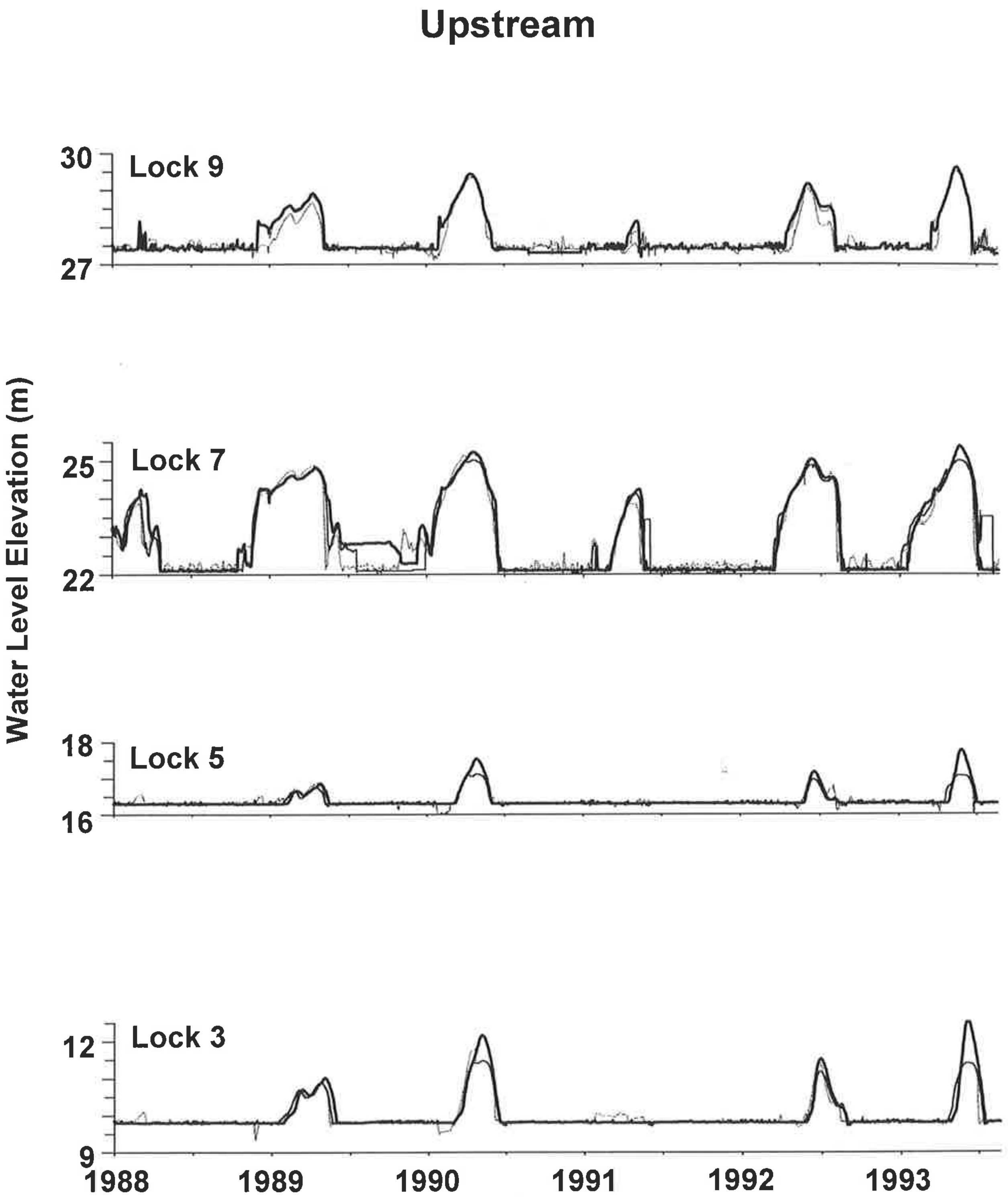


Figure 4.2. Comparison of observed (dashed) and RMHM ouptut for WLE generated with minima (solid, thick) and improved (solid, thin) inputs for upstream of Locks 3, 5, 7 and 9 (see text). Note that Figs 4.2 and 4.3 are aligned at zero error for each Lock (apart from Locks 9 and 10, as the RMHM does not predict levels upstream of Lock 10). The same scale for water level elevation is used in both Figures for comparison.

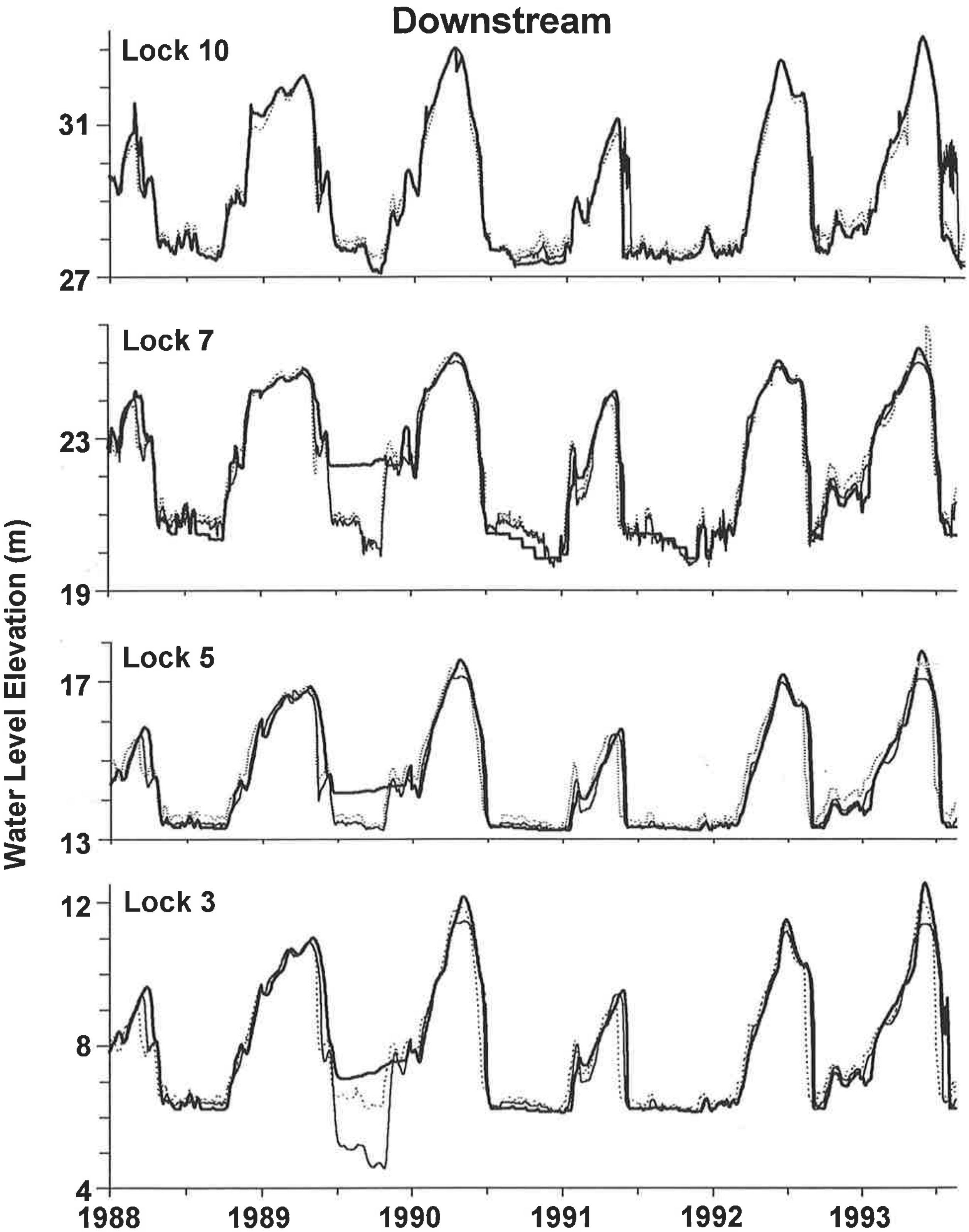
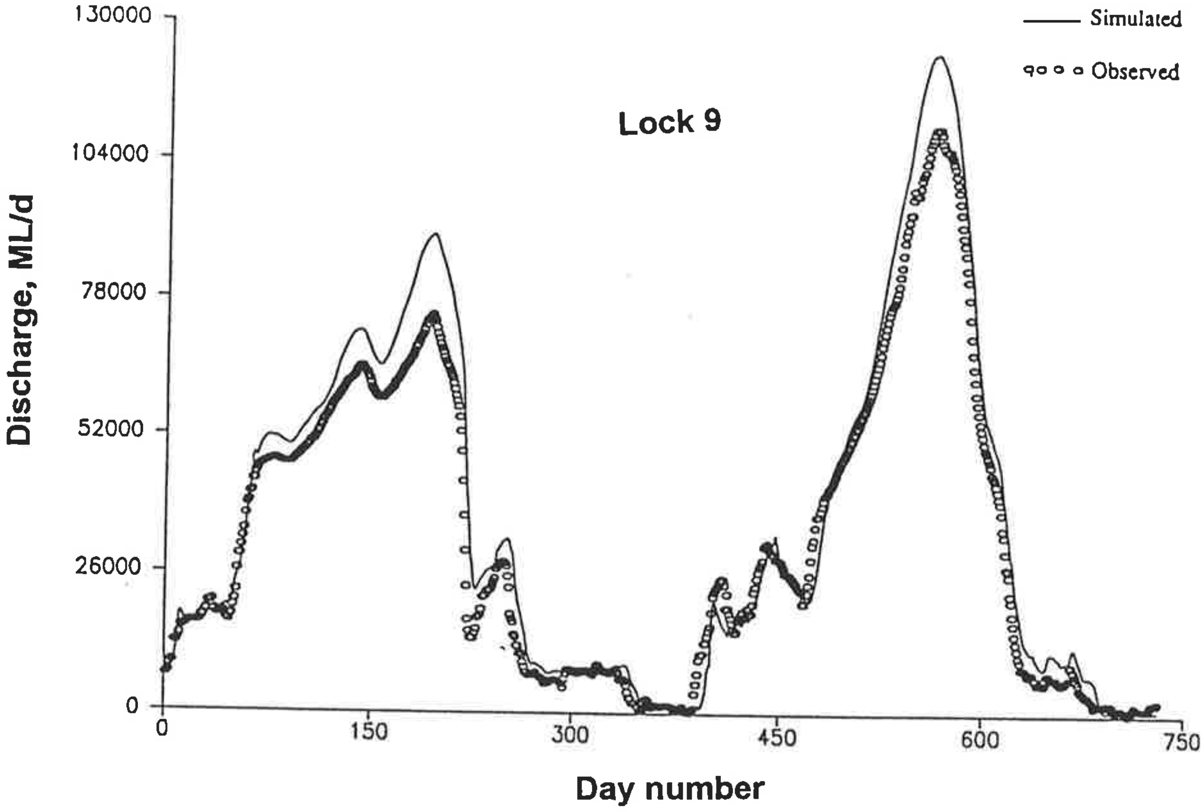


Figure 4.3. Comparison of observed (dashed) and RMHM ouptut generated for WLE with minimal (solid, thick) and improved (solid, thin) inputs for downstream of Locks 3, 5, 7 and 10 (see text).

Figure 4.4. Comparison of observed and predicted RMHM output (minimal inputs) for discharge at Locks 1 and 9. Day 1 refers to 1 April 1989 (from Maheshwari *et al.*, 1993).


Lock 9
Simulated
Observed
Discharge, ML/d
130000
104000
78000
52000
26000
0
0
150
300
450
600
750
Day number

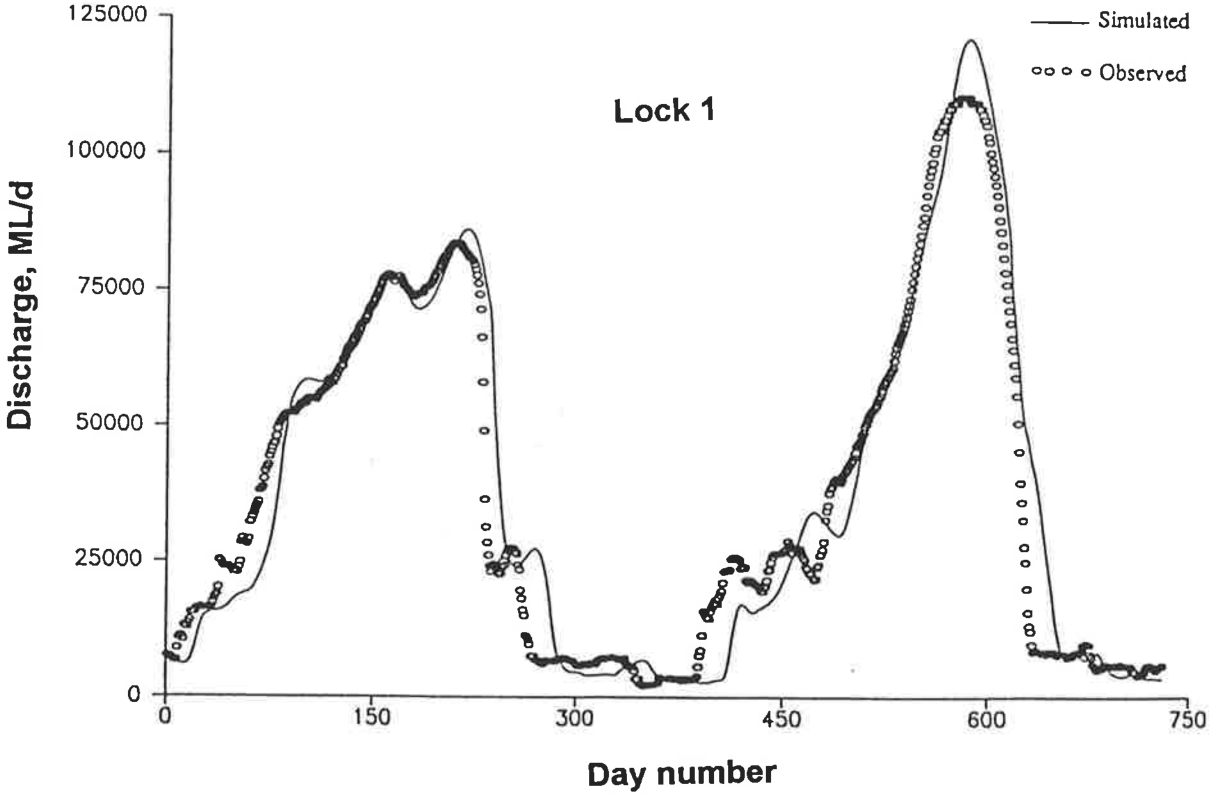

Lock 1
Simulated
Observed
Discharge, ML/d
125000
100000
75000
50000
25000
0
0
150
300
450
600
750
Day number

Figure 4.5. Mean prediction error for a. upstream and b. downstream of Locks. Data are presented for upstream of Locks 3, 5, 7 and 9, and downstream of Locks 3, 5, 7 and 10. Graphs are aligned with respect to zero prediction error for each Lock. The same scale is used for each Lock for comparison. Errors bars are standard errors (*n*=55-180).

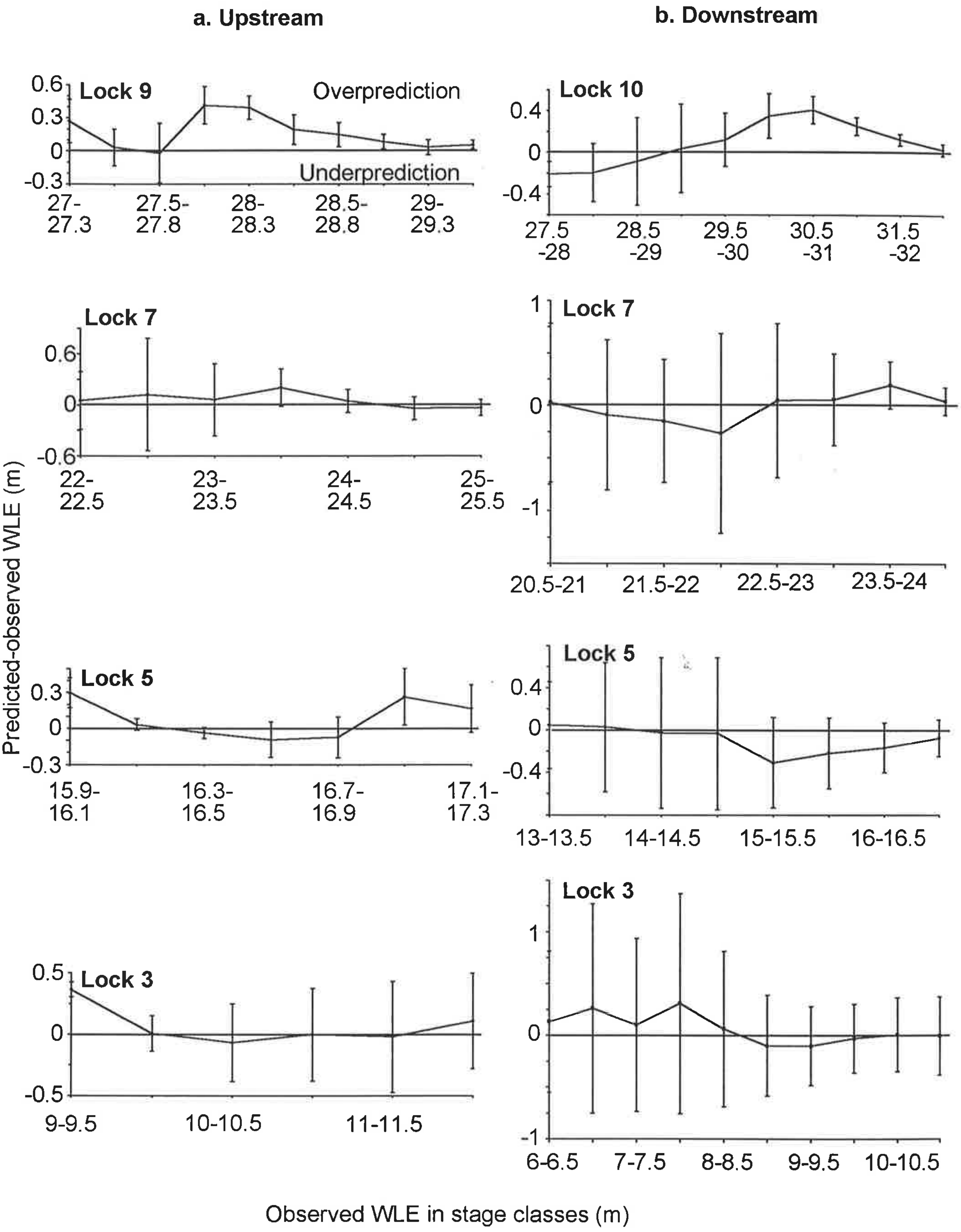

a. Upstream
b. Downstream
Lock 9
Overprediction
Underprediction
0.6
0.3
0
-0.3
27-27.3
27.5-27.8
28-28.3
28.5-28.8
29-29.3
Lock 10
0.4
0
-0.4
27.5-28
28.5-29
29.5-30
30.5-31
31.5-32
Lock 7
0.6
0
-0.6
22-22.5
23-23.5
24-24.5
25-25.5
Lock 7
1
0
-1
20.5-21
21.5-22
22.5-23
23.5-24
Predicted-observed WLE (m)
Lock 5
0.3
0
-0.3
15.9-16.1
16.3-16.5
16.7-16.9
17.1-17.3
Lock 5
0.4
0
-0.4
13-13.5
14-14.5
15-15.5
16-16.5
Lock 3
0.5
0
-0.5
9-9.5
10-10.5
11-11.5
Lock 3
1
0
-1
6-6.5
7-7.5
8-8.5
9-9.5
10-10.5
Observed WLE in stage classes (m)

Figure 4.6. Improved prediction accuracy with increasing distance downstream of Lock 4 for flows <14 000 ML/day. Predictions were generated using minimal inputs to the RMHM. Model output was compared to observed data for Loxton (23 km downstream) and Cobdogla (73 km downstream). The largest underprediction occurred downstream of Lock 4. A quadratic polynomial model of prediction error as a function of distance downstream of Lock 4 explained 76% of the variance.

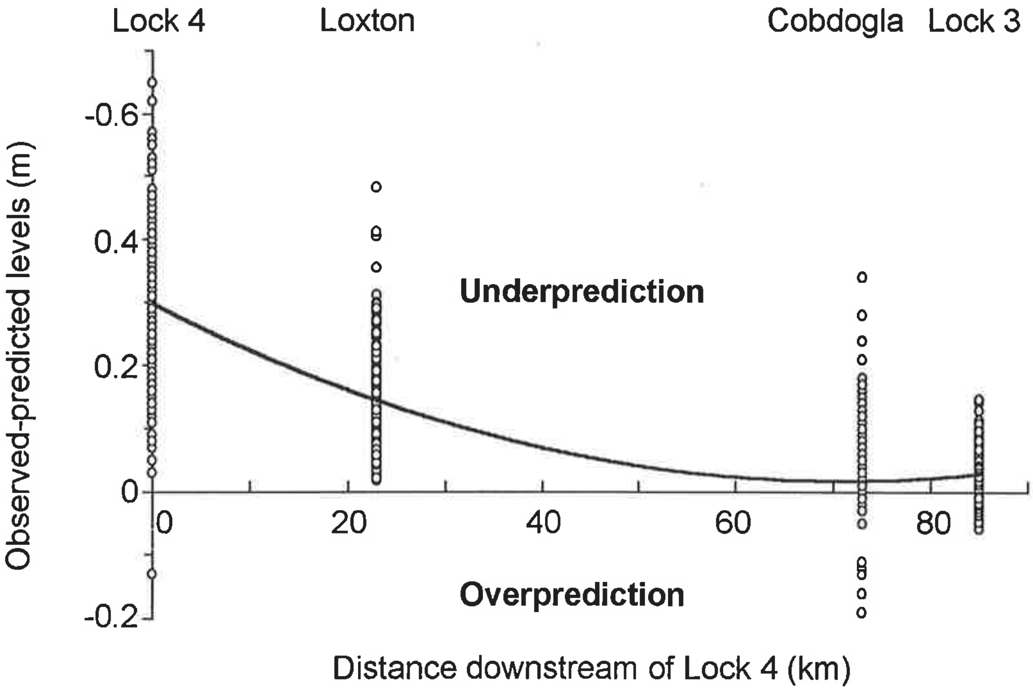

Lock 4
Loxton
Cobdogla
Lock 3
Observed-predicted levels (m)
-0.6
0.4
0.2
0
-0.2
Underprediction
Overprediction
0
20
40
60
80
Distance downstream of Lock 4 (km)

Figure 4.7. Comparison of RMHM output and linear interpolation (■) with observed WLE's at a. Loxton and b. Cobdogla, 23 km and 73 km downstream of Lock 4 respectively. Model output was generated using minimal (●) and improved (□) inputs (see text). Error bars are standard errors (*n*=55-180).

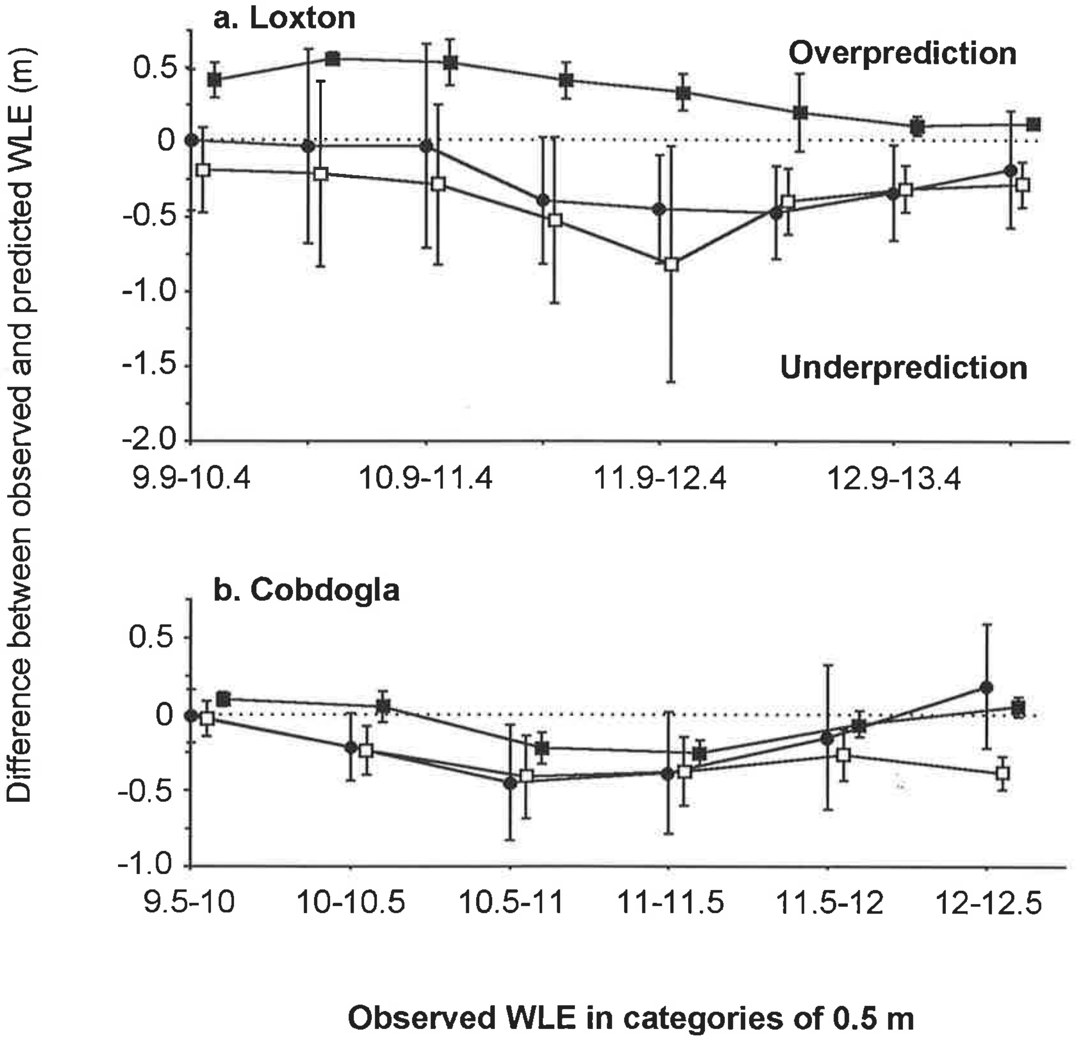

a. Loxton
Overprediction
Underprediction
0.5
0
-0.5
-1.0
-1.5
-2.0
9.9-10.4
10.9-11.4
11.9-12.4
12.9-13.4
b. Cobdogla
0.5
0
-0.5
-1.0
9.5-10
10-10.5
10.5-11
11-11.5
11.5-12
12-12.5
Difference between observed and predicted WLE (m)
Observed WLE in categories of 0.5 m

Figure 4.8. Temporal difference between observed and predicted (using minimal inputs) water level elevations with distance downstream of Lock 10. Locks 3-10 are indicated. Temporal difference, or lead-time, corresponds to the calculated minimal difference between observed and predicted data using least squares regression (r^2=0.971, P<0.0001).

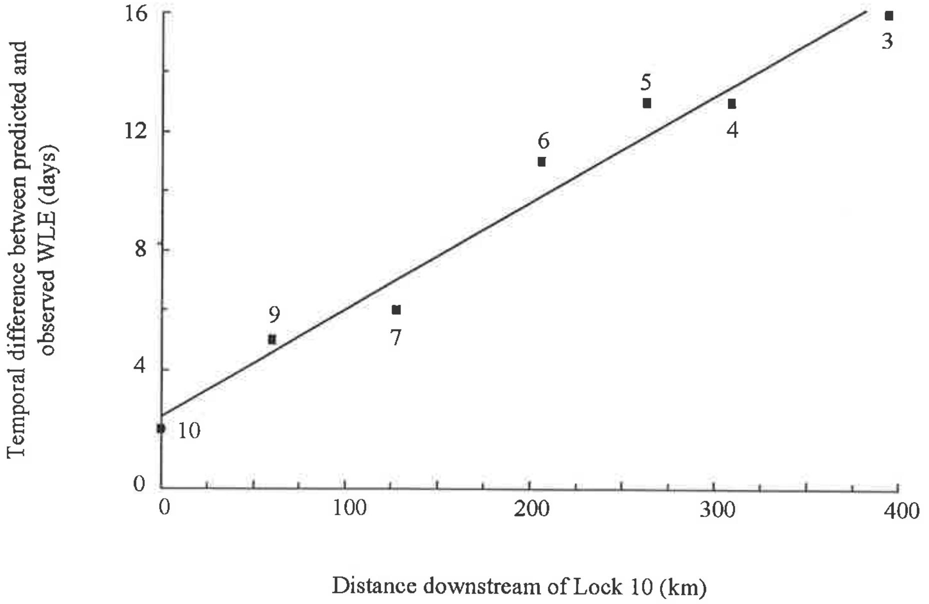
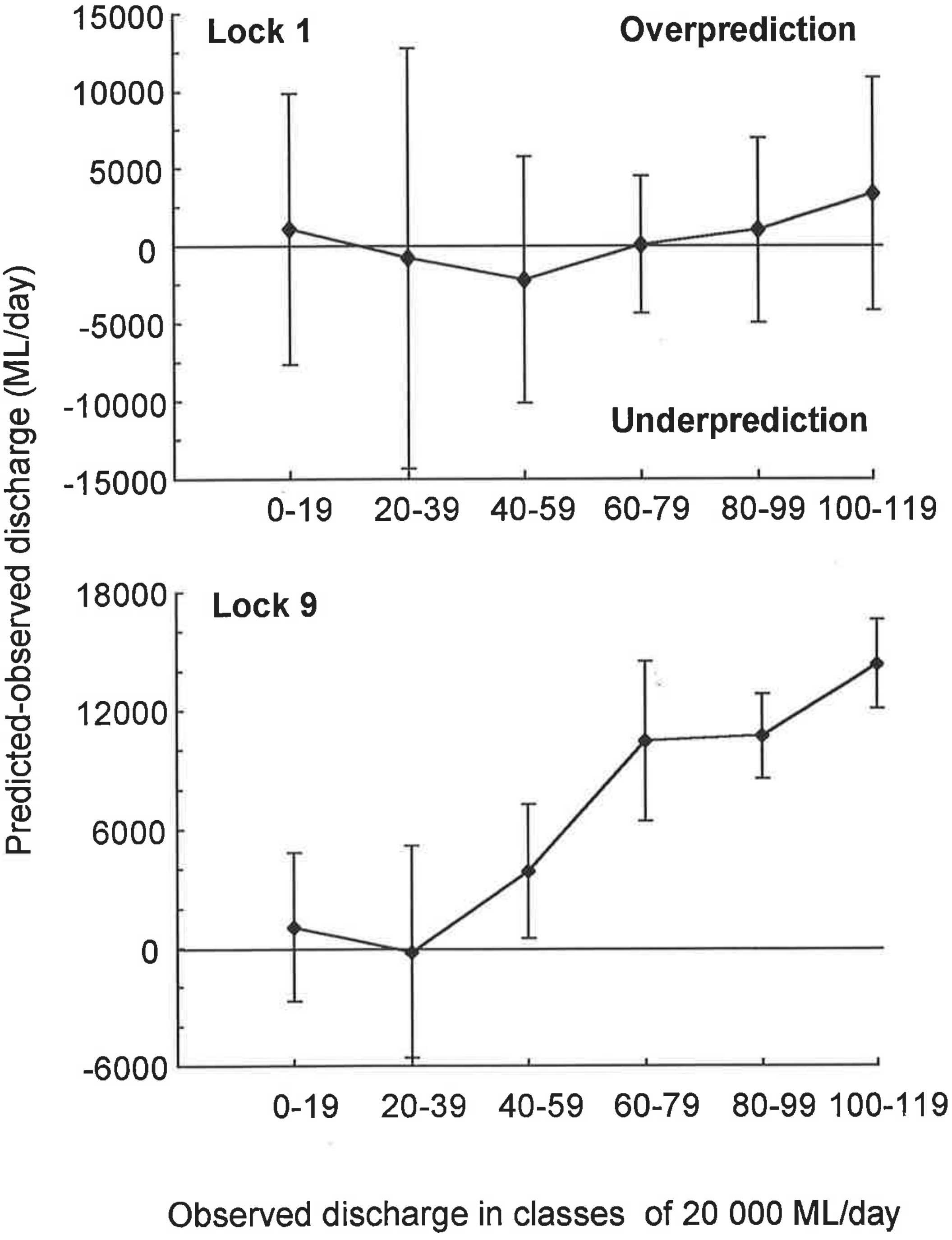

Temporal difference between predicted and observed WLE (days)
16
12
8
4
0
0
100
200
300
400
Distance downstream of Lock 10 (km)
10
9
7
6
5
4
3

Figure 4.9. Mean prediction error for flow rates at Locks 1 and 9. Data are presented for equal sized flow rate classes for each lock. Errors bars are standard errors (*n*=55-180) (from Maheshwari *et al.*, 1993).


Lock 1
Overprediction
Underprediction
15000
10000
5000
0
-5000
-10000
-15000
0-19
20-39
40-59
60-79
80-99
100-119
Predicted-observed discharge (ML/day)
Lock 9
18000
12000
6000
0
-6000
0-19
20-39
40-59
60-79
80-99
100-119
Observed discharge in classes of 20 000 ML/day

Chapter 5

Growth and resource allocation in response to flooding in the emergent sedge *Bolboschoenus medianus**

5.1 Abstract

Potted *Bolboschoenus medianus* plants were grown for 81 days at 20 (exposed), 0, -20, -40 and -60 cm (flooded) relative to the water surface in experimental ponds. Relative Growth Rate (RGR) and culm recruitment were highest at 20, 0 and -20 cm depth. Lower RGR at greater depths was due to reduced access to the atmosphere, suggested by a linear decline in total plant dry weight with emergent leaf area. RGR across the depth gradient was positively correlated with Net Assimilation Rate (NAR) (r =0.973, P <0.0001) but not with Leaf Area Ratio (LAR) (P =0.71). Culm recruitment declined rapidly outside the optimum depth range (0.53 week^{-1} at -20 cm, falling to 0.36 week^{-1} at 20 cm and 0.27 week^{-1} at -40 cm). LAR, a ratio of unit emergent leaf area to unit plant dry weight, remained fairly constant in flooded plants. This indicates a high degree of adaptation to flooding. *Bolboschoenus* adjusts its canopy height by culm extension, more vertical orientation of submersed leaves and higher leaf recruitment in flooded culms.

Carbon assimilation was less in exposed than flooded plants (20.2 *v.* 28.3 µmol CO_2 m^{-2} s^{-1} at 20 and -60 cm, respectively). Assimilation did not differ in plants at -20 cm and -60 cm, confirming that the decline in RGR with depth was due to less emergent leaf area rather than fixation per unit leaf area. With increased depth, percent biomass allocation to culms increased but allocations to tubers, rhizomes and roots decreased. Percent culm and tuber biomass were inversely linearly related (r=-0.957, P<0.0001), suggesting that culm extension is supported by translocation of carbohydrates from tubers. A model of growth and resource allocation is presented to show that *Bolboschoenus* reacts to flooding by altering its morphology to maintain LAR, principally by allocating below-ground biomass to culms despite a lower RGR.

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*Blanch *et al.* (in review, b)

5.2 Introduction

Elongation of stems or leaves in response to flooding is a common adaptation amongst emergent macrophytes (Lieffers and Shay, 1981; Grace, 1989; Blom *et al.*, 1990; Neill, 1990, 1992, 1993; Waters and Shay, 1990; Kirkman and Sharitz, 1993; Armstrong *et al.*, 1994; Crawford and Braendle, 1996). Failure to elevate the canopy above the surface can lead to carbon starvation (Cizkova-Koncalova *et al.*, 1992), causing lower root growth and reduced oxygenation of the sediments (Ernst, 1990). The increase in height of photosynthetic tissues is generally at the expense of below-ground tissues. For example, the marsh grass *Panicum hemitomon* increases its stem height when shallowly flooded, causing a doubling in the above to below ground biomass ratio (Kirkman and Sharitz, 1993).

Description of the morphological responses to flooding in aquatic macrophyte studies generally involves the presentation of basic plant biomass or stem density data. Whilst these may adequately describe the patterns and processes in the given species under the prevailing conditions, accurate comparisons with other studies are difficult. Final biomass depends, *inter alia*, upon initial plant biomass and the length of the experiment. In addition, whilst stem density may not change between depths, the leaf area exposed to atmospheric CO_2 and stem/leaf morphology may change. Thus, comparisons between species, and within species under different conditions, are difficult, and conclusions regarding the relative growth performances can only be tentative. Such data convey little information on response mechanisms - did flooded plants increase the rate at which they produced biomass for the same canopy size, or by adjusting the size of the canopy? The use of growth analyses such as relative growth rate (RGR), net assimilation rate (NAR) and leaf area ratio (LAR), which are widely used in terrestrial studies *e.g.* Poorter and Remkes (1990), would have two major benefits in studies of aquatic plants:

- Firstly, values of RGR, NAR and LAR can be more readily compared between and within species than simple biomass or stem/leaf production data. RGR is the rate of increase in dry weight per unit biomass per unit time (Eq (1), and Harper, 1977; Hunt, 1982; Beadle, 1993). NAR is the increase in plant biomass per unit leaf area per unit time (Eq (2)). LAR is the ratio of assimilatory material to plant biomass, expressed as the ratio of leaf area to total dry weight (Eq (3)). At any instant, RGR is the product of NAR and LAR, and the relative contribution of each to growth across a depth gradient can be ascertained by regressing each against RGR (*e.g.* Poorter and Remkes, 1990). The study by Mason and van der Vaalk (1992) of growth responses in the lily *Nypmhoides indica* across a water depth gradient indicates the benefit of this approach. They found that LAR made the largest contribution to RGR in shallow water, and NAR in deeper water. All three measures also changed over time for each depth due to plant age. These conclusions could not have been drawn using final biomass data, which showed no difference in total biomass across the depth gradient.

- Secondly, these indices describe the functional relationships between biomass production and leaf area over time. As plant biomass is a principal determinant of total respiration, and leaf area of photosynthesis, values of NAR and LAR are particularly insightful in interpreting the effects of submersion on a plant's carbon economy. For example, the poor performance of deeply flooded plants is due to a low NAR as the photosynthetic leaf area above the surface declines, causing a deterioration in its carbon budget.

Bolboschoenus medianus (V. Cook) Soják (formerly *Scirpus medianus*) is a rhizomatous, emergent sedge common throughout southeastern Australia (Fig. 5.1 and Plate 5.1; Black, 1980; Harden, 1993). At the generic level, *Bolboschoenus* is an ecologically important component of many wetland ecosystems in Central and Western Europe (Krisch, 1992; Zakravsky and Hroudova, 1994, 1996; Krahulec *et al.*, 1996), Southern Africa (Krueger and Kirst, 1991; Browning and Gordon-Gray, 1992), and Australia (Brix *et al.*, 1992; Froend *et al.*, 1993 ; Blanch and Walker, in press). *B. medianus* was chosen for this study as it broadly typifies many sedges, rushes, reeds and some grasses in the Murray's littoral, in terms of clonal habit, morphology, height and water regime preference. The study forms part of a broader investigation into plant strategies which permit growth under variable water regimes in semi-arid southeastern Australia (Rea and Ganf, 1994a,b,c; Brownlow *et al.*, 1994; Walker *et al.*, 1994; Blanch and Walker, in press; Blanch *et al.*, 1996; Cooling, 1996).

Species inhabiting the Murray's littoral zone experience frequent partial submersion and exposure (Walker *et al.*, 1994). Subterranean storage organs, such as tubers and corms, are central to their ability to support above-ground growth and for storage and protection during both flooding and exposure (cf. Grace, 1993; Crawford and Braendle, 1996). Many of these exhibit maximum growth and colonisation in shallow water or moist sediments. Taller stems or leaves are produced in deeper water, despite a decline in overall performance. In contrast to this 'reacting' strategy, other species are unresponsive to inundation, appearing rather to await a fall in water level to resume growth *e.g.* the lignified sedge *Baumea juncea* (R. Br.) Palla (Cooling, 1996).

I tested the hypotheses that (a) *Bolboschoenus* reacts to flooding by extending its culms to maintain its above-surface LAR, and (b) that this is achieved through the allocation of resources from tubers to culms. RGR was predicted to be highest in plants at 0 cm depth, and to decrease in deep water due to a reduction in NAR. Resource allocation strategies were examined using 'allocation triangles' (Tilman, 1988) to elucidate trade-offs between tissues under varying levels of resource supply.

5.3 Materials and Methods

5.3.1 Description of Bolboschoenus medianus

Bolboschoenus occurs in fresh to brackish conditions in the littoral zone of rivers, backwaters, wetlands, and floodplains. It has six main tissue types: leaves, culms (or stems), inflorescence and peduncle, tubers, rhizomes and roots (Fig. 5.1). Reproduction is predominantly vegetative. Tubers are 1-5 cm long, to 3 cm wide and have a fresh weight of up to 20 g. They comprise c. 50% of total plant biomass when the water level is at the sediment surface. A tuber generally produces 1 culm and 1-3 rhizomes, but mature tubers in optimal conditions can produce up to 4 culms and 5 rhizomes.

Culms are 0.3-1.5 m high, and to 2 m when flooded. Flowers are produced from October-April, but mainly in October and February (Black, 1980). Plants in the Lower Murray die back to below-ground tissues in May-June, and regrow from tubers from late August. Observations suggest growth occurs to c. 60 cm depth with an apparent optimum within ±20 cm of the water surface.

5.3.2 Experimental design

An experiment was devised to test the effects of flooding or exposure on young plants grown from tubers. Plants were grown in pots across a depth gradient in two outdoor ponds over summer-autumn 1995. These were placed so that the sediment surface was either

20 cm above the water surface, at the surface or 20, 40 or 60 cm below the water surface. The pots of exposed plants had numerous small holes in the base to ensure hydrological connectivity. Seven pots per depth were used, split between the two ponds. *Bolboschoenus* plants were collected from the littoral zone (depth 20-50 cm) in September 1994, near the mouth of the Murray at Tolderol, Lake Alexandrina, South Australia (35°4'S, 139°2'W, Fig. 1.1). These were used to produce vegetative stock by growing plants over summer at high nutrient conditions, high irradiances (noon solar irradiance 1500-2200 µmol m^{-2} s^{-1}) and high air temperature (daytime temperature 20-45°C). In February mature culms were selected and all tissues removed from the tubers (fresh weight 9.8 ± 1.6 g, mean and sd, n=60). A single tuber was placed in each 10 L pot (diameter 33 cm, depth 20 cm) and maintained at depth 0 cm for 3 weeks, till each pot contained 1-3 culms of height 30-70 cm and 1 or 2 tubers. This ensured similar below-ground resources and photosynthetic area between plants. Potting mix was sandy loam topped with 2 cm of commercially-available grey cracking clay. Nutrients were supplied by slow release fertilizer (8-9 month Osmocote®) at 100 g N m^{-2} y^{-1}.

Plants were then flooded or exposed at 10 cm day^{-1} to the final depth in outdoor ponds at the Botany Department. The experiment lasted 81 days (flooding commenced on 23 February and plants were harvested on 15-17 May). The approximate percent leaf area above the water surface was estimated visually: 100% at 20 and 0 cm, 50-70% at -20 cm, 30-40% at -40 cm and 0-10% at -60 cm.

5.3.3 *Morphological measurements*

The height of selected culms was determined approximately every 2 weeks over the experiment. Culm extension was recorded in culm numbers 2, 5, 10 and 25 to examine the effect of culm age on growth. Leaf recruitment and senescence were also recorded in these culms by recording the numbers of new and old leaves relative to a marked leaf. Culms were tagged upon emergence. Height to the highest leaf tip varied daily in an erratic fashion as leaves extended then oriented toward horizontal. Height to the highest visible leaf sheath base varied less and was used instead. Height from the leaf sheath to the highest leaf varied between 10-60 cm.

Numbers of leaves per culm, and data on the length and numbers of rhizomes in plants at selected depths, were recorded at harvest. Submersed leaves were observed in field populations to be oriented more vertically than emergent leaves of similar age, suggesting a mechanism to establish contact with the atmosphere more rapidly. Hence leaf angle relative to culms was measured in the first four mature, fully emergent leaves and wholly or partly submersed leaves in selected plants (*n*=15-25 leaves). Eight initial plants were chosen randomly, harvested and separated into components on 28 February. For calculation of RGR, NAR and LAR, initial plant dry weights were estimated as the mean shoot dry weight (culm+tuber+root+rhizome) x number of culms per plant.

5.3.4 *Carbon assimilation*

The rate of net photosynthesis in emergent leaves of plants at 20 cm, -20 cm and -60 cm was measured using closed-system infra-red gas analysis (IRGA, Li-6200, LiCor, NE, USA). Measurements were made between 1000 and 1400 h on clear autumn days in 6-19 leaves per depth. Leaves were chosen randomly from among the first four fully-extended leaves across several plants for each depth. Rates of light-saturated photosynthesis were compared between the three depths. The irradiance at which light-saturated photosynthesis commenced, I_k, was determined for the combined photosynthesis-irradiance responses for each depth using the hyperbolic tangent model of Jassby and Platt (1976; see Chapter 7).

At harvest, submersed and emergent leaves and culms were separated by clipping at the water surface. Tissues were washed over a 1 mm sieve and sorted via flotation. Tissues were oven dried at 80°C for 72 h to constant weight. Dead roots were infrequent and excluded.

5.3.5 *Analyses*

RGR, NAR and LAR were calculated after Harper (1977):

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

where W_f and W_i are the final and initial plant dry weights over Δt (days). RGR is a 'compound interest' function, expressing growth as a function of initial dry weight.

$$NAR = \frac{W_f - W_i}{\Delta t} \mathrm{x} \frac{\ln A_f - \ln A_i}{A_f - A_i} \qquad (\mathrm{g\ m^{-2}\ d^{-1}}) \qquad (2)$$

where A_f and A_i are the final and initial projected leaf surface areas (only 1 side of each leaf included). NAR is an estimate of net photosynthesis, and expresses the assimilatory efficiency of the plant per unit emergent leaf area.

$$LAR = \frac{A_f - A_i}{W_f - W_i} \mathrm{x} \frac{\ln W_f - \ln W_i}{\ln A_f - \ln A_i} \qquad (\mathrm{m}^2\,\mathrm{kg}^{-1}) \qquad (3)$$

LAR is a measure of the leaf area per unit plant dry weight. Units for RGR, NAR and LAR were chosen to allow for comparison with published data.

The final leaf area employed in calculating NAR and LAR was the emergent leaf area. The contribution of photosynthetic culms was considered to be low. Leaf area was estimated from area *v.* dry weight regressions for emergent leaves in plants grown across the elevation gradient (projected leaf area (cm^2) = (leaf dry weight (g) + 0.0182)/0.0075, r^2=0.917, P<0.0001). Leaf area was measured with a Delta T area meter. Submersed leaves did not photosynthesise in a Clarke-type oxygen electrode. Armstrong *et al.* (1994) reported that some emergent species may be able to fix carbon in partially submersed leaves by obtaining atmospheric carbon from a gaseous film which extends down the leaf from the emergent part. This was not examined for *Bolboschoenus*, but grooves on the surface may assist the development of such a film in calm water.

Growth and recruitment across the depth gradient were examined using linear regression and analysis of variance (Statistica, 1994). For ANOVA normality was tested with the Shapiro-Wilk statistic W and homogeneity of variance with Bartlett's test (Zar, 1996). Bartlett's test was only used when data were normally distributed. Non-parametric Kruskal-Wallis ANOVA was conducted on non-normal data. Significance was tested at a higher P value in the more conservative Kruskal-Wallis ANOVA (P=0.01 in parametric ANOVA and P=0.05 in non-parametric ANOVA). Means separation was conducted with the Tukey Honestly Significant Difference (HSD) test for parametric data and with the Nemenyi test following a Kruskal-Wallis ANOVA (Zar, 1996). The physiological mechanisms underlying growth responses at different flooding depths were examined in plants from 0 cm to -60 cm. As no obvious difference in plant response occurred between ponds (determined by comparing means and se), data were pooled for analyses.

5.4 Results

5.4.1 Growth analyses

Maximum RGR was 43.7 mg g^{-1} d^{-1} at 0 cm (Fig. 5.2a, and Table 5.1 for biomass data). This rate was not significantly different from that at 20 cm and -20 cm (*P*=0.001, Tukey's HSD), but was higher than at -40 cm (*P*=0.001). RGR at -60 cm was 19.5 mg g^{-1} d^{-1}, less than half that at 0 cm. The data suggest *Bolboschoenus* plants growing at 0 cm are able to accommodate fluctuations in water level of ±20 cm without a reduction in growth.

The decline in RGR with depth was due to a reduction in leaf biomass above the surface (Fig. 5.3). Above-surface leaf biomass fell from 43.8 g at 0 cm to 9.7 g at -60 cm (Table 5.1). Plant biomass is a linear function of emergent leaf area (Fig. 5.4). Plants at -40 cm and -60 cm placed considerably less photosynthetic tissue above the surface than shallower plants, and consequently assimilated less. This is reflected in the reduced NAR, and subsequently RGR, with increasing depth (Figs 5.2a,b). The linear relationship between emergent leaf area and plant biomass suggests LAR remains relatively constant regardless of depth, with the slope of 2.56 m^2 kg^{-1} being an approximation of LAR (as calculated by Eq (3)). The magnitude of change in LAR with flooding was small compared to the reduction in NAR (Figs 5.2b,c). Mean NAR declined 54% over the depth range 0 to -60 cm, but LAR remained within 12% of the maximum. This indicates that *Bolboschoenus* responds to flooding by adjusting its canopy height to maintain a fairly constant ratio of leaf area to plant biomass. Note that for interpretation the scale in Fig. 5.2c commences at 2.2 m^{-2} kg^{-1}: the essentially constant nature of LAR over the depth range is obvious when scaled from 0.

The small though statistically significant increase in LAR at -40 cm suggests an adaptation to increase plant leafiness when deeply flooded, which occurs in addition to its ability to maintain an otherwise fairly constant LAR across this depth range. This suggests a high degree of adaptation to flooding. LAR increased from 2.50 m^2 kg^{-1} at 0 cm to 2.74 m^2 kg^{-1} at -40 cm (Fig. 5.2c), despite a reduction in RGR of 55% over this depth range (Fig. 5.2a). However, stem extension was not sufficient to maintain an increase in mean LAR for all plants to -60 cm, where it declined to 2.42 m^2 kg^{-1}. Values of LAR of 2.51 to 2.73 m^2 kg^{-1}

Table 5.1. Biomass partitioning between tissues in *Bolboschoenus medianus* grown across an elevation gradient. Plants were grown at depths from 20 cm above the water surface to 60 cm below the surface. 'Above:below' is the above to below-ground biomass ratio. Data analysis was generally conducted with parametric ANOVA on original or square-root transformed data, but for some tissues with non-parametric Kruskal-Wallis ANOVA (H statistic †). $P<0.0001$ for all tissues. Different letters indicate significant differences at $P=0.01$ using a Tukey test, or at $P=0.05$ using the Nemenyi test following non-parametric ANOVA (mean and se, $n=7$, d.f.= 4, 32).

					Leaves		Culms				
Depth (cm)	Total	Above-ground	Below-ground	Above: Below	Total	Emergent	Total	Emergent	Tubers	Roots	Rhizomes
Dry weight (g)											
20	214.1 ± 0.4^{ab}	82.1 ± 5.3^{b}	132.0 ± 5.7^{ab}	0.62 ± 0.03^{b}	38.3 ± 1.9^{ab}	38.3 ± 1.9^{ab}	43.8 ± 3.5^{b}	43.8 ± 3.5^{a}	102.4 ± 4.4^{b}	17.8 ± 1.6^{a}	11.7 ± 0.6^{b}
0	258.5 ± 2.6^{a}	92.0 ± 5.9^{ab}	166.5 ± 8.6^{a}	0.56 ± 0.03^{b}	43.8 ± 2.0^{ab}	43.8 ± 2.0^{a}	48.2 ± 4.0^{ab}	48.2 ± 4.0^{a}	130.2 ± 8.5^{a}	19.5 ± 1.2^{a}	16.8 ± 1.3^{a}
-20	248.3 ± 9.4^{ab}	106.2 ± 4.5^{a}	142.1 ± 5.7^{ab}	0.75 ± 0.03^{ab}	46.8 ± 1.5^{a}	43.2 ± 1.6^{a}	59.4 ± 3.1^{a}	20.6 ± 1.4^{b}	113.9 ± 5.4^{ab}	15.9 ± 1.1^{a}	12.4 ± 0.5^{ab}
-40	110.3 ± 9.2^{bc}	59.7 ± 4.9^{c}	50.6 ± 4.5^{bc}	1.19 ± 0.04^{a}	25.0 ± 2.1^{bc}	20.7 ± 1.6^{bc}	34.8 ± 3.0^{b}	5.7 ± 0.4^{c}	39.7 ± 3.2^{c}	6.5 ± 0.9^{b}	4.4 ± 0.6^{c}
-60	47.5 ± 4.9^{c}	25.7 ± 3.1^{d}	21.8 ± 3.9^{c}	1.18 ± 0.15^{ab}	9.7 ± 1.1^{c}	7.1 ± 1.0^{c}	16.1 ± 2.0^{c}	2.0 ± 0.4^{c}	18.1 ± 4.1^{c}	2.3 ± 0.5^{b}	1.3 ± 0.2^{c}
F or H	25.19†	28.90	25.64†	22.94†	24.75†	23.69†	17.96	113.82	63.10	33.28	54.11
Percent allocation											
20	100	38.4	61.6	-	17.9	17.9	20.5	20.5	47.8	8.3	5.5
0	100	35.6	64.4	-	16.9	16.9	18.7	18.7	50.4	7.6	6.5
-20	100	42.8	57.2	-	18.8	17.4	23.9	8.3	45.9	6.4	5.0
-40	100	54.1	45.9	-	22.6	18.7	31.5	5.1	36.0	5.9	4.0
-60	100	54.1	45.9	-	20.3	14.9	33.9	4.2	39.2	4.9	2.8

were recorded in several plants at -60 cm which were slightly taller when first flooded, but most had lower values. One plant died at -60 cm because it had no emergent leaves when flooded. Plants with c. 5% of leaf area emergent survived but had low or negative RGR. Plants at -60 cm with 10% leaf area emergent had RGR close to that observed at -40 cm. This suggests that young plants require at least 10% of their leaf area to be emergent, and that a physiological threshold occurs at approximately -60 cm.

RGR was positively correlated with NAR ($F_{1,30}$=527.3, P<0.0001, r^2=0.946) but was independent of LAR ($F_{1,30}$=0.1, P=0.71, r^2=0.01) (Fig. 5.5). The low RGR of deeply flooded plants was due to a low NAR as little photosynthetic surface was exposed. Leaf morphology (expressed as LAR) influenced RGR little, but the morphological plasticity in partially-inundated plants detailed below indicates significant adaptation to flooding.

5.4.2 Plant morphology

In general, the effects of flooding on photosynthetic area were manifested in a change in culm production, rather than in leaf area produced per culm. A single inflorescence was produced during the experiment, in a plant at 0 cm.

Culm recruitment was greatest at 0 and -20 cm (0.48-0.53 culms day^{-1}) (Fig. 5.6). Recruitment at -40 cm was 0.27 culms day^{-1}, half that at -20cm, and at -60 cm only 0.11 culms day^{-1}. Thus for every culm produced at -60 cm, 5 were produced at -20 cm. A weak significant difference existed between recruitment at 0 and 20 cm (P=0.023, Tukey's HSD test). Water stress in plants 20 cm above the water surface reduced recruitment to 0.36 day^{-1} (see below).

A similar pattern occurred for numbers of leaves per plant (Fig. 5.7a). Maximum leaf production occurred at -20 and 0 cm (351 and 340 plant^{-1}, respectively), decreasing in shallower and deeper water. Numbers of leaves per culm was quite uniform in flooded plants, with only a minor, non-significant decline at -60 cm (Fig. 5.7b). Leaf size and length also appeared non-responsive to flooding (pers. obs).

Leaf orientation did vary, however, between fully emerged leaves and those initiated underwater. Emergent leaves tended more toward the horizontal (shown by a larger angle between leaf and culm) than fully or partially-submersed leaves:

Emergent	32.6 ± 4.6°
Partially-submersed	14.4 ± 1.7°
Fully-submersed	15.8 ± 2.7° (mean and sd, n=15-25 leaves)

Thus, adaptation to flooding was manifested as submersed leaves growing more vertically to the surface than in varying leaf number in these culms.

The high number of leaves per culm at 20 cm above the water surface may reflect a strategy to reduce culm production whilst maintaining leaf area production when water stressed (Fig. 5.7b). Culms are not required in the former to breach the water surface as in flooded plants, and are metabolically expensive to produce, having a high structural content.

Whereas leaf recruitment declined with depth in culm 2, which was initiated prior to flooding, recruitment remained quite uniform over the depth range in culms initiated after flooding, with some indication of recruitment peaking in plants flooded to 20 and 40 cm (culms 5 and 10 respectively; Fig. 5.8). This appears to be a mechanism which, in conjunction with culm extension and orienting leaves more vertically when flooded (see below), provides for higher LAR at -40 cm than at 0 cm. This represents an interesting adaptation to flooding. For culms of all ages, recruitment at -60 cm was less than that at -40 cm (except for culm 25 which was not produced at these depths). In plants flooded to 60 cm, recruitment in culms produced soon after submersion was twice that in culms initiated prior to inundation (0.15 day^{-1} and 0.07 day^{-1} for culms 5 and 2, respectively).

Leaf senescence increased with depth in culms 2 and 5 (except at -60 cm in the latter as these were produced late in the experiment). Submersed leaves were generally chlorotic and structurally weaker than emergent leaves, having mostly aerenchymatous tissue composed of enlarged cells. Consequently they senesced more rapidly than emergent leaves. In culm 2 senescence at -60 cm was almost threefold higher than at 0 cm, indicating that submersed, non-photosynthesising leaves are shed more rapidly when submersed to reduce their respiratory demand on the plant. This also occurred in culm 5, which was produced when inundated, indicating this strategy acts independently of whether the culm was initiated when emergent or submersed.

Leaf recruitment declined over time in culm 2, but senescence remained uniform for all depths except -60 cm (Fig. 5.9). Senescence was higher in plants at -60 cm until late March, after which nearly all submersed leaves had been shed. Recruitment rate declined over time for culm 2, falling from 0.4 leaves day^{-1} when flooding commenced to <0.1 day^{-1} by 11 April. Recruitment peaked in late March or early April for most depths in culm 5 (data not shown: the few data available for culms 10 and 25 indicate peak recruitment was attained near or after late April).

5.4.3 Culm height

Bolboschoenus produced longer culms in deep water to elevate photosynthetic tissues above the surface (Fig. 5.10). The elongation of stems and leaves in response to partial submersion has been documented in many emergent species *e.g. Typha* spp. (Grace, 1989), and *Scirpus* spp. (Lieffers and Shay, 1981; Squires and van der Vaalk, 1992). The height of the highest visible leaf sheath in culm 2 was 53 cm at 0 cm depth, rising to 80 cm at -60 cm depth. Culm extension did not completely match flooding depth however: the 20 cm increase in depth from -40 cm to -60 cm elicited only a 7 cm increase in mean culm height in culm 2. Culms recruited later in the experiment showed similar patterns, but were not as high. At -60 cm culms 2 and 5 were of similar height (apart from one 6 cm high culm 5, which lowered the mean height and increased the variance). Culm 10 was <10 cm high at -60 cm whilst no culm 25 was produced. In culm 2, extension was minimal after 17 April at 0 cm and -40 cm (Fig. 5.11). The growth trajectory shows that the youngest culms had adjusted to the water level within 2 months. Culms 5, 10 and 25 had not fully adjusted after 81 days. The data also show the effect of partial submersion on the timing of recruitment. Culms 2 and 5 were recruited at similar times, but culm 10 appeared approximately 7 days later at -40 cm. Culm 25 was produced by 4 April at 0 cm, but not until 4 May at -40 cm.

5.4.4 Carbon assimilation

The photosynthesis-irradiance response in *Bolboschoenus* leaves indicates that light saturation commences at approximately 1000 μmol m^{-2} s^{-1} (Fig. 5.12). As this relationship incorporates rates measured in emergent leaves in plants grown at three depths (which vary with depth), the I_k value is only an approximation. Net photosynthesis measured at irradiances greater than 1000 μmol m^{-2} s^{-1} was similar for the emergent leaves of plants at

Table 5.2. Net photosynthesis and stomatal conductance in emergent leaves of exposed, shallowly flooded and deeply flooded *Bolboschoenus* (mean and se). Letters indicate significance (numbers followed by the same letter are not significantly different at P=0.01; Tukey's HSD test for unequal n).

Depth	Number of leaves	Net photosynthesis (μmol CO_2 m^{-2} s^{-1})	Stomatal conductance (mmol m^{-2} s^{-1})
20 cm (exposed)	16	20.20 ± 0.45^b	770 ± 40^b
-20 cm (shallowly flooded)	6	26.80 ± 0.45^{ab}	1410 ± 290^a
-60 cm (deeply flooded)	19	28.32 ± 0.65^a	1120 ± 40^a

-20 cm and -60 cm, but lower in exposed plants due to lower stomatal conductance (Table 5.2). Lower stomatal conductance in exposed plants indicates water stress: 770 mmol m^{-2} s^{-1} at +20 cm and 1 410 mmol m^{-2} s^{-1} at -20 cm. Internal CO_2 concentrations for the three depths were 290-298 ppm, and did not differ significantly between depths (P=0.25).

5.4.5 *Biomass allocation patterns*

The strategy of *Bolboschoenus* to allocate below-ground biomass to culms when flooded is illustrated in Fig. 5.13 (see also Plate 5.2 and percent allocation data in Table 5.1). Percent allocation to culms increased from 18% at 0 cm to c. 35% at -60 cm (Fig. 5.13a). Culm extension was supported by below-ground tissues. Tuber biomass decreased from 50% at 0 cm to 31% at -60 cm (Fig. 5.13b), and rhizome biomass fell from 6.5% to 2.6% over the same depth range (Fig. 5.13c). Percent root biomass also declined with depth ($F_{1,30}$=11.58, P=0.002, r^2=0.34; Fig. 5.13d), but less than for rhizomes.

Bolboschoenus exhibited up to a 3-fold increase in allocation to above-ground tissues when deeply flooded. Mean above to below-ground biomass ratio at 0 cm was 0.56, doubling to 1.19 at -40 cm (Table 5.1). Culm extension continued at -60 cm in plants which had c. 10% of their leaf area above the surface when flooded. These plants had above to below-ground biomass ratios of 1.5-1.7, three times those at 0 cm. Several plants which had 0-5% of their leaf area above the water surface had lower ratios of 0.8-1.2 due to carbon starvation. The lower ratios in these plants are a consequence of the more rapid biomass loss of culms, leaves and roots than of tubers when flooding increases from 40 to 60 cm. This is shown by the 3% increase in percent tuber biomass from -40 to -60 cm compared to the 10% reduction from -20 to -40 cm. The difference in tissue structure and resilience imparts an advantage to deeply flooded *Bolboschoenus* by preventing carbohydrates being 'wasted' on culm extension when too deeply flooded. Two to three-fold increases in above to below-ground biomass ratios have been reported for other emergent species growing in flood-prone wetlands *e.g.* from 0.43 to 0.83 in the grass *Panicum hemitomon* (Kirkman and Sharitz, 1993), and from 0.54 to 1.27 in *Scolochloa festucacea* (Neill, 1993).

The role of tubers in supporting culm extension is indicated in the allocation triangle in Fig. 5.14a (cf. Tilman, 1988). At 0 cm, allocation to tubers is high (45-60%) and allocation to culms low (15-22%). With increasing flooding depth (left and upwards), which reduces access to atmospheric CO_2 and O_2, allocation to culms increases as allocation to tubers decreases. The positive correlation between rhizome and tuber biomass (high tuber and rhizome allocation at 0 cm, and both decreasing with depth; Fig. 5.14b) underlies the reduction in culm recruitment when flooded to >20 cm (Fig. 5.6). Vegetative spread is curtailed by the preferential allocation of carbohydrates stored in tubers to culm production.

Numbers of tubers produced were highest at depths 20 to -20 cm (66.3-69.1; Table 5.3), and lowest at -60 cm. Numbers of tubers fell 54% from -20 cm to -40 cm. A high ratio of numbers of tubers to culms (*e.g.* 2.36 tubers per culm at 20 cm above the surface) indicates a high allocation to future vegetative growth whilst a low ratio (1.21 at -60 cm) indicates resources are allocated to CO_2 acquisition in extant culms rather than to many tubers for growth in the following season. The mean dry weight of individual tubers was greatest when the water level was within ±20 cm of the water surface (1.58-1.90 g, Table 5.3). Depletion of carbohydrate stores for culm extension reduced mean weight to 1.08 g at -60 cm.

5.4.6 Rhizome length and number

Mean and sum rhizome length per plant were higher at -20 cm than at 0 cm and -60 cm (Table 5.4). A single plant in the former produced a total of 11.9 m of rhizome, with a

Table 5.3. Number of tubers per plant, ratio of the number of tubers to number of culms, and mean individual tuber biomass across a depth gradient (mean and se, n=7). Letters indicate significance (numbers followed by the same letter are not significantly different at P=0.05 for numbers of tubers using the Nemenyi test following a Kruskal-Wallis ANOVA, or P=0.01 for the last two columns; Tukey's HSD test).

Depth (cm)	Number of tubers	Ratio of numbers of tubers to culms	Mean tuber biomass (g dry weight)
20	66.3 ± 12.6^{a}	2.36 ± 0.32^{a}	1.58 ± 0.10^{abc}
0	68.4 ± 6.7^{a}	1.80 ± 0.17^{b}	1.90 ± 0.09^{a}
-20	69.1 ± 7.3^{a}	1.65 ± 0.10^{bc}	1.65 ± 0.04^{ab}
-40	31.7 ± 8.3^{ab}	1.40 ± 0.11^{cd}	1.28 ± 0.08^{bc}
-60	12.0 ± 2.9^{b}	1.21 ± 0.21^{d}	1.08 ± 0.06^{c}

mean length of 19 cm (Plate 5.3). This fell to 1.5 m and 10.9 cm respectively at depth -60 cm.

Rhizomes were thicker and stronger in 0 cm plants, as indicated by the reduction in biomass investment per unit length in deeper water (0.016 to 0.006 g cm^{-1} at -60 cm). Mean rhizome biomass production was 16.8 g at 0 cm, falling to 1.3 g at -60 cm (Table 5.1). Irrespective of depth, the maximum number of meristems available for rhizome growth was five.

The longest rhizomes were produced by the first daughter tubers at -20 cm (mean, 22.9 cm, Table 5.4). These tubers produced the greatest number of rhizomes longer than 30 cm, followed by the second and third tubers (6, 5 and 4 rhizomes respectively). Rhizomes were generally shorter at depth 0 and -60 cm, with a maximum mean length at 0 cm of 17.5 cm. The effect of depth on vegetative spread is also indicated by the left-skewed frequency distribution of rhizome lengths in Fig. 5.15. Many of the shorter rhizomes were young and still extending. However, many short rhizomes had also produced tubers with rooted culms which suggests their maximum length had been attained. RGR in the plant at -20 cm was lower than in the 0 cm plant (35 v 43 mg g^{-1} d^{-1}, respectively). Hence, rhizome length was not a direct function of increasing growth. The reason for a higher proportion of long rhizomes in plants flooded to 20 cm is not clear, but may indicate a strategy to disperse

Table 5.4. Mean and sum rhizome length and number per plant at depths 0, -20 and -60 cm. Rhizome number refers to the position in the plant's rhizome network: the original and first daughter tuber are connected by rhizome 1, the first and second daughter tubers by rhizome 2, and so on. Data are for one plant per depth.

Depth:			**0 cm**					**-20 cm**					**-60 cm**		
Rhizome number:	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
mean length (cm)	9.2	16.1	17.5	12.8	11.4	10.0	22.9	20.2	17.5	17.2	0.1	10.0	12.8	17.4	0
sd	9.6	10.7	11.9	5.8	5	9.9	11.0	12.7	13.1	12	0	4.7	8.3	2.8	-
Number of rhizomes >30 cm	0	1	2	0	0	0	6	5	4	1	0	0	0	0	0
Sum rhizome length per plant (m)			**9.34**					**11.9**					**1.5**		
Number of rhizomes per plant			66					63					14		
Mean rhizome length per plant (cm)			14.2					19.0					10.9		
Biomass investment per cm (rhizome dry weight/sum length) (g/cm)			0.016					0.011					0.006		

culms across the elevation gradient to ensure survival at the plant level should water levels rise further. Such a 'bet-hedging' strategy appears to be exhibited only in plants growing within their optimum depth range. The inability of *Bolboschoenus* to pressurise its culms for the convective flow of oxygen to rhizomes (Brix *et al.*, 1992) may explain the much shorter rhizomes produced at -60 cm.

5.5 Discussion

5.5.1 Optimum depth range for growth and recruitment

Experimental data contrast with observed distributions of *Bolboschoenus* across the elevation gradient of the littoral zone in Pool 5. RGR peaked within a narrow depth range (within ±20 cm of the sediment surface; Fig. 5.2a), whereas plants occurred in six of seven water regime groups (Fig. 3.6). The experimental data indicate recruitment was highest approximately one month before surveying during and immediately after flooding. Hence growth was stimulated across the littoral.

High RGR in this range was due to a high leaf dry weight above the water surface, producing a high NAR (Fig. 5.2b; 15-20 $g\ m^{-2}\ d^{-1}$). Lower RGR in flooded plants was principally due to a reduction in NAR; lower biomass assimilation occurred as emergent leaf area available for photosynthesis declined (Fig. 5.4), rather than in the rate of assimilation per unit emergent leaf area (Table 5.2). Rates of net photosynthesis were higher in the emergent leaves of deeply flooded plants than plants exposed by 20 cm and water stressed, thereby reducing stomatal conductance. The ability of *Bolboschoenus* to maintain a fairly constant LAR across a wide range of flooding conditions indicates a high degree of morphological plasticity. This is demonstrated by the linear relationship between emergent leaf area and plant biomass in Fig. 5.4. Whilst the reduction in NAR was much greater than the increase in LAR, this plasticity is a significant adaptation for survival in the Murray's littoral. The three principal means by which partially submersed *Bolboschoenus* increased the size of its emergent canopy were by extension of its culms, growing submersed leaves more vertically to breach the surface, and higher leaf recruitment. Culm extension, arguably the most effective means of improving LAR, was supported by the export of biomass from tubers to culms (Fig. 5.14a).

A summary model of growth and resource allocation in *Bolboschoenus* grown across an elevation gradient is shown in Fig. 5.16. RGR, culm production and below-ground biomass are optimal in the depth range +20 to -20 cm. With increasing depth below-ground tissues and culm production decline, but culm height increases. The length of the arrow indicates the relative extent of the plant's reaction to flooding in allocating carbohydrates in tubers to culms extension.

Maximum RGR was 43.7 mg g^{-1} d^{-1} at 0 cm (Fig. 5.2a). This rate is low compared to that reported for many other aquatic macrophytes grown under favourable conditions *e.g.* *Juncus effusus*, 147 mg g^{-1} d^{-1} (Grime and Hunt, 1975); *Carex* spp., 61-83 mg g^{-1} d^{-1} (Konings *et al.*, 1989); *Nymphoides indica*, 41-64 mg g^{-1} d^{-1} (Mason and van der Vaalk, 1992); and a range of annual and perennial species from eastern North America, 170-280 mg g^{-1} d^{-1} (Boutin and Keddy, 1993). As well as innate rapid growth in these species, these values may in part reflect the favourable nutrient, light and temperature conditions employed in these studies. The present study was conducted mainly over autumn, when solar irradiance and air temperatures were below optimum for *Bolboschoenus*. Noon irradiances were 400-1800 µmol m^{-2} s^{-1}, and thus frequently below that required to saturate photosynthesis (I_k for *Bolboschoenus* is c. 1 000 µmol m^{-2} s^{-1}, Fig. 5.12). Daytime air temperatures were in the range 15-28°C, whereas *Bolboschoenus* grows tallest and perennates most rapidly over summer in the Lower Murray (Plate 5.4), when air temperatures frequently reach 40°C. Hence rates of carbon assimilation were below maximum. Nevertheless, the low maximum RGR agrees with lower observed rates of colonisation compared with common reed *Phragmites australis* and grasses *Paspalum distichum* and *Cynodon dactylon*. They occupy similar elevations to *Bolboschoenus* in the Murray's littoral, but generally spread more rapidly and have more extensive stolon/rhizome systems.

In contrast to RGR, NAR observed in shallow water plants is higher than that reported for 24 terrestrial C_3 species by Poorter and Remkes (1990; 7.4-12.1 g m^{-2} d^{-1}). Given that RGR was highly correlated with NAR (Fig. 5.5a) this is surprising. *Bolboschoenus* also possesses C_3 photosynthetic metabolism (J. Bruhl, Department of Botany, University of New England, Australia, pers. comm.), but has a much lower allocation to leaves than the species in Poorter and Remkes' study: 16.9-22.6% of total biomass in this study (Table 5.1) and 43-66% in the latter (shown as leaf weight ratio). Hence NAR, which is a measure of the ability to produce biomass per unit leaf area per day, is high in *Bolboschoenus* due to a low leaf area per unit total biomass. The low LAR in *Bolboschoenus* compared to that in Poorter and Remkes' study (2-3 $m^2\,kg^{-1}$ and 14-36 $m^2\,kg^{-1}$, respectively) and in *Nymphoides indica* (4-11 $m^2\,kg^{-1}$, Mason and van der Vaalk, 1992) is similarly due to a low allocation to leaves.

Weir operations in the regulated Murray impose regular and rapid changes in level of up to 20 cm over several days (Maheshwari *et al.*, 1993; Blanch and Walker, in press). The ability of *Bolboschoenus* to accommodate frequent exposure and partial inundation are due in part to its morphology. For a culm growing at 0 cm, a 20 cm rise in water level would submerge relatively little photosynthetic area as most leaves are produced higher on the culm. Culms are also strong but flexible for withstanding currents, and dense stands afford mutual protection by buffering wave motion. Plants exposed by 20 cm in this study had lower culm recruitment than those at 0 cm (Fig. 5.6) due to lower rates of carbon fixation. However, the sandy-loam potting sediment used in this study has a much lower water holding capacity than littoral sediments which commonly occur in the Murray. These are composed of grey clays and clay-loams, and have a high organic matter content. Growth can persist in these sediments for long periods following flooding and drawdown. In a field study of the effects of the rate of flood recession on *Bolboschoenus* growth, plants grown 44 cm above the surface extended roots to the water table when water levels fell slowly (c. 2.5 cm day^{-1}; Chapter 6). Biomass production after 2 months was similar in plants at 44 cm and 0 cm when partially flooded and exposed. In conjunction, these data suggest that the ability of *Bolboschoenus* to tolerate water level fluctuations of up to 40 cm in the Murray's littoral is due in large part to a morphology which accommodates minor water level fluctuations with minimal loss in growth.

Water stress in plants exposed by 20 cm reduced stomatal conductance, and consequently rates of light-saturated photosynthesis (Table 5.2). Culm recruitment was 32% lower in plants exposed by 20 cm than plants flooded by 20 cm. Whilst RGR was not significantly different between these two treatments (Fig. 5.2a), it can be concluded that lower rates of assimilation in water stressed plants act to reduce recruitment. The absence of any difference in RGR despite much lower recruitment rates in exposed plants suggests that culms were structurally denser.

Culm recruitment had a narrower optimum depth range than RGR, and was skewed toward deeper water (Fig. 5.6), *i.e.* recruitment fell more rapidly in deep water than it did at 0 cm or 20 cm. The right-skew in recruitment across the elevation gradient departs from the classic Gaussian response used in ordination techniques to model responses across environmental gradients (*e.g.* Austin, 1985). The skewed distribution reflects the different physiological stresses imposed on growth, though ultimately both induce carbon starvation (from reduced stomatal conductance when exposed, and reduced emergent leaf area available for photosynthesis when flooded). Non-Gaussian response curves were recently reported by Hoagland and Collins (1997) in wetland vegetation occurring across moisture and nutrient gradients. Skewed distributions have also been reported for a wide range of species and environments *e.g.* in eucalypt species growing across elevation gradients in Australia (Austin *et al.*, 1994), and in the shrub *Periploca* (Asclepiadaceae) across gradients of aspect and altitude (Ferrer-Castán *et al.*, 1995). The data for *Bolboschoenus* and these studies indicate that endeavours to model the effects of water depth and exposure on wetland vegetation must first determine the shape of the response curve for each species or community.

5.5.2 *Biomass allocation*

Bolboschoenus responded to flooding by producing longer culms to maintain a high LAR and thus a more favourable carbon economy (Figs 5.4, 5.10 and 5.16). Stem elongation during flooding has been reported in many emergents (*e.g.* Grace, 1989; Waters and Shay, 1990; Rea and Ganf, 1994a). Elongation is stimulated by the increase in ethylene concentration, which diffuses 10^4 times more slowly in water than in air. Ethylene indirectly stimulates cell production and elongation by sensitising meristems to giberellic acid, and increases the elasticity of cell walls (Armstrong *et al.*, 1994). Thus long, structurally weaker stems are produced. *Bolboschoenus* culms produced during flooding are up to 2 m tall, and lodge when floodwaters recede. Elongation is due to an increase in internode length, indicated by the absence of significant changes in leaf production per culm across the depth gradient (Fig. 5.7b).

Three-fold higher above to below-ground biomass ratios in two of the seven deeply flooded plants than at 0 cm indicate a high degree of adaptation to flooding. The lower increase in the mean ratio across all plants at -60 cm (0.56 at 0 cm to 1.18 at -60 cm, Table 5.1) indicates how sensitive *Bolboschoenus* is to water level fluctuations at the extreme of its depth range. Plants with 0-5% leaf area emergent at -60 cm died or had negative or low RGR, whereas growth was relatively high when 10% of the leaf area was emergent.

The inverse relationship between percent tuber biomass and percent culm biomass (Fig. 5.14) suggests culm extension was supported by allocation of carbohydrates from tubers. This resulted in fewer, smaller tubers being produced in deep water (Table 5.3). A similar inverse relationship between petiole and storage root, expressed as a percent, occurs in the lily *Villarsia reniformis* R. Br. (Menyanthaceae) (Cooling, 1996).

The highly significant relationship between emergent leaf area and plant biomass indicates the importance of elevating the canopy above the surface for gas exchange (Fig. 5.4). Grace (1989) suggested that lower growth in deeply flooded *Typha latifolia* was due to light limitation of photosynthesis (in submersed leaves?). Lower RGR in deeply flooded *Bolboschoenus* is more likely due to reduced availability of emergent leaf area for the acquisition of CO_2 and O_2, however. Carbon fixation is hypothesised to be low (negligible?) in the submersed section of emergent leaves, as *Bolboschoenus* is unable to transport air *via* convective flow from emergent to submersed tissues (see below). Despite an apparent reduction in cuticle thickness over time in submersed leaves, the direct uptake of dissolved CO_2 is also unlikely to contribute significantly to fixation. Squires and van der Vaalk (1992) also argued that emergent leaf area rather than light was the proximate factor in limiting growth in flooded emergent macrophytes.

The relationship in Fig. 5.4 indicates significant adaptation to flooding in *Bolboschoenus*. It suggests that, regardless of depth, *Bolboschoenus* maintains a LAR of c. 2.56 $m^2 kg^{-1}$ (or slightly higher at -40 cm), and that this occurs until so deeply inundated that RGR becomes negative. At this point, the more rapid loss of culms, leaves and roots in plants with <10% of their leaf area emergent indicates an important strategy to prevent all carbohydrates being used for culm extension when too deeply flooded. In contrast to the 10% fall in percent tuber biomass from -20 to -40 cm, a 3% increase in percent tuber biomass occurred from -40 to -60 cm. This represents a mechanism to preserve resources in tubers for growth when the water level falls.

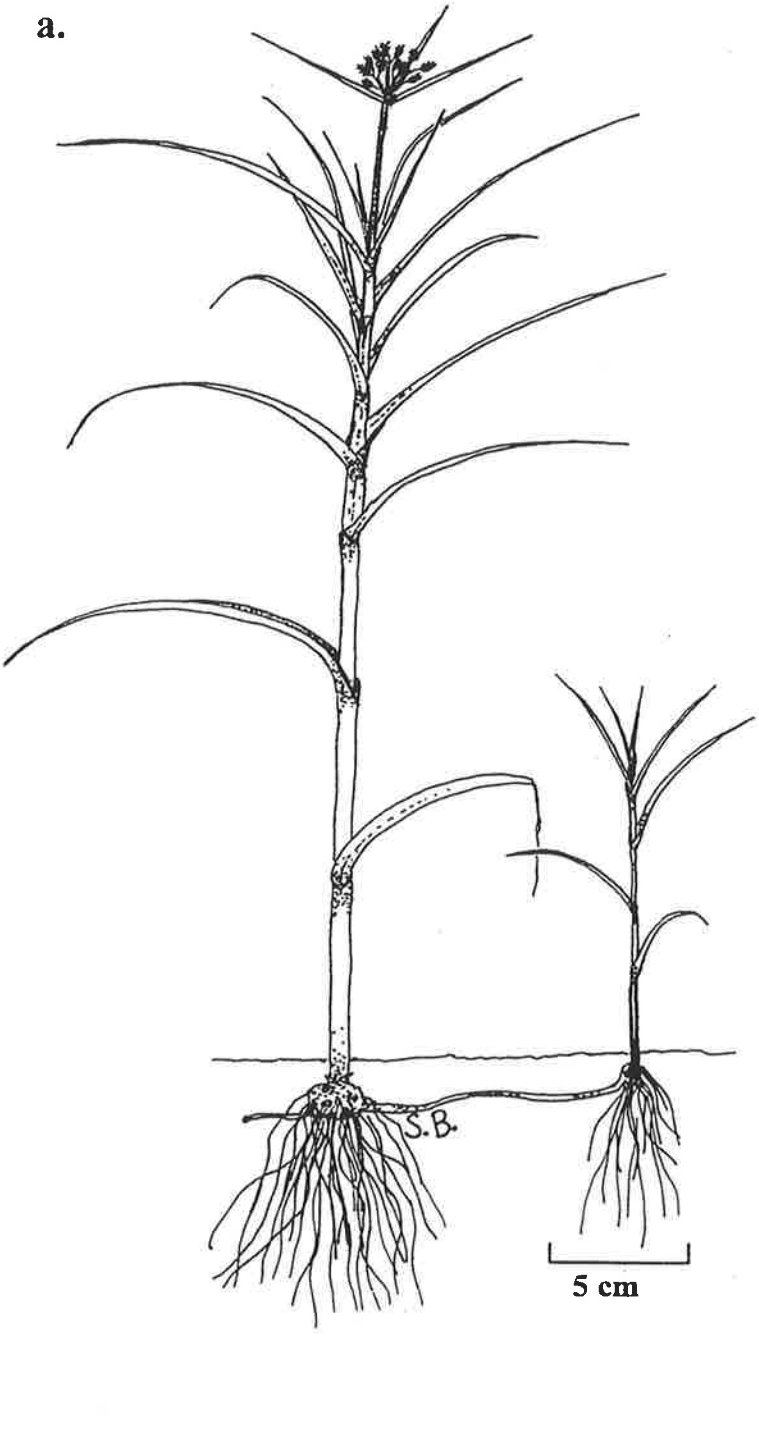
The sharp decline in LAR at -60 cm suggests the onset of a physiological stress operating to curtail culm extension. Whilst *Bolboschoenus* exhibits minor pressurisation (Brix *et al.*, 1992), its lacunal morphology is unsuitable for pumping air to the root zone. Internal pressurisation and convective through-flow occurs in emergents with cylindrical stems or linear leaves such as *Phragmites australis, Schoenoplectus* spp. and *Eleocharis* spp. (Brix *et al.*, 1992). *Bolboschoenus* does not possess either. *Bolboschoenus* plants with <10% of their leaf area emergent when deeply flooded may be unable to maintain sufficient oxygen concentrations in the rhizosphere for foraging by the roots. Activity of aerobic nitrifying bacteria will also decline resulting in lower nitrogen availability in the sediments (Armstrong *et al.*, 1994).

Percent tuber and rhizome biomass were positively correlated across the depth gradient, with both decreasing with depth. The correlations between percent tuber biomass and percent culm and rhizome biomass highlights the importance of tubers for storing and allocating carbohydrates for growth. Grace (1993) suggests the primary roles of tubers are protection and storage followed by anchorage, numerical increase and dispersal. *Bolboschoenus* tubers afford protection from grazing and fire, and are desiccation resistant for up to one season (according to Aston, 1973). In a study of medium-term viability, tubers were stored in dry soil for 2.5 y to simulate the flooding frequency of medium-sized flows on the Lower Murray's floodplain. None produced culms when wetted at 30°C. Regeneration from seed is therefore hypothesised to be the dominant form of regrowth in floodplains inundated only every second year. In contrast, Zakravsky and Hroudova (1996) found tubers of *Bolboschoenus maritimus* ssp. *compactus* remained viable after 2 y without wetting. Also, tubers of the closely related *Scirpus maritimus* were found to remain viable for 20-25 y in northern temperate wetlands (Squires and van der Vaalk, 1992). An improved understanding of tuber and seed viability and germination success in *Bolboschoenus medianus*, and floodplain vegetation in general, is essential in understanding the effects of reduced flooding frequency on vegetation dynamics on the Murray floodplain.

Plants flooded to 20 cm produced lower rhizome biomass than those at 0 cm (Table 5.1), but had longer sum and mean rhizome length (Table 5.4). The high frequency of long, thin rhizomes produced at -20 cm suggests a 'bet-hedging' strategy whereby culms+tubers are spread laterally to ensure some are positioned favourably in the event of deeper inundation (Table 5.4, Fig. 5.15). Lateral spread of 1 m in the Lower Murray's littoral may place culms+tubers from 0.2-2 m higher (or lower) on the bank. This represents an important mode of dispersal, albeit only local, and the plasticity in length indicates an important adaptation to shallow flooding. This contrasts with the reduction in rhizome length in couch grass *Cynodon dactylon* under low light and nutrients observed by Dong and de Kroon (1994). The response of *Bolboschoenus* rhizomes at lower CO_2 supply (flooded to 20 cm) rather resembled that of *Cynodon* stolons, which were longer under low light. The conclusion of Dong and de Kroon, that of foraging for higher light by stolons, may be tentatively applied to *Bolboschoenus* rhizomes foraging for improved CO_2 supply.

Figure 5.1 Habit of *Bolboschoenus medianus*. a. Non-submersed and b. Partially-submersed plants. Leaves and flowers are borne by culms (stems) arising from tubers. Vegetative spread is by subterranean rhizomes. Partially-submersed culms are taller and weaker than non-submersed culms. Submersed leaves grow more vertically than emergent leaves. Tubers are smaller and rhizomes thinner and shorter in submersed culms.

a.



b.

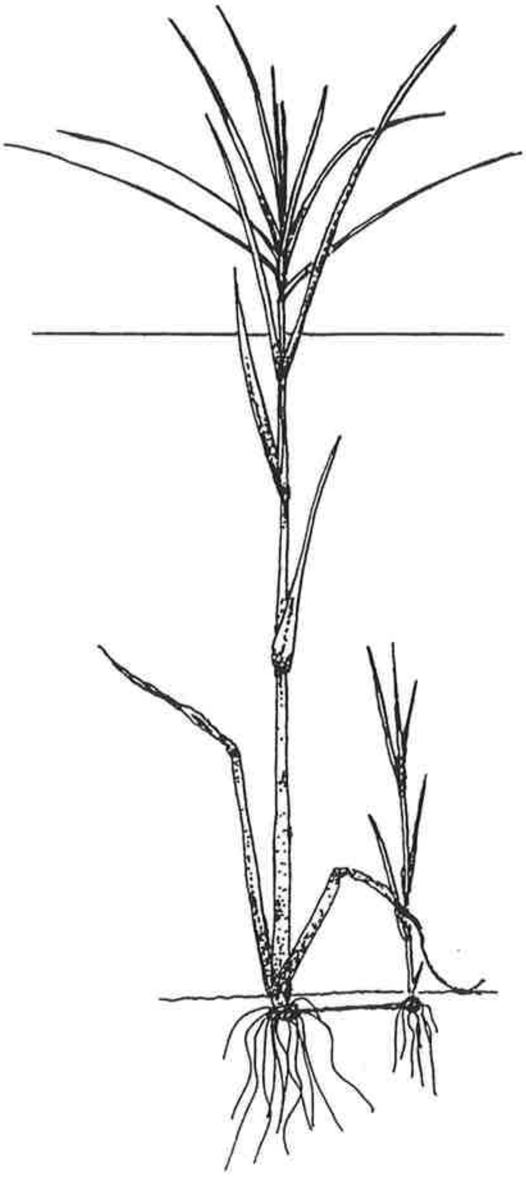


Plate 5.1. Young *Bolboschoenus medianus* plants and experimental setup. Note that pots without culms were part of a separate study (not reported). The photograph was taken on the second day of rising water levels. Pots on the far left were flooded to a final depth of -60 cm, and those elevated in the left-foreground were exposed by 20 cm. Note plants in only one pond are shown.

Plate 5.2. The effect of water depth on the below-ground tissues of *Bolboschoenus*. Carbon starvation in plants flooded to 60 cm reduces the production of tubers, rhizomes and roots. Culms were longer, due to the export of biomass from tubers to culms, and had fewer leaes due to higher rates of senescence.


BOTANY FIELD
0 cm
-60cm

Plate 5.3. Rhizome and tuber network in a vigorously growing plant, flooded to 20 cm. The parent tuber is in the centre. A 1 m rule is shown.

Plate 5.4. *Bolboschoenus* plants growing on a floodplain of the Lower River Murray after summer flooding. Culms are up to 1.3 m tall. Scattered *Phragmites australis* stems are shown on the left.

Figure 5.2. a. Relative growth rate (RGR), b. net assimilation rate (NAR) and c. leaf area ratio (LAR) in *Bolboschoenus* plants grown across a depth gradient (see Eqs (1), (2), and (3)). The same letter indicates no significant difference at P=0.01 (Tukey's HSD test) (mean and se, n=7).

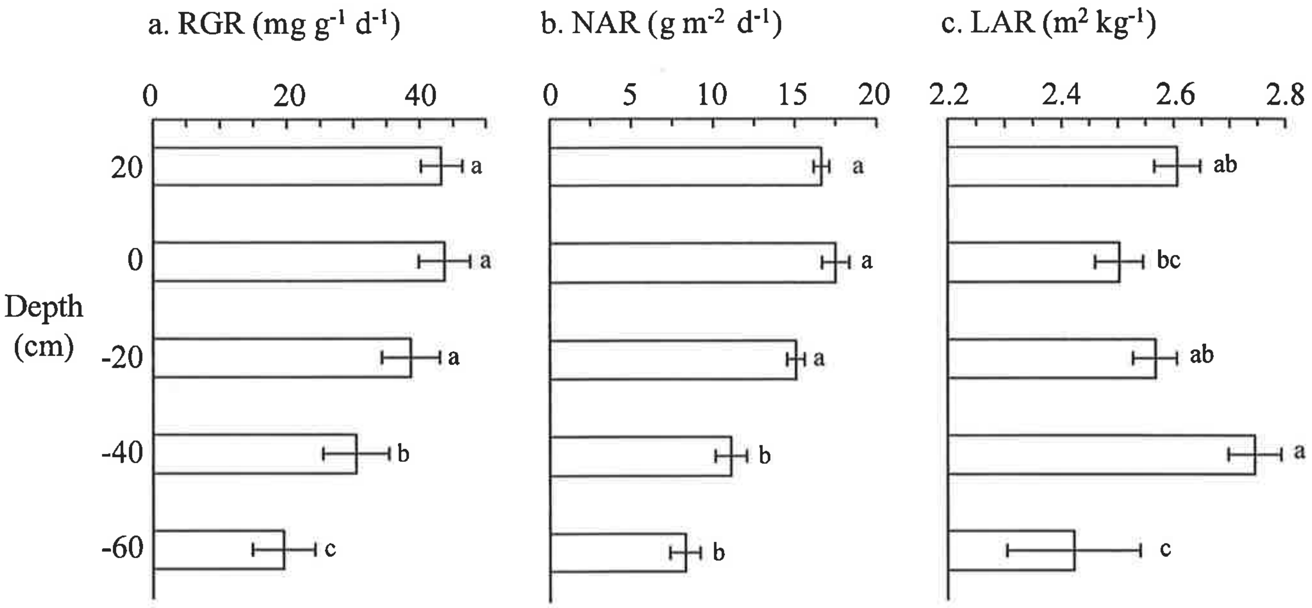

a. RGR (mg g-1 d-1)
0
20
40
b. NAR (g m-2 d-1)
0
5
10
15
20
c. LAR (m2 kg-1)
2.2
2.4
2.6
2.8
Depth (cm)
20
0
-20
-40
-60
a
a
a
b
c
a
a
a
b
b
ab
bc
ab
a
c

Figure 5.3. Biomass of emergent leaves in plants grown across a depth gradient. Data are oven dry weights. The same letter indicates no significance difference at P=0.01 (Tukey's HSD test) (mean and se, n=7).

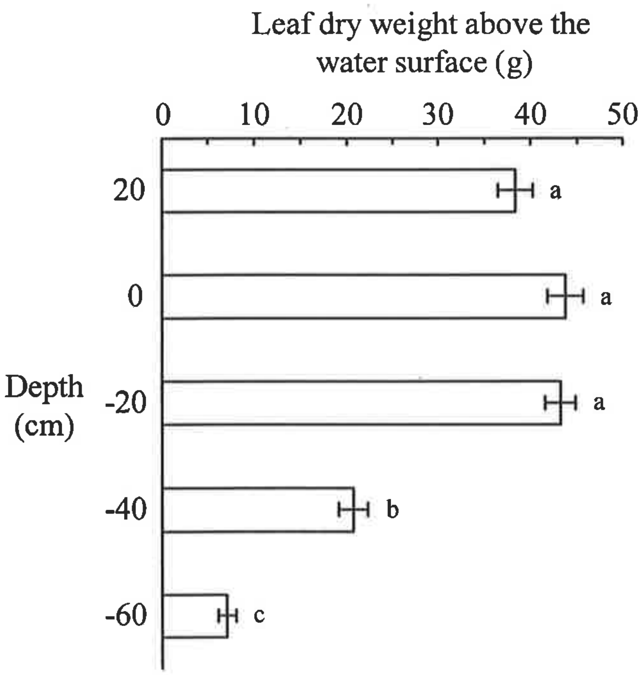

Leaf dry weight above the water surface (g)
0
10
20
30
40
50
Depth (cm)
20
0
-20
-40
-60
a
a
a
b
c

Figure 5.4. Relationship between emergent leaf area and total plant biomass across a depth gradient. The linear fit and ninety-five percent confidence intervals are shown.

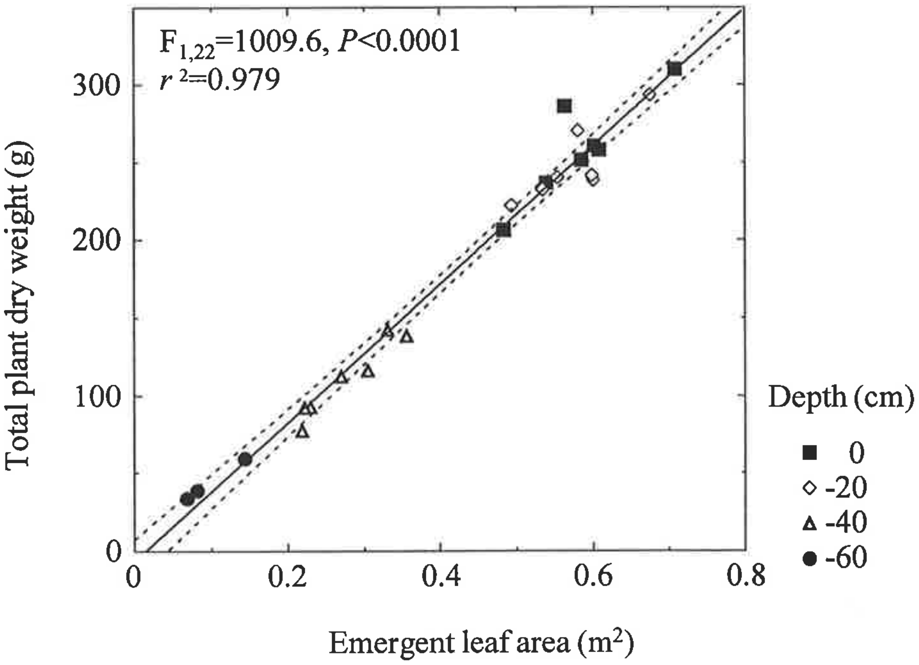

F1,22=1009.6, P<0.0001
r 2=0.979
Total plant dry weight (g)
0
100
200
300
0
0.2
0.4
0.6
0.8
Emergent leaf area (m2)
Depth (cm)
■ 0
◇ -20
△ -40
● -60

Figure 5.5. NAR and LAR as functions of RGR. RGR was highly positively correlated with NAR, but not with LAR.

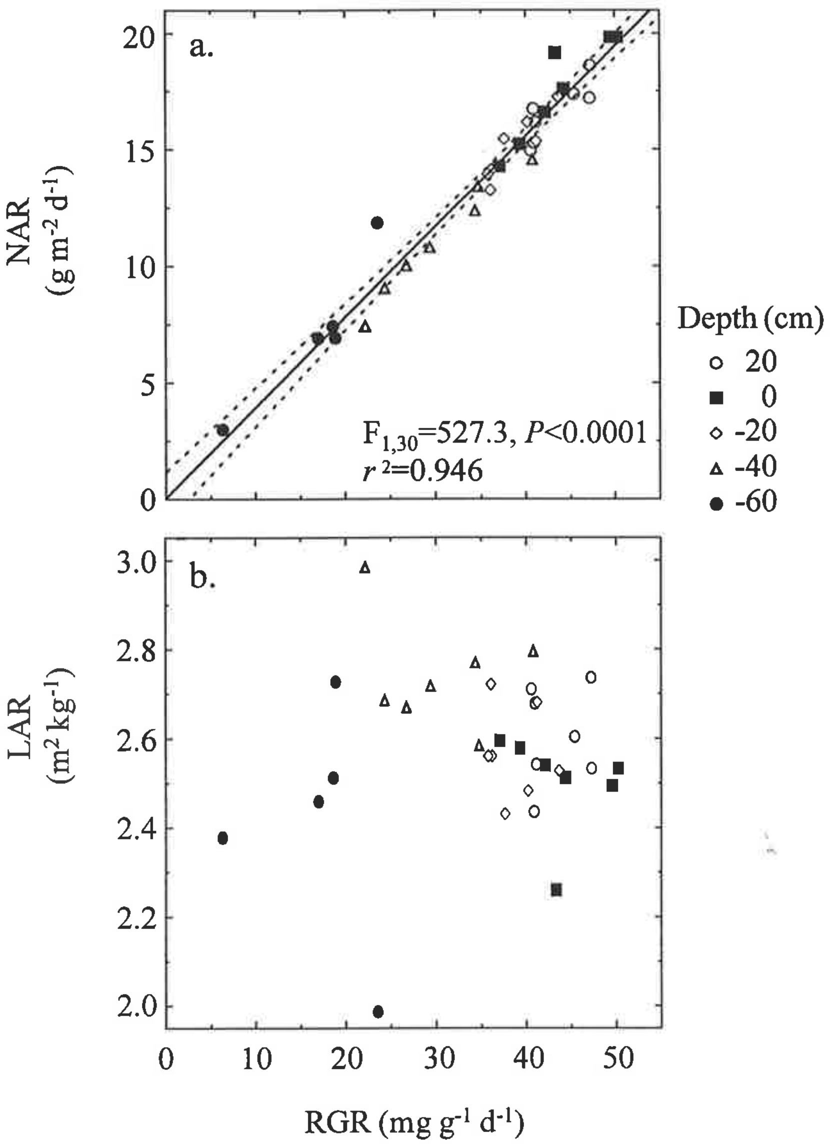

a.
NAR (g m-2 d-1)
0
5
10
15
20
F1,30=527.3, P<0.0001
r 2=0.946
Depth (cm)
○ 20
■ 0
◇ -20
△ -40
● -60
b.
LAR (m2 kg-1)
2.0
2.2
2.4
2.6
2.8
3.0
0
10
20
30
40
50
RGR (mg g-1 d-1)

Figure 5.6. Culm recruitment rate in *Bolboschoenus* plants grown across a depth gradient. The same letter indicates no significance difference at P=0.01 (Tukey's HSD) (mean and se, n=7).

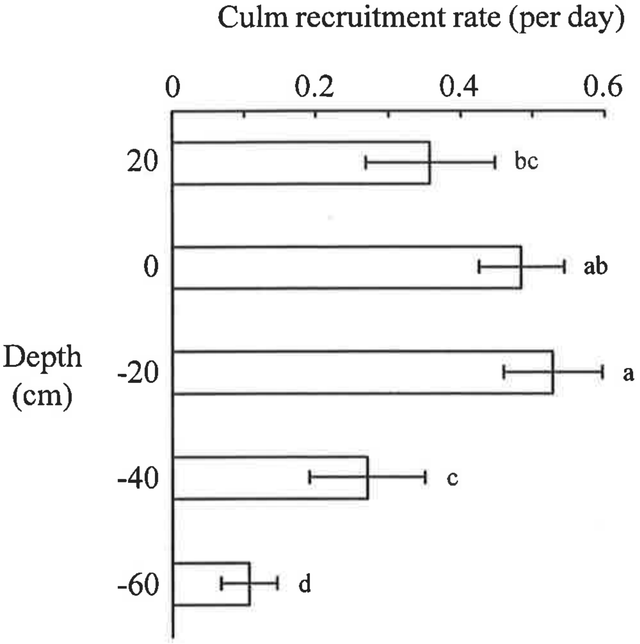
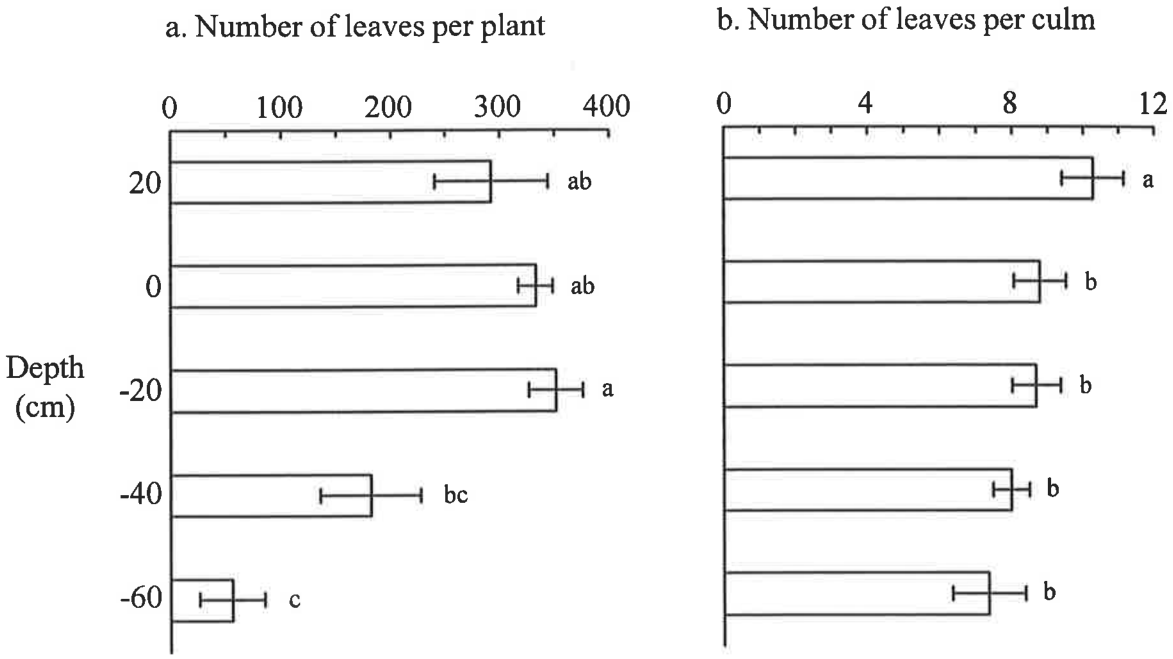

Culm recruitment rate (per day)
0
0.2
0.4
0.6
Depth (cm)
20
0
-20
-40
-60
bc
ab
a
c
d

Figure 5.7. Leaf production as a function of water depth in *Bolboschoenus*. a. Number of leaves per plant and b. Number of leaves per culm (= number of leaves per plant/number of culms). The same letter indicates no significance difference at P=0.05 for a. (Nemenyi non-parametric test); and P=0.01 for b. (Tukey's HSD test) (mean and se, n=7).



a. Number of leaves per plant

b. Number of leaves per culm

Figure 5.8. Leaf recruitment and senescence as functions of culm age and depth. Recruitment and senescence were calculated as the change in numbers of leaves per day once the culm was produced. For example, in culm 2, which was initiated prior to flooding, this was over 64 days, but only over 30-40 days for culm 10. Data are mean±se (*n*=3-7).

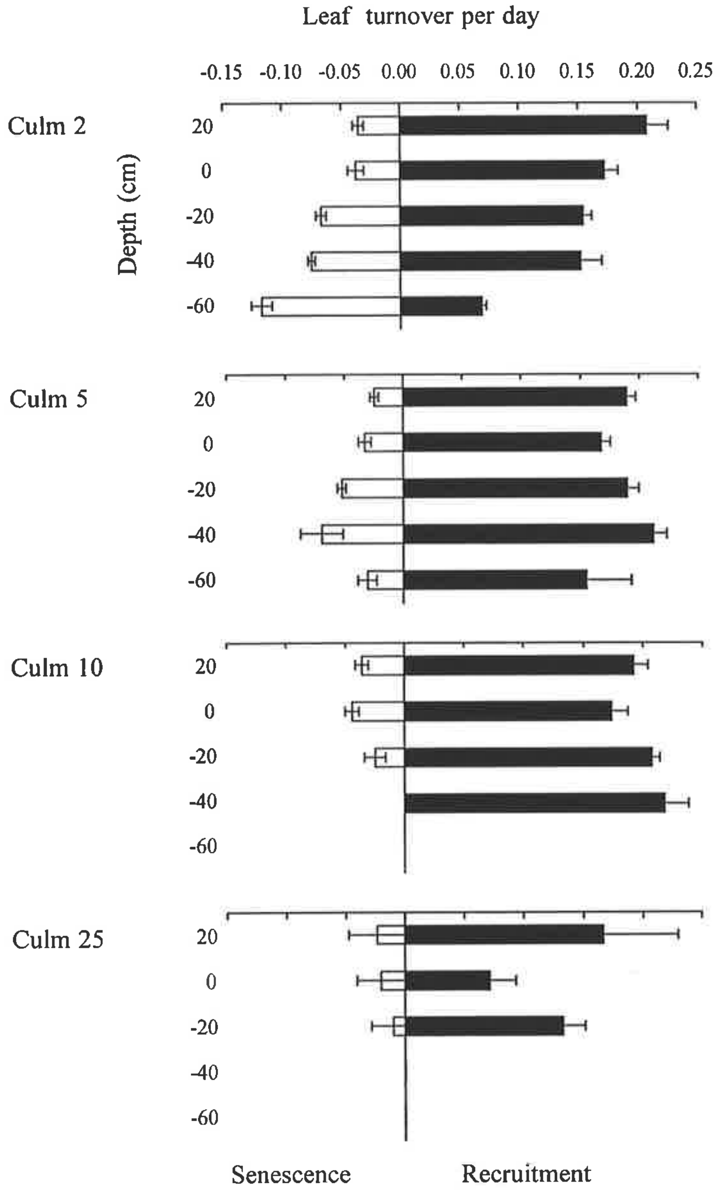

Leaf turnover per day
-0.15
-0.10
-0.05
0.00
0.05
0.10
0.15
0.20
0.25
Culm 2
Depth (cm)
20
0
-20
-40
-60
Culm 5
20
0
-20
-40
-60
Culm 10
20
0
-20
-40
-60
Culm 25
20
0
-20
-40
-60
Senescence
Recruitment

Figure 5.9. Rates of leaf recruitment and senescence in culm 2 over time and across the depth gradient. Data are mean±se (*n*=5-7).

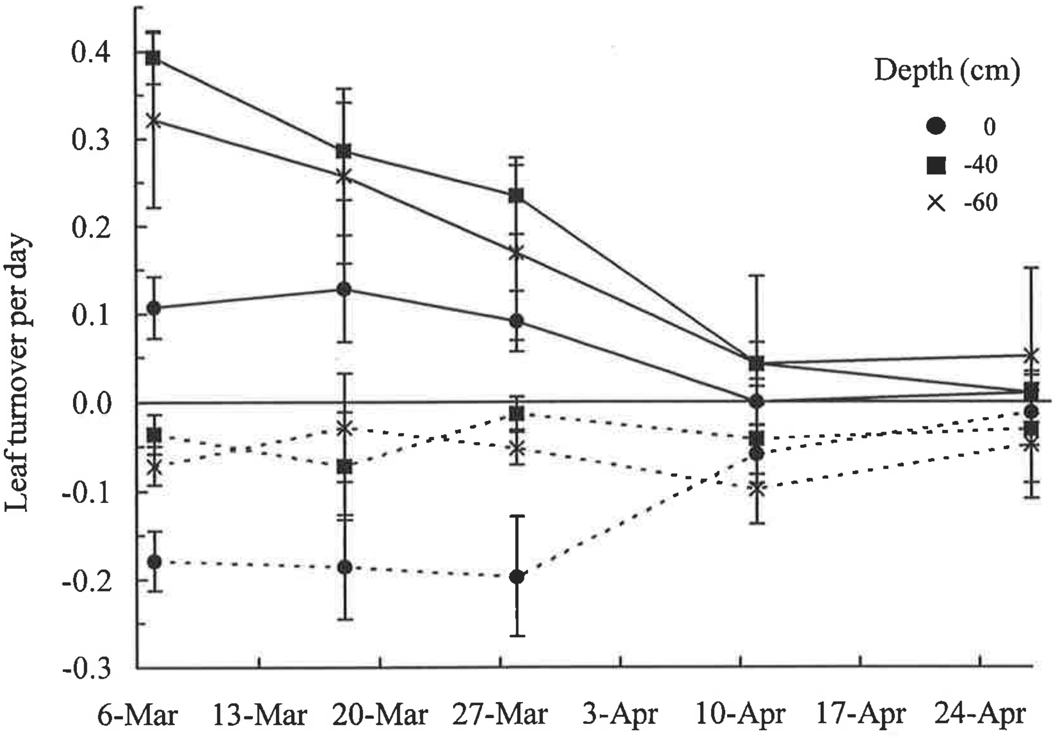

Depth (cm)
● 0
■ -40
× -60
Leaf turnover per day
0.4
0.3
0.2
0.1
0.0
-0.1
-0.2
-0.3
6-Mar
13-Mar
20-Mar
27-Mar
3-Apr
10-Apr
17-Apr
24-Apr

Figure 5.10. Culm extension in culms of varying ages in *Bolboschoenus* plants grown across a depth gradient. Culm number 2 was the second culm produced, and culm 25 was produced toward the end of the experiment. Dashed lines indicate the water depth. Height is to the highest visible leaf sheath base. Data are mean and se. n=7 for most culms, but 3-6 for plants in deeper water in which fewer culms were produced.

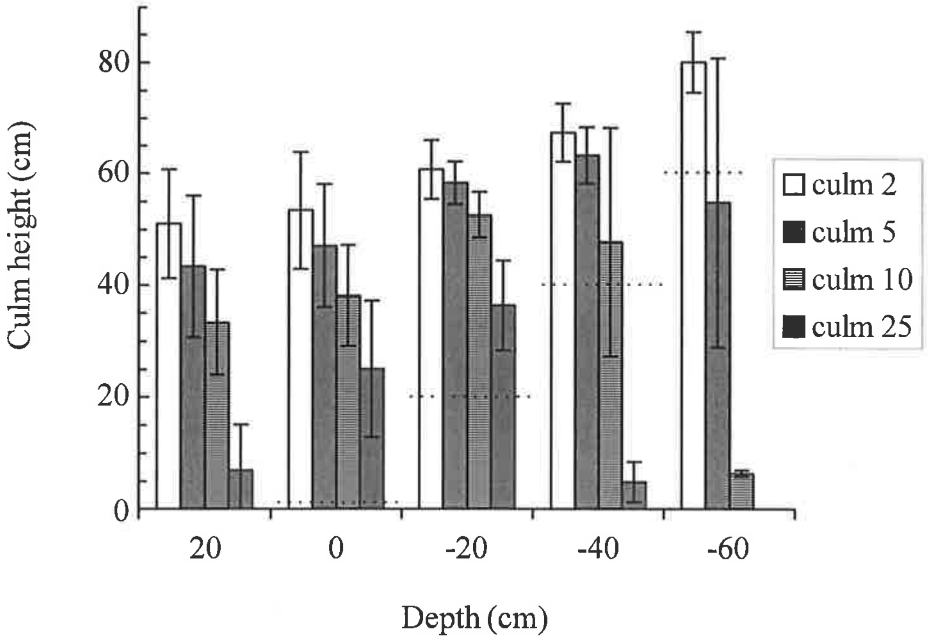

Culm height (cm)
80
60
40
20
0
20
0
-20
-40
-60
Depth (cm)
culm 2
culm 5
culm 10
culm 25

Figure 5.11. Culm extension over time in culms of varying ages in plants at depths 0 and -40 cm. Height is to the highest visible leaf sheath base. Data are mean height (*n*=7). Error bars are not shown for clarity.

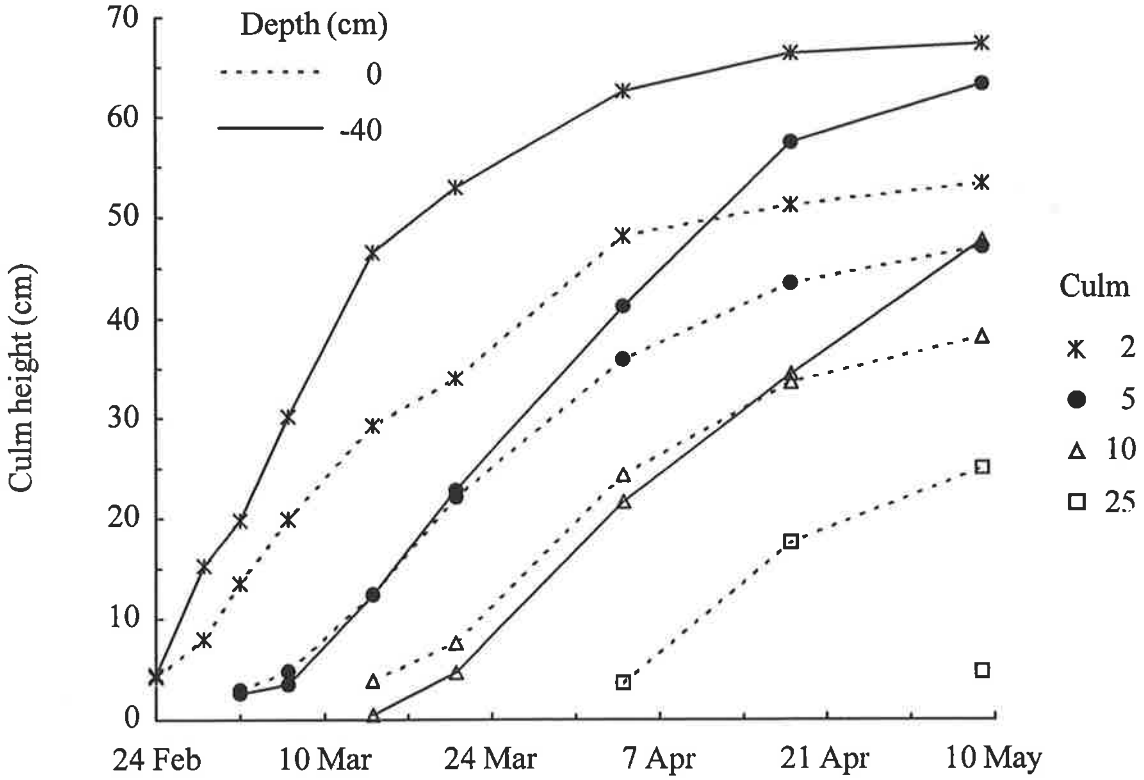

Culm height (cm)
70
60
50
40
30
20
10
0
24 Feb
10 Mar
24 Mar
7 Apr
21 Apr
10 May
Depth (cm)
0
-40
Culm
2
5
10
25

Figure 5.12. Photosynthesis-irradiance response in *Bolboschoenus*. Data are modelled with the hyperbolic tangential model of Jassby and Platt (1976). Maximum photosynthetic rate was 27.8 μmol CO_2 m^{-2} s^{-1}.

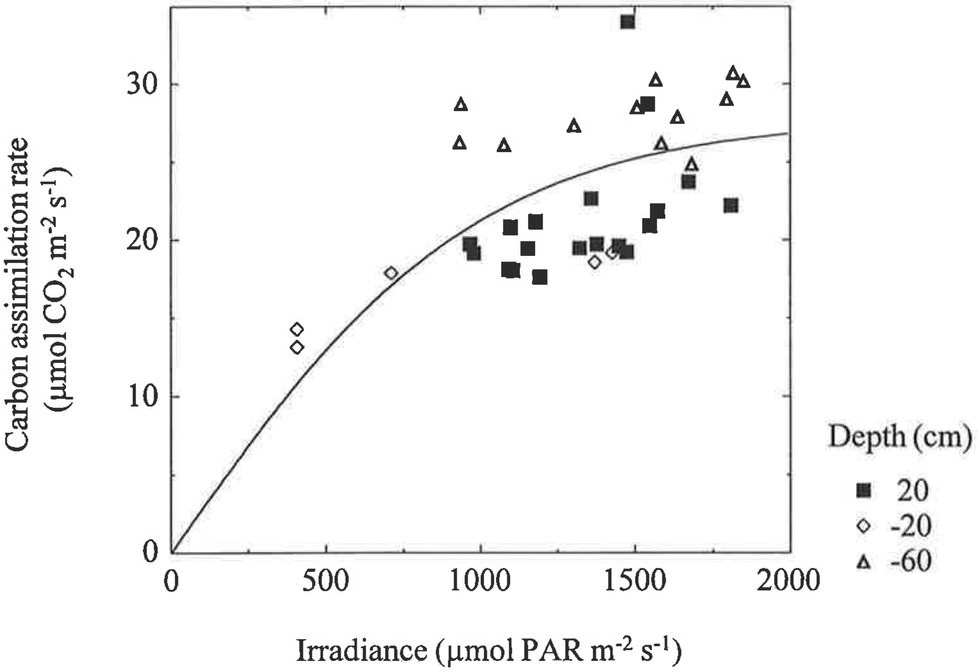

Carbon assimilation rate
(μmol CO$_2$ m^{-2} s^{-1})
0
10
20
30
0
500
1000
1500
2000
Irradiance (μmol PAR m^{-2} s^{-1})
Depth (cm)
■ 20
◇ -20
△ -60

Figure 5.13. Influence of water depth on percent biomass in a. culms, b. tubers, c. rhizomes, and d. roots. Data are presented for plants flooded to 0 to -60 cm. The linear fit and ninety-five percent confidence intervals are shown. d.f = 24 for all plots. See Table 5.1 for mean percent allocations.

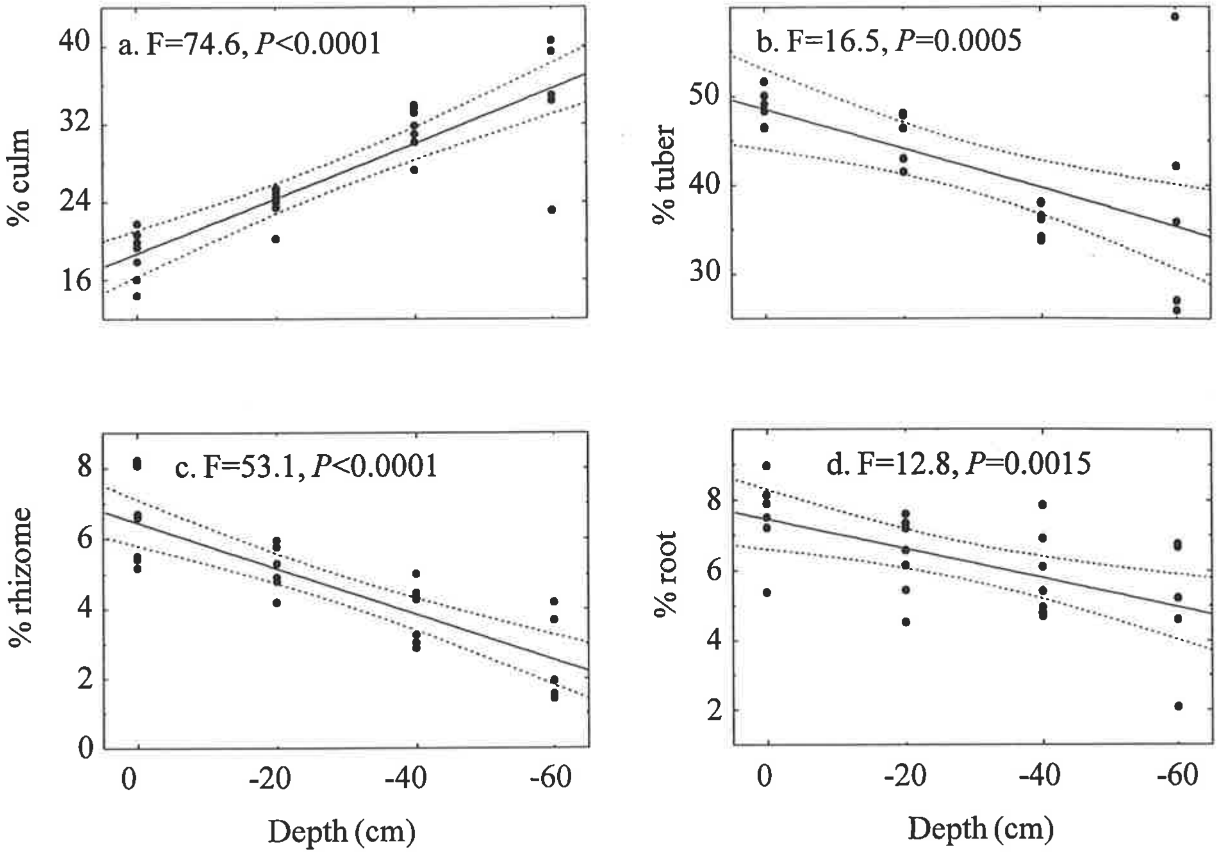

a. F=74.6, $P<0.0001$
% culm
40
32
24
16
b. F=16.5, $P=0.0005$
% tuber
50
40
30
c. F=53.1, $P<0.0001$
% rhizome
8
6
4
2
0
d. F=12.8, $P=0.0015$
% root
8
6
4
2
0
-20
-40
-60
Depth (cm)
0
-20
-40
-60
Depth (cm)

Figure 5.14. a. Inverse linear relationship between percent culm biomass and percent tuber biomass. b. Positive relationship between percent rhizome biomass and percent tuber biomass. Data are presented for plants flooded from 0 to -60 cm. d.f. = 24. See Table 5.1 for mean percent allocations. The linear fit and ninety-five percent confidence intervals are shown.

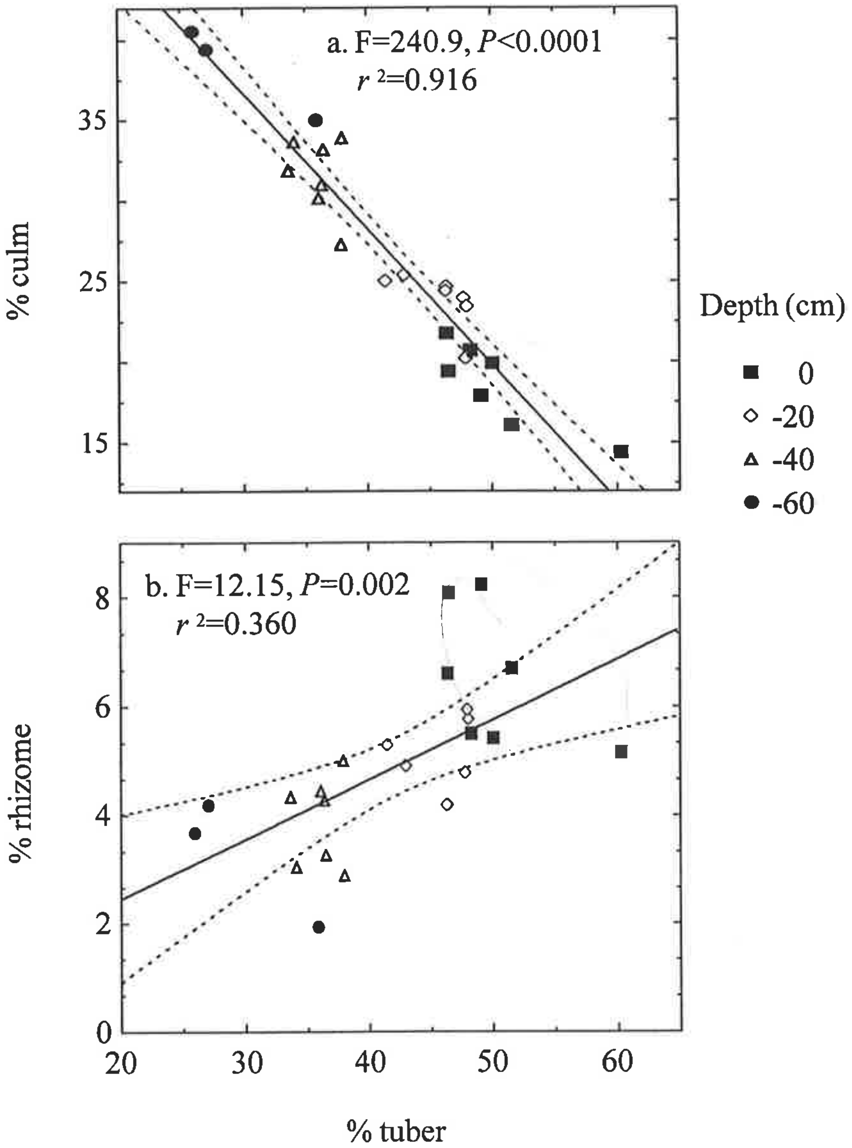

a. F=240.9, $P<0.0001$
$r^2=0.916$
% culm
35
25
15
Depth (cm)
■ 0
◇ -20
△ -40
● -60
b. F=12.15, $P=0.002$
$r^2=0.360$
% rhizome
8
6
4
2
0
20
30
40
50
60
% tuber

Figure 5.15. Frequency distribution of rhizome lengths in plants grown at the water surface (0 cm), and 20 and 60 cm below the surface.

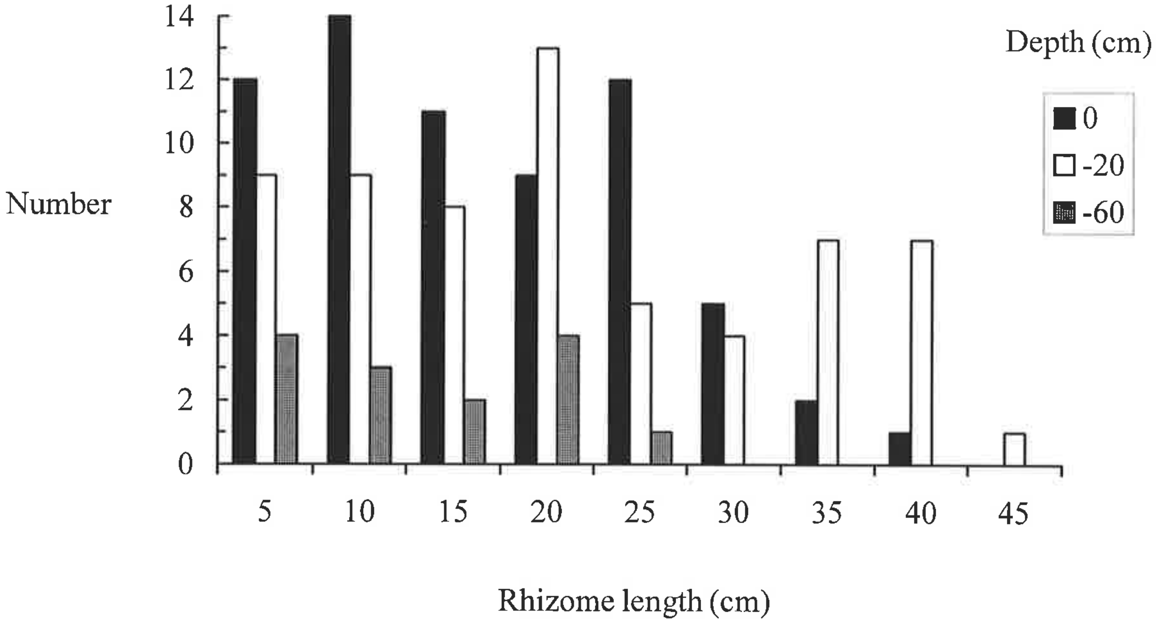
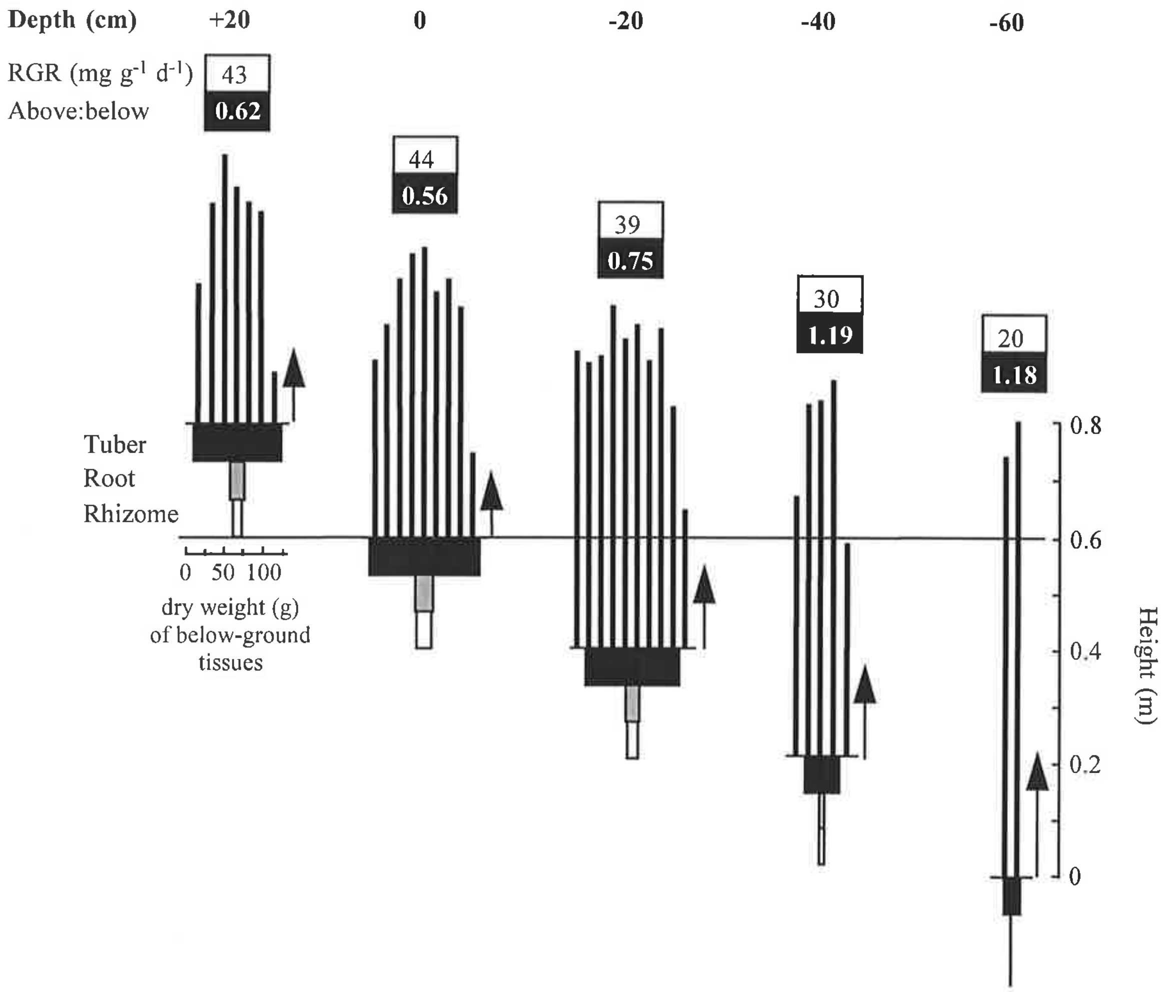

Number
14
12
10
8
6
4
2
0
5
10
15
20
25
30
35
40
45
Rhizome length (cm)
Depth (cm)
0
-20
-60

Figure 5.16. Model of growth and resource allocation in *Bolboschoenus* plants grown across an elevation gradient. Culms are represented as vertical lines, with ten 'culms' representing maximum recruitment at -20 cm (see Fig. 5.6). Plants react to inundation by producing longer culms (see Fig. 5.10). Leaves are omitted for clarity. The biomass of below-ground tissues are indicated by the width of bars. The relative extent to which *Bolboschoenus* allocates biomass from tubers to culms increases with depth, represented by the length of the arrow (Fig. 5.14a). Plant RGR data are shown in Fig. 5.2 and above to below-ground biomass ratios in Table 5.1.


Depth (cm)
+20
0
-20
-40
-60
RGR (mg g-1 d-1)
Above:below
43
0.62
44
0.56
39
0.75
30
1.19
20
1.18
Tuber
Root
Rhizome
0 50 100
dry weight (g) of below-ground tissues
0.8
0.6
0.4
0.2
0
Height (m)

Chapter 6

A field study of the effects of depth of flooding and rate of exposure on *Bolboschoenus medianus*

6.1 Introduction

Plants inhabiting the littoral zone of semi-arid floodplain rivers must tolerate exposure and flooding of variable duration and depth (Mitchell and Rogers, 1985). The temporal juxtaposition of limited access to atmospheric gases followed by low soil moisture exerts strong selective pressure on plants to develop morphological adaptations which permit survival and growth under both regimes. This chapter investigates the morphological responses and resource allocation patterns in *Bolboschoenus medianus* in a variable water regime. The allocation of carbohydrates from tubers to culms when flooded indicates a high degree of plasticity in this species (Chapter 5, Fig. 5.14a). Conversely, culm recruitment declined when exposed due to lower stomatal conductance. Of particular interest in this Chapter are the changes in resource allocation, recruitment and morphology which occur under a variable water regime, when access to atmospheric gases then soil moisture are limiting.

Studies of macrophytes in xeric environments, though few in number compared to those from mesic climes (cf. Mitchell and Rogers, 1985), have identified the dynamic nature of growth and reproduction under varying water regimes. The growth rate of couch (*Cynodon dactylon*) on the Pongolo River floodplain, South Africa, declines exponentially 51 days after flooding, due to falling soil moisture (Furness and Breen, 1985). Flexibility of both morphology and mode of reproduction are important traits (cf. Grime, 1979, Rørslett, 1989) allowing the semi-emergent milfoil *Myriophyllum variifolium* and the charophyte *Chara australis* to persist in temporary wetlands (Brock, 1991; Casanova, 1994; see also Briggs and Maher, 1985; Rea and Ganf, 1994a,b,c). Studies from mesic environments have also revealed a range of life-history strategies in plants occupying the littoral zone of variable water bodies (Day *et al.*, 1988; Hultgren, 1988; Shipley *et al.*, 1989; Wilcox and Meeker, 1991; Hroudova *et al.*, 1996).

Given the ubiquity of *Bolboschoenus* in the Murray's littoral zone (Blanch and Walker, in press; Chapter 3), one may expect a range of morphological adaptations and resource allocation strategies to enable rapid responses to changing levels of resource supply (Mitchell and Rogers, 1985; Brock, 1991; Rea and Ganf, 1994c).

Increasing flow variability to approximate aspects of pre-regulation conditions is essential in the rehabilitation of highly regulated rivers (Toth, 1993; Toth *et al.*, 1993; Brookes 1995; Schiemer, 1995; Bornette and Amoros, 1996). Reregulation of impounded rivers involves, in part, modifications to the hydrograph to improve connectivity between rivers and their floodplains, and is increasingly being proposed and implemented in river remediation (Bayley, 1995; Nilsson, 1996; Nilsson and Brittain, 1996; Stanford *et al.*, 1996). Flow regulation and increased abstractions in the Lower Murray have reduced the frequency of small-medium flows by 70% (Jacobs, 1989; Walker and Thoms, 1993; Murray Darling Basin, 1995). Preliminary trials are being conducted by water management agencies to increase wetting of the floodplain through weir manipulations and releases from storages (A. Jensen, Lower Murray Flow Management Flow Working Group, Department of Environment and Natural Resources, Adelaide, pers. comm.). However, scant ecological information exists on the flooding requirements of littoral and floodplain vegetation to guide such efforts for the Lower Murray.

Accordingly, the effects of flooding depth and rate of recession on growth, resource allocation and reproduction in *Bolboschoenus* were examined in a field experiment. Both strongly influence growth (Grace, 1989; Middleton, 1990; Kirkman and Sharitz, 1993; Neill, 1993; Rea and Ganf, 1994c), and are amenable to manipulation by managers. The experiment was designed to compare performance under regimes of controlled flooding and no flooding, and conducted in conjunction with SA Water and the SA Department of Environment and Natural Resources. This was to be accomplished by raising the level of a weir 0.5 m in one pool (flooding regime), whilst maintaining a stable level in three control pools (no flooding). Plants were grown at three elevations above pool level to examine plant responses at different positions on the river bank with respect to the hydrograph. Growth was hypothesised to be greatest in plants shallowly flooded then exposed. Under such conditions, culm recruitment would be high (cf. Chapter 5), and biomass production correlated with the time in which the water level remained within ±20 cm of the sediment.

However, higher than expected spring flows prevented complete control of water levels. Consequently, analysis of the data was modified to examine growth and resource allocation with respect to the different flooding depths and rates of exposure in 1each pool.

6.2 Materials and Methods

6.2.1 Planned water-level manipulations

The experiment was originally designed to compare growth and recruitment in plants flooded to 0.5 m for 6 weeks then gradually exposed, with plants which were not flooded. Four weir pools between Locks 4 and 10 were chosen for the study (cf. Fig. 1.1). Pool 8 was chosen for the weir manipulation owing to its sparse population and low irrigation demand (Ohlmeyer, 1991). Pools 4, 6 and 9 were assigned as control pools, in which water levels were to be maintained within 5 cm of pool level. Data for Pool 6 were later excluded from the analyses as the site chosen was too far upstream of Lock 6 (cf. Blanch *et al.*, 1996), and hence water levels varied much more than recorded at Lock 6 (see below). Consequently, water levels fell below the bases of pots on several occasions.

6.2.2 Experimental Design

Potted plants were grown at elevations of 2, 22 and 44 cm above weir pool level in Pools 4, 8 and 9 (Fig. 6.1 and Plate 6.1). Sites were chosen within 5 km of the upstream side of a weir (cf. Blanch *et al.*, 1996), and the stage hydrograph assumed to be the same as that recorded by SA Water at the weir.

Plants were grown from tubers in a glasshouse at the Department of Botany. Tubers were collected the previous spring (1995) from the Murray at Swan Reach. A single tuber with culm was placed in each pot. Plants bore 10 cm of rhizome, live roots, and a culm 0.3-0.5 m high. To facilitate comparison with the pond experiment, sediments and nutrient conditions were identical for both studies (cf. Chapter 5).

Six black plastic pots (25.5 cm high x 28 cm wide) were used in the 2 and 22 cm elevations (Fig. 6.1, Plate 6.1). Five cylinders of reinforced spiral-bound Ribloc® tubing (60 cm high x 33 cm wide) with plastic pot saucers underneath were used in the 44 cm elevation treatment. Plastic bags were used to retain the sediments (Plate 6.1). In the 22 and 44 cm elevation treatments, the bases of bags were punctured to allow the passage of water.

Trenches were close to the water's edge and connected by a small channel. Plants experienced changes in river level by means of a small channel connecting the trenches to the river. The 44 cm elevation pots were on the southern side of the trench to prevent shading of the lower elevations. Trenches were dug behind logs, sand bars and reeds to reduce wash by waves. Sites were chosen on the inside of river bends or on straight sections to reduce current effects. A 1.1 m high fence of 25 mm mesh wire excluded grazers. Nearby shading vegetation was removed and the pots weeded regularly. Following the flood, deposited silts were removed from on top of the pots and from within the trench.

6.2.2 Growth measurements

The experiment lasted 156 days (25 June-30 November, 1995). Culm density was recorded on three occasions: 28 September (immediately after flooding), 3 and 29 November. At harvest, components were separated by washing over a 1 mm sieve. If required, below-ground tissues were further separated by flotation in the laboratory. Numbers of tubers were recorded. Tissues were oven dried at 80°C to constant weight (72 h).

NAR and LAR at the end of the experiment were calculated using the leaf area *v.* dry weight relationship determined from the pond study. For the calculation of RGR, NAR and LAR (cf. Chapter 5), initial plant dry weights and leaf area were determined from eight initial plants harvested on 24 June.

6.2.3 Photosynthesis and stomatal conductance

Net photosynthesis and stomatal conductance in 1 young, fully expanded leaf per plant were measured on 20-21 November using IRGA (cf. Section 5.3.4). Measurements were made from 1000-1600 h in the absence of cloud.

6.2.4. Data analyses

Biomass, culm density and culm height data were analysed (Statistica, 1994) using weighted two-way ANOVA on original or ln transformed data in a fully-factorial design.

The factors were elevation above pool level and Pool. 'Pool' is a complex variable, signifying the pattern of flooding and exposure (*i.e.* the hydrograph), as well as other biotic and abiotic factors operating at each site. Within a weir pool, the *water regime* is dependent upon elevation, *i.e.* the water regime experienced by a plant at elevation 2 cm in Pool 9 is different to that experienced at 22 cm in the same pool (Chapter 3). Hence growth in *Bolboschoenus* was examined in nine water regimes (three pools x three elevations).

Difficulties are associated with analysis of the data using both two-way and one-way nested ANOVA. In the latter, the main effect may be considered to be the rate of recession (constant within a pool), with maximum water depth the nested factor (calculated as peak flood height - pot elevation). An advantage of this approach is that it dissects the three hydrographs into components of biological interest, and compares their effects on growth. However, nested ANOVA assumes that the levels of the nested factor are randomly chosen (Sokal and Rohlf, 1969), whereas maximum depths are related in this design. Nested ANOVA also assumes interactions between main and nested factors are not important. In this experiment, plant performance could only be explained by reference to both depth and rate of exposure, however. Two-way ANOVA presents a more defensible option (A. Verbyla, Department of Statistics, University of Adelaide, pers. comm.), with factors being pool and elevation. The influence of elevation is tested at three levels: 2, 22 and 44 cm above pool level. In effect, pool is treated as a 'black box', and the effects of depth and rate of exposure are only examined when interpreting the biological significance of interactions between main factors from data means.

Normality was tested with the Shapiro-Wilk statistic or Lilliefors variant of the Kolmogorov-Smirnov test (Zar, 1996) when the former was judged overly conservative. Homoscedasticity was tested using Bartlett's test (see Section 5.3.5). Culm recruitment over the three censusing occasions was examined using two-way repeated measures weighted ANOVA on ln transformed data (Zar, 1996). Relationships between RGR and NAR, and between LAR and above to below-ground biomass ratio, were fit using a nonlinear estimation procedure (Statistica, 1994).

6.3 Results

6.3.1 Changes in water level at each site

As planned, weir operations lowered the water level in Pool 8 to 0.3 m below pool level in early July (Fig. 6.2). However, an increase in discharge, greater than that forecast by SA Water during the planning stage, prevented the completion of the study as planned. Discharge increased from <3 000 ML/day in early July to 66 000 ML/day in Pool 8 in early September. Stage peaked at 1.4 m in Pool 8 at this time, and at 0.85 in Pool 4. The weir at Lock 9 was lowered over this period to reduce the rise in water level in Lake Victoria (cf. Fig. 1.6) to protect Aboriginal burial sites just above normal lake level. This precipitated the greater rise in Pool 8, immediately downstream. Following the minor flooding, the rate of exposure was higher in Pools 4 and 8 (12 and 10 cm day^{-1} for 7 and 13 days, respectively). Exposure was more gradual in Pool 9, and occurred over a longer period: 2.5 cm day^{-1} for 24 days (Fig. 6.2).

6.3.2 Biomass production

As one may expect, performance of *Bolboschoenus* plants grown at various elevations relative to a range of hydrographs can not be explained by reference to either main factor alone (Table 6.1). The highly significant interaction terms (P<0.008) for all measures of plant performance indicate that biomass production and recruitment depend upon both depth of flooding and rate of recession, as well as other aspects of water regime not related to these two components.

Total plant biomass and the biomass of each component are shown in Fig. 6.3. Total biomass was greatest at elevation 22 cm in Pools 9 and 8, and at 44 cm in Pools 9 and 4 (Fig. 6.3a). Plants in these treatments were flooded from 0-40 cm for 2-6 weeks in August and early September (Fig. 6.2). Top-flooding for 2 weeks or more in the remaining treatments reduced biomass production. ANOVA indicated elevation but not pool significantly affected total biomass (Table 6.1). A strong interaction (P<0.001), however, indicates that the pattern of flooding and exposure is very important, albeit modified by elevation.

Table 6.1. Results of two-way analysis of variance for selected growth and recruitment parameters. The factor 'Pool' indicates the different flooding patterns at each site. Note that *F* values are marginally higher for factors when the interaction is significant. d.f.=2,41.

Source of variation	*F*	*P*
Total plant biomass		
Pool	0.916	0.822
Elevation	12.158	<0.001
Pool x Elevation	0.365	<0.001
Above:below-ground biomass		
Pool	5.739	0.006
Elevation	46.680	<0.001
Pool x Elevation	3.983	0.008
Cumulative culm height		
Pool	3.605	0.036
Elevation	17.129	<0.001
Pool x Elevation	11.982	<0.001
Number of culms		
Pool	9.888	<0.001
Elevation	10.156	<0.001
Pool x Elevation	14.121	<0.001
Number of tubers		
Pool	0.252	0.778
Elevation	21.326	<0.001
Pool x Elevation	4.746	0.003

Two of the six replicate plants at 2 cm elevation in Pool 9 died after prolonged top-flooding, with a further 3 showing low growth. This suggests a slower drawdown, whilst favouring plants in shallow water, will prolong CO_2 and O_2 limitation in plants lower on the elevation gradient, leading to low growth or mortality through post-anoxic stress (Armstrong *et al.*, 1994; Crawford and Braendle, 1996). Survival was 100% in Pools 4 and 8 despite longer periods of top-flooding, presumably as drawdown was more rapid.

The longer period of flooding at 2 cm reduced the time available for culm recruitment. Once water levels had returned to pool level, however, recruitment at 2 cm in Pools 4 and 8 increased rapidly, but less so at 22 and 44 cm (see below). This is likely to have led to higher biomass at the lowest elevation had the experiment been allowed to proceed for a further 1-2 months.

Plants at 44 cm elevation in Pool 8, which were the only plants at the two higher elevations to have comparatively low biomass, were top-flooded for 3 weeks, then rapidly exposed.

The water level then remained 30-40 cm below the pot base for a further 7 weeks. Hence, low growth in these plants is attributed to the temporal juxtaposition of the stresses of low access to atmospheric CO_2 and O_2, and low soil-moisture.

As in the pond experiment (Chapter 5), partial submersion stimulated the allocation of biomass to culms. Mean and cumulative culm height were greatest at 22 cm elevation in Pool 9 (Fig. 6.4 d and e), as was above-ground culm biomass (Fig. 6.3e). Hence the conditions favouring the greatest culm extension was shallow flooding for 4-6 weeks, followed by exposure at 2.5 cm day^{-1} for 24 days. In addition, flowering only occurred in this treatment, with the average height to the highest visible leaf sheath of flowering culms being 72 cm (or 1.3-1.5 m to the highest leaf). The stimulus for flowering, therefore, appears to be 4-6 weeks shallow flooding followed by a month of high soil moisture. The first culms to flower were c. 70-90 cm high (to the highest sheath), after which shorter culms in the plant flowered. Few culms in other treatments were >70 cm high (Fig. 6.4d)). However, plants in shallow (<10 cm), stable water bodies do flower without flooding (pers. obs.). Flower production in *Scirpus maritimus*, a close relative of *Bolboschoenus*, is depth dependent, with most flowers produced in deeper water (Lieffers and Shay, 1981; Zakravsky and Hroudova, 1996). This suggests that culm extension may be important, but not essential, for flowering in *Bolboschoenus*.

Below-ground biomass, and that for each below-ground tissue, was generally highest at higher elevations (Fig. 6.3c). This observation is temporally confounded, however, by growth commencing 1-3 weeks earlier at these elevations, which were exposed first. Above to below-ground biomass ratios were 0.85-1.22 at 44 cm, increasing to 2.04-2.51 at 2 cm (Table 6.2). This confirms the highly plastic nature of resource allocation in *Bolboschoenus* under a variable water regime. For Pools 4 and 8, ratios were similar at 22 and 44 cm elevations. The ratio at 22 cm in Pool 9, however, was twice that at 44 cm (0.85 and 1.83, respectively). Plants at both elevations in Pools 4 and 8 had 7-8 weeks to adjust to exposure, whilst the more gradual recession in Pool 9 (Fig. 6.2) induced a range in allocation patterns across the elevation gradient. This indicates that a more gradual recession (2.5 cm day^{-1}) permits sufficient time for allocation strategies to be altered in *Bolboschoenus*, whilst rapid recession (10-12 cm day^{-1}) does not.

Table 6.2. Above-ground to below-ground biomass ratios. Data are mean and one standard error (*n*=4-6).

Pool	Elevation above pool level (cm)		
	2	22	44
9	2.13 ± 0.26	1.83 ± 0.13	0.85 ± 0.07
8	2.51 ± 0.22	1.47 ± 0.20	1.22 ± 0.10
4	2.04 ± 0.22	1.03 ± 0.05	0.93 ± 0.10

Leaf to root biomass ratios offer a complementary indication of the plant's response to changing water levels. Specifically, the ratio compares a plant's allocation to tissues responsible for photosynthesis, and for obtaining water and nutrients. Plants 2 cm above pool level allocated 5.03-6.01 times their root weights to leaves (Table 6.3). Allocation to roots was higher at the two higher elevations (ratios of 2.72-4.04), reflecting lower soil moisture.

The high leaf and below-ground dry weights at 44 cm elevation in Pool 4 indicate that plants directed resources to leaves when flooded, then to roots and rhizomes when exposed and soil moisture was declining (Figs 6.3 c, d, h and i). In this treatment, plants were flooded 0−40 cm for 3 weeks, then exposed, albeit rapidly. Roots were concentrated deeper in the pot in these plants than in other treatments (pers. obs.). One mechanism whereby this was achieved was to place tubers deeper, thereby placing roots in zones of higher moisture. Consequently the below-ground component of culms were longer and had a greater dry weight than found in other treatments (Fig. 6.3f). Similarly, the rhizomes which enable

Table 6.3. Leaf to root biomass ratios. Data are mean and one standard error (*n*=4-6).

Pool	Elevation above pool level (cm)		
	2	22	44
9	5.07 ± 0.51	4.04 ± 0.48	2.93 ± 0.20
8	6.01 ± 1.04	3.61 ± 0.53	3.68 ± 0.54
4	5.03 ± 0.35	2.72 ± 0.11	3.09 ± 0.23

such downwards growth had the highest dry weight in this treatment (Fig. 6.3h). Hence growth may not be reduced by rapid exposure more than by gradual exposure, provided that it is preceded by a period of shallow flooding when recruitment and RGR are high.

Percent biomass data for each tissue also indicates a flexible allocation strategy with respect to water regime (Fig. 6.5). Allocation above-ground formed 65-73% of total biomass at 2 cm elevation across the three elevations, falling to 45-55% at 44 cm. In contrast, percent tuber biomass increased from 10-13% at 2 cm to 20-30% at 44 cm. Higher percent tuber biomass at 44 cm indicates a strategy to store carbohydrates for future growth as soil moisture declines. This suggests that given sufficient time, *Bolboschoenus* will maximise future vegetative reproductive success by producing many large tubers. Similar numbers of tubers were produced at 22 and 44 cm in Pool 9 (Fig. 6.4c), but were of considerably greater weight in the latter (Fig. 6.3g). This did not occur in Pools 4 and 8 where exposure was more rapid. Interestingly, pool alone did not significantly influence the number of tubers (P=0.778; Table 6.1), but position on the elevation gradient with respect to flooding pattern was highly significant (P=0.003).

6.3.3 RGR, NAR and LAR

Relative growth rate was in the range 0.2-23 mg g^{-1} d^{-1} (Fig. 6.6). Peak values were lower than those determined for the pond experiment (cf. Fig. 5.2a) due to minimal growth over winter. However, if RGR is calculated assuming growth commenced only in spring (Δt=92 days; 1 September-29 November), then peak RGR is 39 mg g^{-1} d^{-1}. As biomass production is assumed exponential over Δt according to Eq (1) in the formulation of RGR in Chapter 5 (Beadle, 1993), which is unlikely over winter, this value probably more truly represents the maximum observed rate over the period in which growth occurred.

The relationship between RGR and NAR describes an hyperbola, with a predicted tangential maximum RGR of 26 mg g^{-1} d^{-1} according to the model of Jassby and Platt (1976) (RGR_{max} = 44 mg g^{-1} d^{-1} assuming Δt is 92 days, and approximates RGR_{max} in Chapter 5). No physiological basis exists for assuming that RGR varies with NAR according to this expression, however, and the predicted maximum must be viewed with caution.

As demonstrated for total plant biomass (Fig. 6.3), maximum RGR occurred at 22 and 44 cm elevations due to high recruitment and culm extension during, and in the month following, flooding (Fig. 6.6a). Values of NAR were 0.9-8 g m^{-2} d^{-1}, with maximum values coinciding with maximum RGR. The plateau in RGR (which is equivalent to the product of NAR and LAR at any instant: Beadle, 1993) at high values of NAR appears to be due largely to a corresponding decline in LAR (Fig. 6.6b). LAR was highest in plants at 2 cm elevation in Pools 4 and 8 (4-4.5 m^2 kg^{-1}), which corresponds to RGR values of 10-18 mg g^{-1} d^{-1}. The rapid decline in LAR at higher elevations was due to a reduction in culm (hence leaf) recruitment during November (Table 6.4, see below) and increasing allocation of resources below-ground as soil moisture declined (Table 6.2).

Minimum LAR occurred in plants at 22 and 44 cm elevations, coinciding with the lowest above to below-ground biomass ratios (Fig. 6.7). These indices are somewhat correlated in that both describe a relationship between allocation to photosynthesising tissues and biomass. However, allocation to culms is not included in the denominator in calculating LAR (cf. Section 5.3.5), which was higher at 22 and 44 cm, due to culm extension during September and October, than at 2 cm. Changes in the density of leaf tissue due to water availability were not examined in this study, and may also have influenced this relationship. A Michaelis-Menten model suggests a maximum LAR of 5.1 m^2 kg^{-1}. As noted above, such predictions are based on empirical rather than theoretical relationships.

6.3.4 Culm recruitment

Culm recruitment increased from winter to late-spring (Table 6.4). Recruitment was essentially zero over winter and up to late September, but increased markedly in October. Rates were considerably higher at 22 and 44 cm over this period, coinciding with higher air temperatures and flooding between 30 and -40 cm. The highest rate in October occurred in plants flooded between 30 and -20 cm (0.23 day^{-1}; 22 cm elevation in Pool 9). Low rates at 2 cm over this period suggest post-flooding stress (Armstrong *et al.*, 1994; Crawford and Braendle, 1996), and contrast markedly with higher production in November at this elevation. Rates of 0.47 and 0.51 day^{-1} occurred in Pools 8 and 4 at 2 cm elevation, and are equivalent to maximum rates observed at -20 cm depth in stable water levels in the pond experiment (Fig. 5.6). In contrast, rates were approximately 50% lower at 22 and 44 cm over this period (0.21-0.26 day^{-1}), presumably due to water stress.

Table 6.4. Culm recruitment rate at three elevations above pool level in three weir pools. Data show the rate for each censusing period (mean and se (n=4-6)). The value '0.00' indicates datum <0.005. Results of the repeated measures ANOVA are also given.

		Culm recruitment rate (day^{-1})		
Pool	Elevation (cm)	25 June - 28 September	28 September - 3 November	3 November - 29 November
9	2	0.00 ± 0.00	0.01 ± 0.02	0.09 ± 0.07
	22	0.01 ± 0.00	0.23 ± 0.04	0.24 ±0.03
	44	0.00 ± 0.00	0.16 ± 0.02	0.21 ± 0.08
8	2	-0.01 ± 0.00	0.07 ± 0.02	0.51 ± 0.03
	22	0.00 ± 0.00	0.21 ± 0.03	0.21 ± 0.04
	44	0.00 ± 0.00	0.11 ± 0.02	0.26 ± 0.06
4	2	0.00 ± 0.00	0.06 ± 0.01	0.47 ± 0.11
	22	0.00 ± 0.00	0.15 ± 0.02	0.22 ± 0.01
	44	0.00 ± 0.00	0.15 ± 0.01	0.25 ± 0.04

Source of variation	d.f. Effect	MS Effect	d.f. Error	MS Error	*F*	*P*
Pool	2	0.01167	36	0.00526	2.220	0.1233
Elevation	2	0.00288	36	0.00526	0.549	0.5821
Censusing period	2	0.60411	72	0.00450	134.161	0.0000
Pool x Elevation	4	0.02067	36	0.00526	3.931	0.0095
Pool x Censusing period	4	0.01924	72	0.00450	4.274	0.0037
Elevation x Censusing period	4	0.04386	72	0.00450	9.741	0.0000
Pool x Elevation x Censusing period	8	0.01114	72	0.00450	2.474	0.0198

Low recruitment at 20 cm elevation in the stable water level experiment coincided with lower rates of net photosynthesis and stomatal conductance (but see below). The data suggest that the post-flooding depression of recruitment lasted approximately one month.

Results of the repeated measures ANOVA confirm that the effects on recruitment of the pattern of flooding and exposure specific to each pool and elevation are complex, with significant interactions between pool, elevation and time (Table 6.4). Neither pool nor elevation significantly affected recruitment alone (P=0.12 and 0.58, respectively), but both did *via* an interaction with censusing period. The weak three-way interaction (P=0.0198) reflects the dependence of recruitment on water regime (the interaction between pool and elevation) and season.

The interaction between the three main factors in influencing recruitment is shown by plotting the rate over time for each pool (averaged across the three elevations), and for each elevation (averaged across Pools) (Figs 6.8 a and b). Mean recruitment rate for each pool showed similar increases from 25 June to early November, but was considerably lower in Pool 9 over the last 3 weeks of the study due to depressed production at 2 cm (Fig. 6.4b).

Immediately after flooding, recruitment was higher at higher elevations (averaged across all Pools) (Fig. 6.8b). From one to two months after flooding (3-29 November), recruitment was highest in plants close to pool level, reflecting higher soil moisture. Culm production started to plateau over this period at elevations 22 and 44 cm.

6.3.5 Photosynthesis and stomatal conductance

A high degree of variation in the rate of carbon fixation and stomatal conductance was observed across elevations and pools (Fig. 6.9), though water regime-related patterns are evident~~s~~. Rates of net photosynthesis ranged from 10.8 to 38.1 μmol CO_2 $m^{-2}s^{-1}$, but were quite similar across treatments. The mean rate was generally lowest at 22 cm elevations, although this is probably biologically significant only in Pool 4. Although assimilation rates two months after water levels had fallen were similar across all elevations and pools, differences may have occurred across treatments immediately after the return to pool level. Had measurements been made in October and early November, differences in assimilation related to water regime may have been detected.

Conductance appears to be higher at 2 cm elevation treatments, presumably due to greater water availability (cf. Chapter 5). In Pools 8 and 9 plants in the 22 and 44 cm elevations appear to exhibit lower conductance as stomata close to conserve water. Data for Pool 4 suggest *Bolboschoenus* reduces water loss at 22 cm (and thereby reducing CO_2 assimilation) due to water stress, but not at 44 cm. This indicates water was not limiting in the latter, perhaps because roots were placed deeper in the soil *via* long below-ground culms (see Fig. 6.3f). This warrants further investigation.

6.4 Discussion

6.4.1 The importance of ecological experiments in large rivers

The intention of the original experimental design was to examine the effects of minor engineered flooding on plant growth in the Lower Murray. The design provides for a well controlled and statistically powerful analysis of flooding effects during low flows. Incorporation of within-pool replicate sites would increase its power. To be of greatest benefit to the littoral zone, a flooding *regime*, rather than a single manipulation, needs to be imposed over several years (Stanford *et al.*, 1996; Nielsen and Chick, 1997).

Difficulties encountered during the study include natural spring flooding, high habitat heterogeneity, limited road access on the floodplain, sediment deposition of up to 10 cm during flooding, the confounding effects of waves, currents and shading vegetation, and vandalism. In addition, permission from water managers for water-level manipulations was granted only for winter and early spring, prior to the irrigation season. Flooding responses are muted at such times due to low temperatures and short day-lengths.

Long–term studies at an appropriate scale are essential for improving our understanding of the patterns and processes shaping vegetation of rivers and floodplains. Whilst several surveys have been made along the Lower Murray over the past 15 years (see Chapter 1), these have been conducted for different purposes and used divergent techniques. Whilst patterns have been demonstrated, causal processes remain largely unknown (but see Nielsen and Chick, 1997). Despite being the principal river in south–eastern Australia, no long–term ecological studies of vegetation processes and the impacts of flow regulation on these processes have been undertaken. Notwithstanding the difficulties encountered in this study, such investigations are essential in developing strategies for rehabilitating vegetation of the Lower Murray.

6.4.2 Resource allocation in variable water regimes

Many studies report the importance of flexibility of growth form and biomass allocation in macrophytes for survival in variable water regimes (Mitchell and Rogers, 1985; Rørslett, 1989; Grillas, 1990; Brock, 1991; Madsen, 1991; Rea and Ganf, 1994a,c). However, the effects of flooding and exposure on plants, and plant responses to changing resource availability, are not well understood.

The degree of allocation to resource–acquiring tissues reflects the level of resource availability (Chapin *et al.*, 1987, 1993; Rea and Ganf, 1994c). Above to below–ground biomass ratios ranged five–fold in *Bolboschoenus* plants which were flooded and exposed (0.6-3.2, Fig. 6.7). Mean ratios ranged two to three–fold in both the stable and variable flooding experiments (Tables 5.1 and 6.2). Leaf to root biomass ratios were lower when water was limiting; 2.93–3.68 at 44 cm elevation, and 5.03–6.01 at 2 cm (Table 6.3). Similarly, LAR varied from 2.7–4.5 m^2 kg^{-1} (Fig. 6.6b), considerably more than observed in stable water levels (Fig. 5.2). Values for LAR were also higher, and those of NAR lower, than observed in Chapter 5, probably due to differences between leaf area and dry weight relationships. All three measures of resource allocation indicate that *Bolboschoenus* reacts to changing availability of both atmospheric gases and soil moisture.

Bolboschoenus responded to flooding by allocating carbohydrates from tubers to culms (Fig. 5.14a), and to exposure by sequestering carbohydrates in tubers for future growth (Grace, 1993). Percent tuber biomass increased much more than did percent root biomass when exposed (Fig. 6.5), indicating a strategy to ensure resilience at the population level at the expense of growth in individual culms. This is reminiscent of the apparent stragety to conserve carbohydrates in tubers when flooded to 60 cm (Chapter 5).

Rea and Ganf (1994c) and Cooling (1996) also concluded that tubers and corms are critical for accommodating long-term changes in water level in southern Australian wetlands. Other morphological and physiological adaptations exhibited by plants in variable water regimes include stem or leaf extension (Kirkman and Sharitz, 1993), propagule longevity and desiccation tolerance, rapid root penetration, dependence upon predictable seasonal cues such as temperature (Mitchell and Rogers, 1985), and changes in stem diameter and structural strength. In a variable regime, possession of a range of such traits would permit recruitment over a longer period than in a species possessing few. Such an approach to investigating plant responses to variability could form the basis for a general model of plant performance with respect to water regime in southern Australia. Several models of plant–environment relationships using functional attributes or life–history strategies have been developed for northern hemisphere aquatic systems (*e.g.* Day *et al.*, 1988, Rørslett, 1989, Shipley *et al.*, 1989; Wilcox and Meeker, 1991; Boutin and Keddy, 1993).

Despite possessing a high capacity for altering resource allocation in response to a variable resource supply, *Bolboschoenus* was unable to match the rapid recession rate in Pools 4 and 8 (10-12 cm day^{-1}). Data from both pond and field investigations indicate *Bolboschoenus* has a narrow optimum depth range for culm recruitment. Clonal growth declines rapidly once exposed (Table 6.4) and when submersed by 0.40 m or more (Fig. 5.6). Hence the key to maintaining populations of *Bolboschoenus* across the littoral zone is to ensure frequent, shallow flooding followed by high soil moisture.

Whilst stable water levels have favoured *Bolboschoenus* growth within a narrow elevation range around pool level, the reduction in frequency of small–medium floods (Jacobs, 1989, 1990) has reduced growth higher on the littoral and floodplain. Comparisons of pre– and post–regulation vegetation are hampered by a lack of scientific data. However, the consensus amongst residents of the Lower Murray is that major contractions in floodplain vegetation have occurred over the last 60 years, coinciding with regulation and a concommitant increase in abstraction for irrigation and domestic use.

Current storage operations which harvest the falling limb of the hydrograph, and thereby increase the rate of recession (Jacobs, 1989; Maheshwai *et al.*, 1993, 1995), may be reducing genetic diversity amongst *Bolboschoenus* populations by reducing sexual reproduction in individuals high on the river bank. *Bolboschoenus* only invested in flowers under a regime of shallow flooding (0–40 cm) for 6–7 weeks, followed by gradual recession (2.5 cm days^{-1}) for 24 days. Hence, genotypes adapted to highly variable environments are less likely to be successful than those with traits which confer a competitive advantage in the dense littoral close to pool level. Such traits could include aggressive rhizome extension and rapid elevation of the canopy (Grime, 1979; Rørslett, 1989). Genetic traits which enable rapid changes in resource allocation, necessary in variable regimes, are less likely to be successful under a predominantly stable regime.

Figure 6.1. Arrangement of pots at experimental sites. See also Plate 6.1.

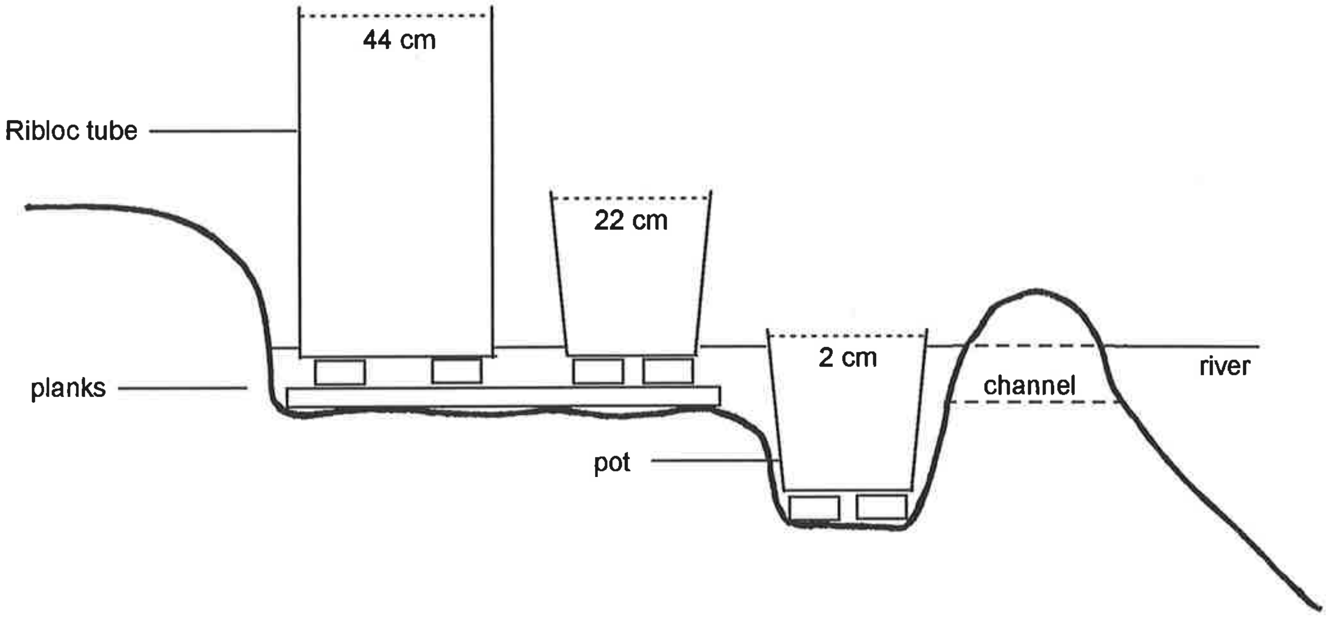

44 cm
Ribloc tube
22 cm
2 cm
planks
channel
river
pot

Plate 6.1. Experimental site showing arrangement of pots, and initial (upper photograph) and final culm densities (see Fig. 6.1). The 44 cm elevation treatments are on the left. Note that 2 cm elevations are submersed.

Figure 6.2. Stage hydrographs at experimental sites in Pools 9, 8 and 4. Plants were grown at elevations 2, 22 and 44 cm above pool level. Data are for the upstream sides of weirs. Hydrographs are standardised to weir pool level. The arrow indicates the approximate commencement of growth in *Bolboschoenus*. * indicates occasions for censusing culm recruitment.

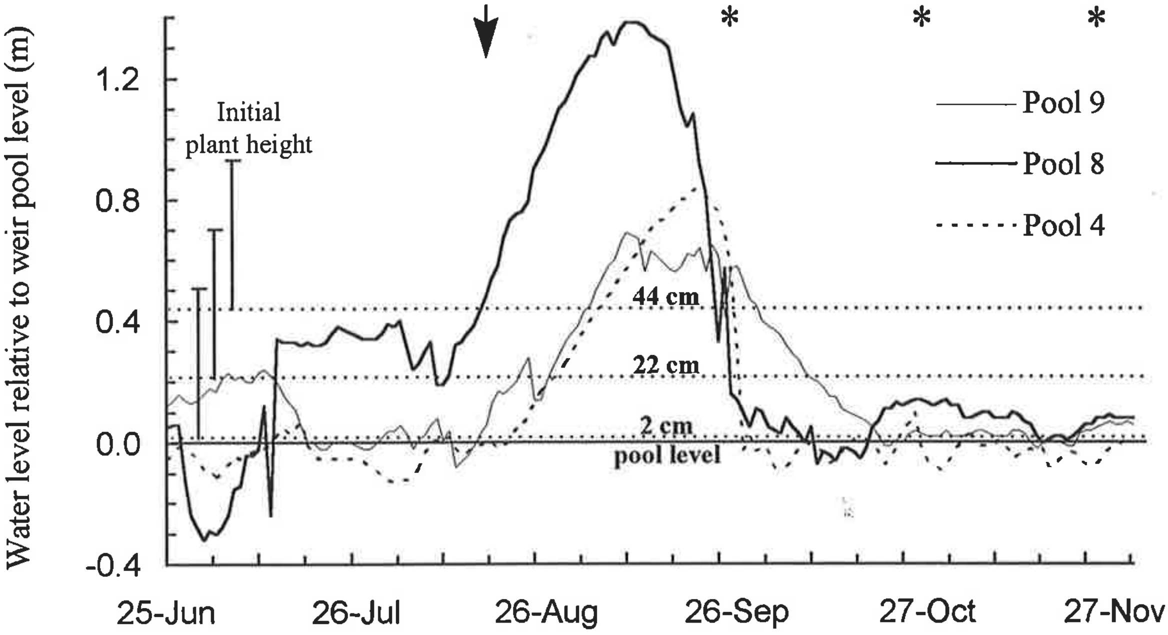

Water level relative to weir pool level (m)
1.2
0.8
0.4
0.0
-0.4
25-Jun
26-Jul
26-Aug
26-Sep
27-Oct
27-Nov
Initial plant height
Pool 9
Pool 8
Pool 4
44 cm
22 cm
2 cm
pool level
*
*
*

Figure 6.3. Biomass partitioning between tissues in *Bolboschoenus* (see Fig. 6.2). Error bars are one standard error (*n*=4–6).

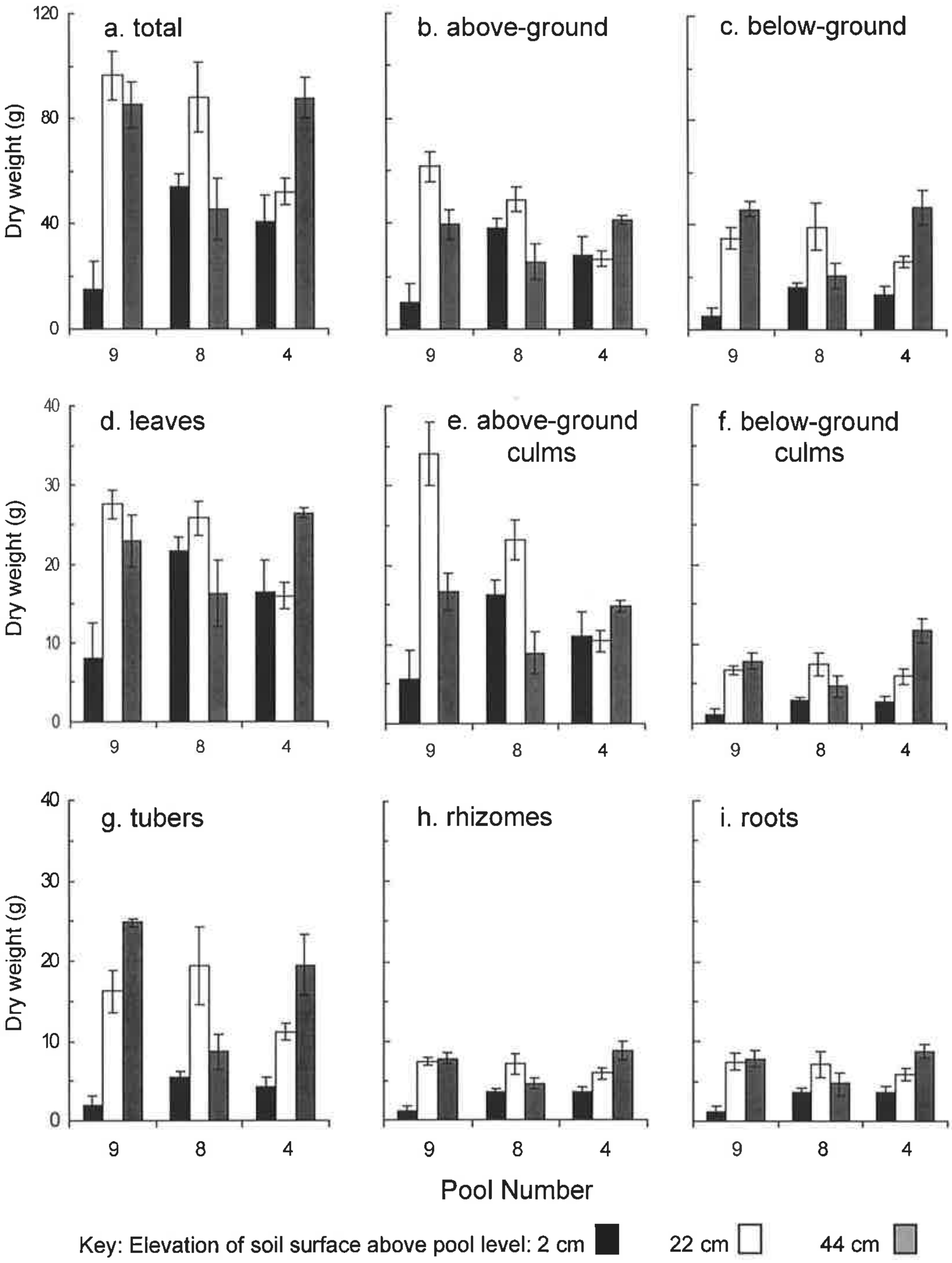

a. total
b. above-ground
c. below-ground
d. leaves
e. above-ground culms
f. below-ground culms
g. tubers
h. rhizomes
i. roots
Dry weight (g)
120
80
40
0
40
30
20
10
0
9
8
4
Pool Number
Key: Elevation of soil surface above pool level: 2 cm ■
22 cm □
44 cm ▨

Figure 6.4. Leaf, culm and tuber production in *Bolboschoenus*. See Fig. 6.3 for details.

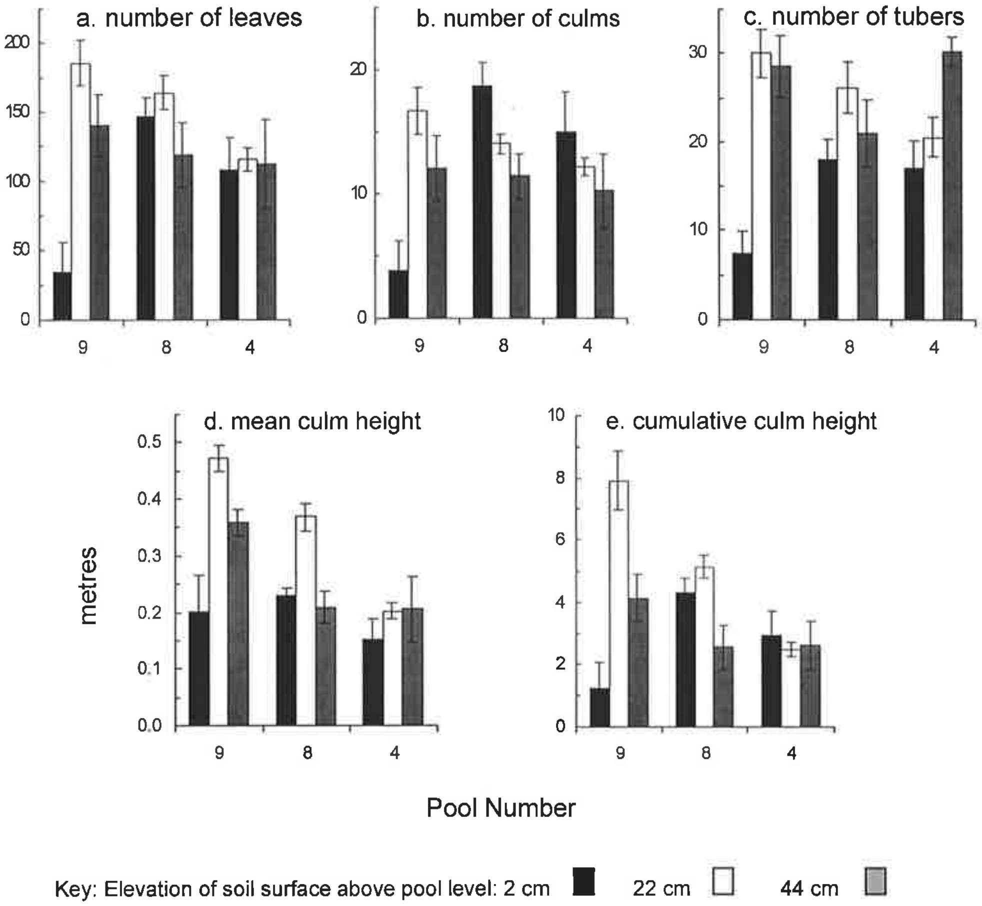

a. number of leaves
200
150
100
50
0
9
8
4
b. number of culms
20
10
0
9
8
4
c. number of tubers
30
20
10
0
9
8
4
d. mean culm height
metres
0.5
0.4
0.3
0.2
0.1
0.0
9
8
4
e. cumulative culm height
10
8
6
4
2
0
9
8
4
Pool Number
Key: Elevation of soil surface above pool level: 2 cm ■ 22 cm □ 44 cm ▨

Figure 6.5. Biomass allocation between tissues, expressed as a percent. A change in percent biomass per tissue between elevations indicates a change in resource allocation.

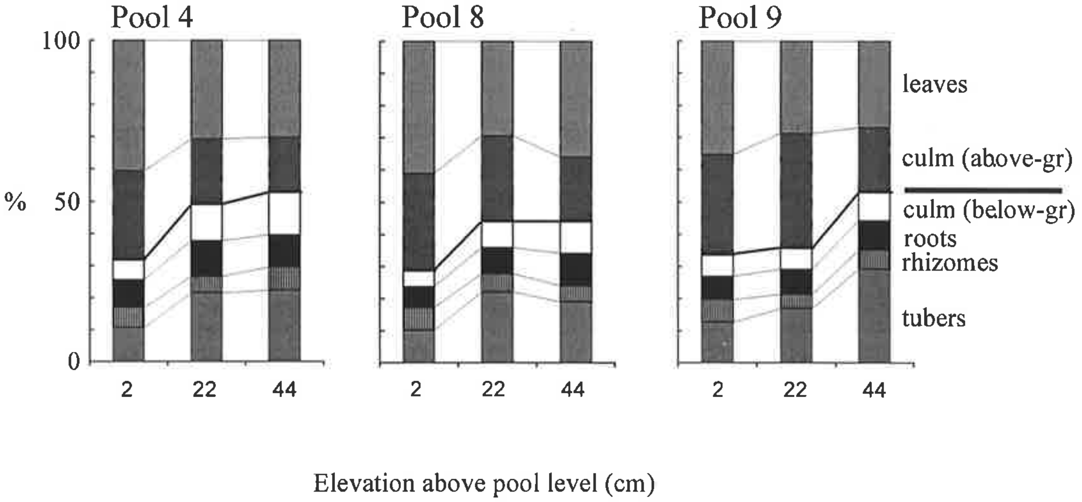

Pool 4
Pool 8
Pool 9
100
%
50
0
2
22
44
leaves
culm (above-gr)
culm (below-gr)
roots
rhizomes
tubers
Elevation above pool level (cm)

Figure 6.6. Relationships between a. relative growth rate (RGR) and net assimilation rate (NAR) and b. RGR and leaf area ratio (LAR) in *Bolboschoenus*. Numbers show the elevation above pool level. An hyperbolic tangent model explains 92.6% of the variance between RGR and NAR.

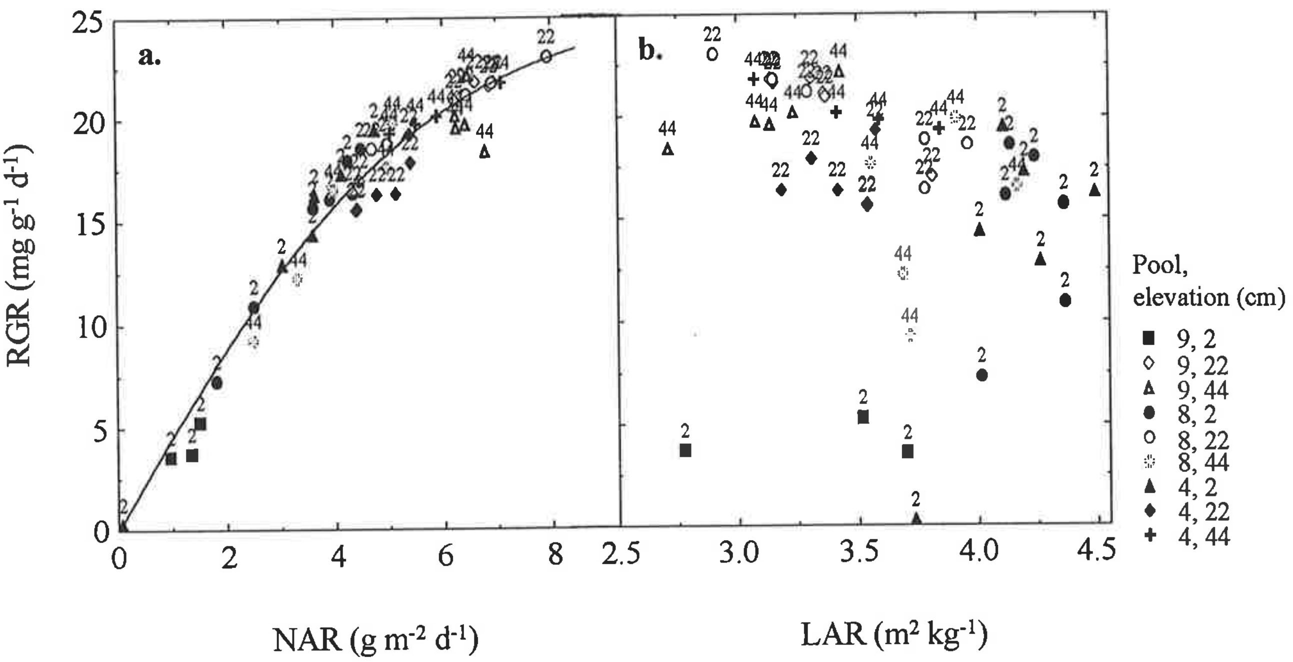

a.
b.
RGR (mg g⁻¹ d⁻¹)
25
20
15
10
5
0
0
2
4
6
8
NAR (g m⁻² d⁻¹)
2.5
3.0
3.5
4.0
4.5
LAR (m² kg⁻¹)
Pool, elevation (cm)
■ 9, 2
◇ 9, 22
△ 9, 44
● 8, 2
○ 8, 22
✲ 8, 44
▲ 4, 2
◆ 4, 22
+ 4, 44

Figure 6.7. Relationship between LAR and above to below–ground biomass ratio in *Bolboschoenus* (r^2=0.835).

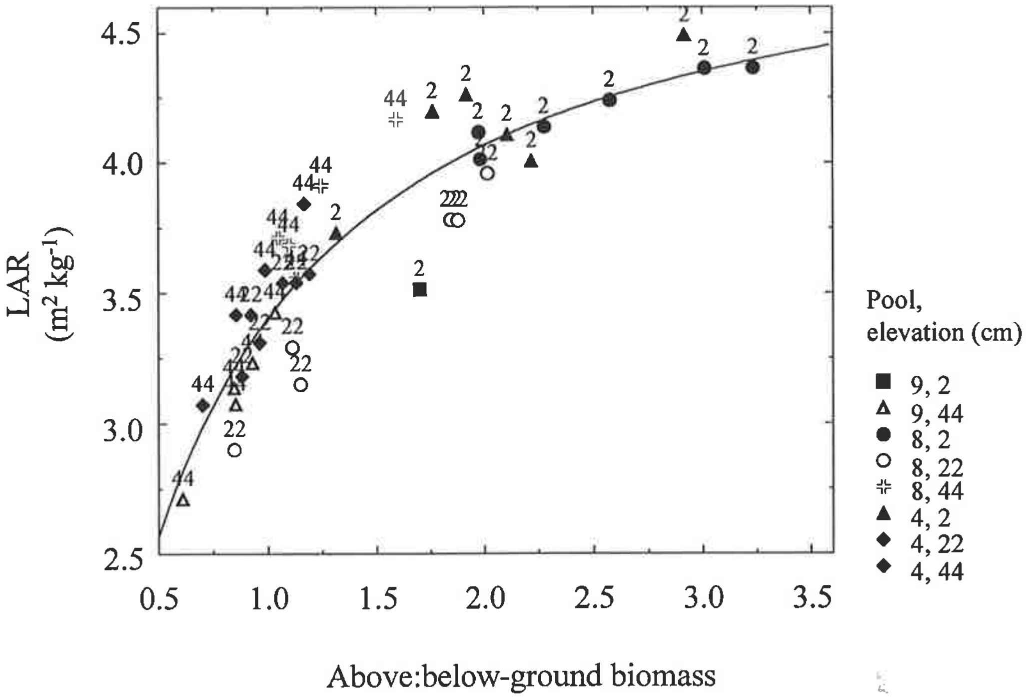

LAR
(m^2 kg^{-1})
4.5
4.0
3.5
3.0
2.5
0.5
1.0
1.5
2.0
2.5
3.0
3.5
Above:below-ground biomass
Pool,
elevation (cm)
■ 9, 2
△ 9, 44
● 8, 2
○ 8, 22
⁜ 8, 44
▲ 4, 2
◆ 4, 22
◆ 4, 44

Figure 6.8. Mean culm recruitment rate per censusing period. Means are shown for factors a. Pool (averaged across elevations), and b. Elevation (averaged across pools). Note that the scale of the abscissa does not reflect the length of each period.

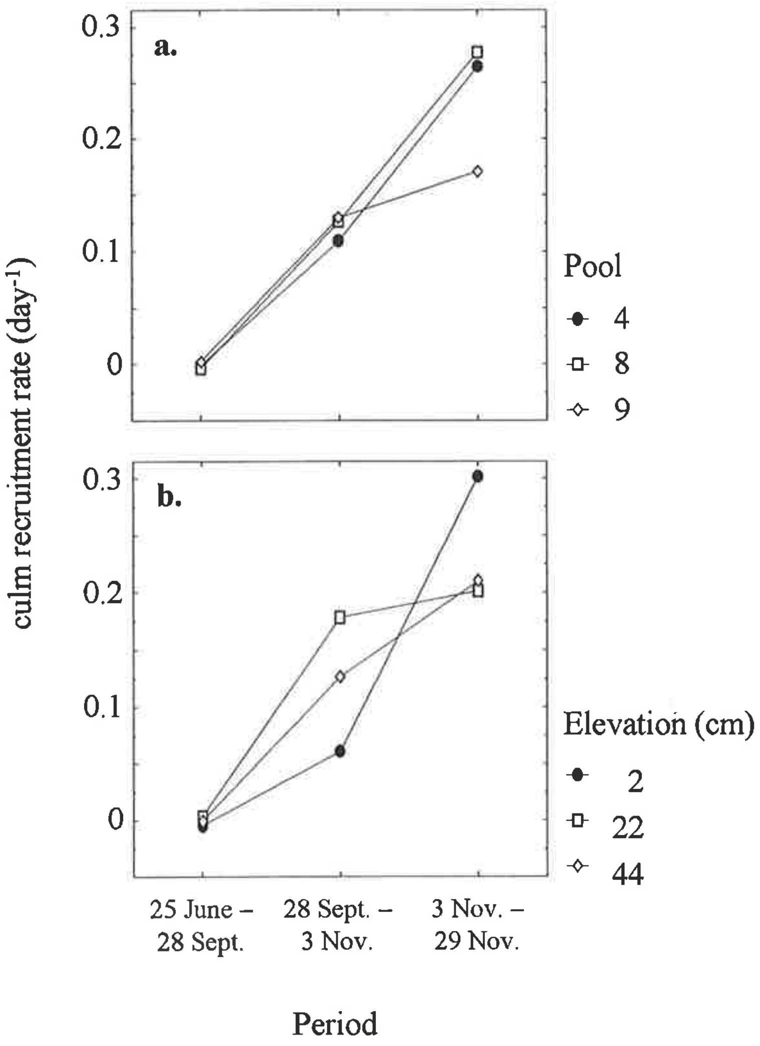
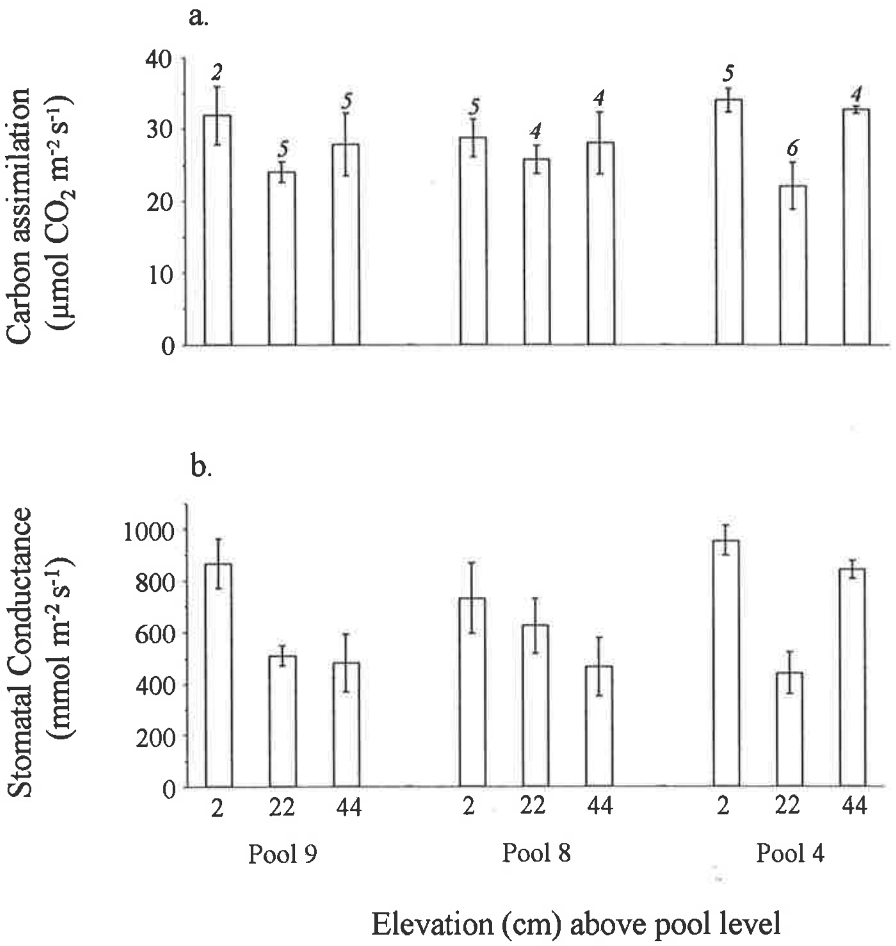

culm recruitment rate (day^{-1})
a.
b.
0.3
0.2
0.1
0
Pool
4
8
9
Elevation (cm)
2
22
44
25 June – 28 Sept.
28 Sept. – 3 Nov.
3 Nov. – 29 Nov.
Period

Figure 6.9. a. Net photosynthesis and b. Stomatal conductance in *Bolboschoenus*. Numbers of replicates are shown. Data are mean and one standard error.


a.
Carbon assimilation (µmol CO$_2$ m^{-2} s^{-1})
0
10
20
30
40
2
5
5
5
4
4
5
6
4
b.
Stomatal Conductance (mmol m^{-2} s^{-1})
0
200
400
600
800
1000
2
22
44
2
22
44
2
22
44
Pool 9
Pool 8
Pool 4
Elevation (cm) above pool level

Chapter 7

Growth and recruitment in *Vallisneria americana* as functions of the average irradiance over the water column*

7.1 Abstract

Growth and recruitment in the submersed macrophyte *Vallisneria americana* Michx. var. *americana* were examined in plants grown at three turbidities and five depths in a pond experiment. A new approach to estimating the light environment of a submersed plant was investigated using $\bar{I}$ (μmol photons $m^{-2}s^{-1}$), the average irradiance between the water surface and sediment in the absence of vegetation. $\bar{I}$ originates from phytoplankton studies and is determined from the depth, mean subsurface irradiance and rate of downwelling extinction. The relationship between whole plant relative growth rate (RGR) and $\bar{I}$ followed the theoretical P-I relationship, with 89.3% of the variance in RGR explained by $\bar{I}$. This was principally due to the causal relationship between net assimilation rate (NAR), an estimate of net plant photosynthesis, and $\bar{I}$, according to the P-I response (r^2=0.934). The compensation irradiance $\bar{I}_c$ of the NAR-$\bar{I}$ response was similar to the laboratory-determined mean I_c value for leaves (26 μmol $m^{-2}s^{-1}$). The change in leaf area ratio (LAR) across the range in $\bar{I}$ was smaller than for NAR. However, changes in LAR with $\bar{I}$ indicate *Vallisneria* is able to alter its canopy morphology in response to fluctuations in turbidity and depth in the Lower River Murray, southeastern Australia.

The biological validity of $\bar{I}$ is its relationship with B_e, the photosynthetically effective proportion of the canopy biomass B. $\bar{I}$ was significantly correlated with the proportion of B estimated to receive greater than compensation level irradiances, averaged over the day.

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*Blanch *et al.* (in review, a)

RGR, and shoot and leaf recruitment increased with $\bar{I}$ due to an increasing B_e.

Despite being a simplistic estimate of a plant's light environment, $\bar{I}$ may prove useful in studies of the light requirements of submersed plants, particularly in shallow turbid water. Its utility is enhanced by it being a single number, which can be compared graphically and statistically with growth data. It is calculated from easily measured parameters. Parametres of the RGR-$\bar{I}$ curve, such as RGR_{max}, α, $\bar{I}_c$ and $\bar{I}_k$ can be compared within and between species.

The RGR-$\bar{I}$ relationship in experimental plants was used to predict the change in biomass of *Vallisneria* plants in the Lower Murray under a range of flooding depths, durations and K_d. The simple model accurately predicted the colonised depth and general performance of *Vallisneria* under a typical turbidity regime, and the reduction in vigour at high turbidities.

7.2 Introduction

The relationship between photosynthesis and irradiance in submersed macophytes is well documented (Adams *et al.*, 1974; Rogers and Breen, 1980; Barko and Smart, 1981; Goldsborough and Kemp, 1988; Boston *et al.*, 1989; Sand-Jensen, 1989; van der Bijl *et al.*, 1989; Madsen and Sand-Jensen, 1991; Schwarz and Howard-Williams, 1993; Dunton and Tomasko, 1994; Harley and Findlay, 1994; Zimmerman *et al.*, 1994; Masini *et al.*, 1995; Schwarz *et al.*, 1996). Less is known concerning growth-irradiance relationships in submersed macrophytes at the whole plant scale over the long term (e.g. Carter and Rybicki., 1985; Kimber *et al.*, 1995a; Carter *et al.*, 1996). How are short-term metabolic processes observed in P-I responses translated into biomass accumulation? Previous studies have generally grown plants in clear water and characterised the plant's light environment as the amount of photosynthetically active radiation PAR (400-700 nm) falling on the leaf tips, and assumed negligible light attenuation with depth or by the canopy (Barko and Smart, 1981; Sand-Jensen and Madsen, 1991; Madsen and Sand-Jensen, 1994; but see Tanner *et al.*, 1993). Rapid light extinction in turbid water however, necessitates a different approach as irradiances may be several orders of magnitude lower near the sediments. One option in predicting growth in turbid water involves constructing a

Table 7.1. Symbols and parameters. RGR, NAR and LAR are calculated after Harper (1977, p 310) (see also Chapter 5).

Symbol	Description	Units
$\bar{I}$	Average irradiance between the water surface and sediments in the absence of plants.	μmol m^{-2} s^{-1}
$\bar{I}_o'$	Mean daily subsurface irradiance, averaged over the daylight hours.	μmol m^{-2} s^{-1}
$\bar{I}_c$	Minimum $\bar{I}$ for growth (analagous to the minimum light requirement for growth in Sand-Jensen and Madsen, 1991).	μmol m^{-2} s^{-1}
$\bar{I}_k$	Onset of light-saturated growth (calculated as RGR_{max}/α).	μmol m^{-2} s^{-1}
I_{ini}	Mean noon irradiance received at the leaf tips at the start of the experiment.	μmol m^{-2} s^{-1}
I_c	Light compensation point in leaf pieces.	μmol m^{-2} s^{-1}
I_k	Onset of light-saturated photosynthesis in leaf pieces.	μmol m^{-2} s^{-1}
K_d	Rate of downwelling extinction (or attenuation) coefficient.	ln m^{-1}
z_m	Depth to sediment $_m$ reflects the origin of $\bar{I}$ in phytoplankton studies, which estimate the *mixed* depth. See text (The convention is observed here for consistency).	m
α	Growth efficiency; numerically the linear slope of the light-limited section of the RGR-$\bar{I}$ curve.	mg g^{-1} d^{-1}(μmol m^{-2} s^{-1})$^{-1}$
RGR	Whole-plant relative growth rate; calculated as instantaneous growth per initial dry weight.	mg g^{-1} d^{-1}
RGR_{max}	Maximum light-satured RGR.	mg g^{-1} d^{-1}
NAR	Net assimilation rate; the assimilatory efficiency per unit leaf area.	g cm^{-2} d^{-1}
LAR	Leaf area ratio; the ratio of the assimilatory area of a plant per unit total dry weight.	cm^{2} g^{-1}

carbon balance model for the whole plant from measured net photosynthesis rates, biomass and light profiles within depth strata of the canopy (Adams *et al.*, 1974; van der Bijl *et al.*, 1989; Fourqurean and Zieman, 1991; Zimmerman *et al.*, 1994). This is essentially a reductionist approach. Whilst this allows an insight into the depth distribution of assimilation within the canopy, its use in accurately predicting long-term growth patterns over a range of turbidities and depths is limited.

This study instead employs an holistic approach by calculating the average irradiance $\bar{I}$ (μmol m^{-2} s^{-1}) between the water surface and the sediments, in the absence of plants, as a measure of the light available for growth (Table 7.1, Riley, 1957; Oliver and Ganf, 1988; Mallin and Paerl, 1992). No assumption is made concerning the depth distribution of biomass; $\bar{I}$ is simply an estimate of the average level of available resource (PAR) over the depth to the sediments, z_m. $\bar{I}$ is a function of the mean daily subsurface irradiance $\bar{I}_o{}'$, z_m, and the downwelling extinction coefficient K_d (Table 7.1) according to the expression

$$\bar{I} = \frac{\bar{I}_o{}'(1-e^{-K_d.z_m})}{K_d.z_m} \tag{1}$$

$\bar{I}$ approaches $\bar{I}_o{}'$ as z_m decreases, and equals $\bar{I}_o{}'$ in perfectly clear water (K_d=0) at all z_m (Fig. 7.1).

Its utility lies in it being a single number which can be compared graphically and statistically with growth data (Oliver and Ganf, 1988). It was suggested by Riley (1957) as an estimate of the mean irradiance encountered by an algal cell circulating freely through the mixed depth z_m. Hence it assumes an homogenous distribution of photosynthetic material. Of necessity $\bar{I}$ was used without assuming an homogeneous depth distribution of biomass in this study.

As plant density increases, absorption by the canopy will reduce the actual $\bar{I}$ over z_m, thereby impinging upon growth (Titus and Adams, 1979; van der Bijl *et al.*, 1989; Beadle, 1993). Incorporating the specific absorption coefficient K_s of leaf biomass B (per m^3 over z_m) into Eq (1) yields

$$\bar{I} = \frac{\bar{I}_o{}'(1-e^{-(K_d.z_m+K_sB)})}{K_d.z_m+K_sB} \tag{2}$$

The 'effective' $\bar{I}$ experienced by a plant depends on the depth distribution of B. Plants with a surface canopy will increase the interception of light, resulting in a higher effective $\bar{I}$. Plants in deeper water with mainly short leaves will experience an effective $\bar{I}$ lower than that suggested by Eq (2). The apparent optical properties K_d and K_s are assumed to be additive, due to the close relationship between the inherent and apparent optical properties of a water body (Kirk, 1983, p18; Oliver, 1990).

Plants able to place the majority of their photosynthetic tissue close to the surface in turbid water maximise carbon assimilation. With increasing depth or turbidity, in the absence of photoadaptation, the plants' photosynthesis:respiration will decline and biomass accumulation will slow. Hence at high $\bar{I}$ growth is expected to be high, and to decrease with decreasing $\bar{I}$ (increasing z_m and/or K_d).

Growth is determined by both the efficiency of a plant's canopy to assimilate carbon and the size of that canopy relative to total biomass (Harper, 1977; Beadle, 1993). The former is calculated as NAR, and the latter as LAR (Table 7.1). Growth is expressed as RGR. NAR is a crude estimate of net photosynthesis (Harper, 1977), and would be expected to increase with irradiance due to an increase in photosynthesis at higher irradiance. If this is true, the NAR-$\bar{I}$ response would essentially follow a P-I response curve (Kirk, 1983). A species' capacity to change its canopy morphology in a changing light environment would be detected in changes in LAR with $\bar{I}$. Under low irradiances an increase in leaf length and reduction in width, causing an increase in LAR, is predicted as a strategy to place maximum photosynthetic tissue at the surface. In shallow water, $\bar{I}$ is higher and plants can maximise light interception by producing many short, thick leaves, thereby reducing LAR.

Vallisneria americana Michx. *americana* (ribbonweed or American wild celery, Hydrocharitaceae) is a common submersed macrophyte in the Lower Murray (Lowden, 1982; Catling *et al.*, 1994; Jacobs and Frank, in press). It produces long ribbon-like leaves from basal meristems which form a canopy at the surface. Growth is typically limited to 1-2 m depth, but when the tributary Darling River is in flood, its extremely turbid waters limit growth to <1 m (Walker *et al.*, 1994). The Darling's sediment load is comprised of mainly non-settling montmorillonite clays, 90% of which are less than 2 µm in diameter (Woodyer, 1979). At such times, turbidities range from 100-600 nephelometric turbidity units (NTU) and downwelling extinction coefficients from 6 to 25 m^{-1} (Mackay *et al.*, 1988; Oliver, 1990). Diminished light penetration and deep submersion greatly reduce the average irradiance $\bar{I}$ received by *Vallisneria* at such times.

In this chapter the influence of turbidity and depth on growth and shoot and leaf recruitment in *Vallisneria* is examined by investigating the relationship between $\bar{I}$ and RGR. Three turbidity (thus K_d) levels and 5 depths were used in a pond experiment which lasted 102 days, with the RGR-$\bar{I}$ relationship determined at the end of the experiment. Depths were selected to vary the proportion of the canopy receiving sufficient light for net photosynthesis (based on laboratory-determined compensation irradiances, I_c, cf. Chapter 8). In the deepest treatments the majority of the canopy was below the depth of penetration of compensation-level irradiances. This allowed the determination of the whole plant compensation irradiance.

As identical $\bar{I}$ values can occur for a range in z_m by altering K_d, the RGR-$\bar{I}$ relationship was investigated at three K_d levels to test its applicability from mid to very high turbidities. Data are plotted against both $\bar{I}$ and depth as an aid to interpretation of the data.

The effect of turbidity is initially examined for constant z_m, the hypothesis being plant performance declines with increasing turbidity. I then test the hypothesis that growth is a function of the average irradiance $\bar{I}$, and the RGR-$\bar{I}$ response follows the standard P-I curve as formulated by Jassby and Platt (1976). $\bar{I}$ is the proximal and turbidity the distal factor determining growth. Consequently the formers' influence on performance is examined in greater detail.

As $\bar{I}$ increases, the proportion of the canopy receiving sufficient light for net photosynthesis decreases. This suggests that the relationship between RGR and $\bar{I}$ may be examined by comparing growth and recruitment with the proportion of the canopy biomass receiving irradiances greater than compensation levels. This proportion of the canopy is B_e, the photosynthetically effective leaf biomass. Evidence for such a relationship exists in seagrasses, where growth has been related to the time per day plants receive light exceeding saturating or compensating irradiances (Dennison and Alberte, 1982; Dunton and Tomasko, 1994; Zimmerman *et al.*, 1994). Thus the biological significance of $\bar{I}$ is hypothesised to be its relationship to B_e.

If $\bar{I}$ is an ecologically meaningful estimate of the mean water column irradiance, then the RGR-$\bar{I}$ response for a species should be described by the same RGR_{max}, photosynthetic efficiency α and onset of photosaturation $\bar{I}_k$ for all values of K_d (at similar temperature, inorganic carbon and nutrient conditions). If this is true, RGR-$\bar{I}$ curves could be a simple yet powerful predictive tool for researchers and managers of aquatic macrophytes. The utility of the RGR-$\bar{I}$ response for prediction was tested by modelling growth in natural populations of *Vallisneria* under a range of flooding depths, durations and K_d in the Lower Murray.

7.3 Methods

7.3.1 Description of Vallisneria *and experimental design*

Vallisneria americana is a perennial, diocieous monocot with basal meristems (Fig. 7.2). The recent classification of Jacobs and Frank (in press) is followed, who consider it pan-Pacific and native to southeastern Australia. Others have claimed it native to eastern North America however (Lowden, 1982; Catling *et al.*, 1994). Until just prior to submission of this thesis, plants used in the study were named *Vallisneria spiralis* according to Black (1980). One aim of the study was to compare growth-light responses in the dominant *Vallisneria* species of southestern Australia with that in eastern North America (*Vallisneria americana*). Only recently have I become aware that Lower Murray *Vallisneria* plants are grouped with the North American species. Jacobs (Royal Botanic Gardens, Sydney, pers. obs., 1997) observed considerable morphological plasticity in *Vallisneria*, and ascribed it to differences in sediment type and organic content, depth and current velocity. Canopy formation seems more prevalent in Lower Murray populations than North American plants (cf. Titus and Adams, 1979; Madsen *et al.,* 1991; Carter *et al.,* 1996). Lokker *et al.* (1994) found high genetic diversity in a *Vallisneria* bed in the Detroit River, northern USA. Phenotypic variation between continents is unsurprising given this diversity.

Variation in leaf size is common; from short and narrow (< c. 0.5m and c. 15 mm wide) to long and wide (to 2 m and 25 mm). Leaves comprise more than three-quarters of total biomass. The prime function of stolons is vegetative spread rather than carbohydrate storage. *Vallisneria* does not appear to store carbohydrates in subterranean organs for the purposes of resource allocation above-ground in deep water and/or low light.

Vallisneria shoots between 30 and 50 cm high were collected in December 1995 from a single population in the littoral zone of the Lower Murray at Blanchetown, South Australia (34°25'S, 139°40'W). Plants were kept in shallow water and covered with damp hesian for 48 hours before planting. Stolons and roots were trimmed to 5 and 10 cm respectively to standardise initial performance. A single shoot was planted per 10 L pot (30 cm wide by 18 cm deep). Sediments were sandy-loam with a 2 cm cap of grey clay to reduce leaching of nutrients and emulate littoral sediments. Slow-release fertilizer pellets (Osmocote®, 9 month release) were thoroughly mixed into the sandy-loam at 3 g per litre, equivalent to a loading of 100 g N $m^{-2}y^{-1}$.

Shoots were established for 3 months in clear water 20-35 cm deep in an outside pond in summer (water temperatures 20-30°C, noon irradiance 1500-2500 µmol $m^{-2}s^{-1}$). In mid-May three vigorous non-flowering shoots were selected, to reduce the effect of age, and the remainder removed. All shoots were female. Leaves were trimmed to 10 cm a week prior to being placed in turbid water. This standardised the initial canopy distributions with respect to light and simulated the inundation of plants by turbid floodwaters with leaves naturally trimmed to similar lengths by exposure in the wash zone. Flooding in the Lower Murray generally occurs in late winter-early spring (though floods may occur throughout the year). Hence the study was conducted over winter to foster predictions of the effects of winter floods on field populations.

7.3.2 Constant downwelling extinction regimes

Clay suspensions were used to simulate the light regime in the Lower Murray when receiving turbid water from the Darling River. Bentonite was the finest commercially-available clay, and simulated the extremely fine montmorillonites, illites and kaolinites which dominate Darling water (Woodyer, 1979; Thoms and Walker, 1993).

Powdered clay was manually stirred in tapwater in large tanks until thoroughly wetted, then regularly agitated with an electric drill and paint stirrer. The concentrated clay suspension was added to tapwater in large outdoor ponds (3m x 4m x 1.1m deep, volume $13m^3$). A submersible pump (Ebara Best-Zero, 33 mm outlet, pond turnover time 1.5 h) stirred each pond continuously. Rapid settling ensued without constant stirring in the high conductivity tapwater (600-700 µS cm^{-1}). Clay suspension was also added regularly, and settled sediments resuspended with a broom. Damage to plants was prevented by directing the pump flow underneath plants and around the pond walls.

As turbidity was simpler to measure than K_d, it was determined every 1-3 days with a Hach 2100A turbidimeter and K_d estimated from an empirical relationship between turbidity and K_d (Fig. 7.3). K_d was also measured twice weekly to validate the estimations. Turbidity measurements made at different sites in each pond confirmed an homogeneous distribution of particles.

7.3.3 *Average irradiance* $\bar{I}$ *treatments*

$\bar{I}$ and z_m treatment levels for each K_d are shown in Table 7.2. The range in K_d values span those observed in the Lower Murray during flooding with Darling water (Oliver, 1990; M. Shaffron, Murray Darling Basin Commission, Canberra, pers. comm.). Values for K_d and turbidity in the Lower Murray are generally 2-5 ln units m^{-1} and 20-100 NTU.

Levels of $\bar{I}$ for each K_d were determined by placing plants such that the tips of their 10 cm-long leaves received a mean initial irradiance I_{ini} of 450, 100, 20, 5 or 0.1 µmol $m^{-2}s^{-1}$ between 10 am and 2 pm, when initially flooded with turbid water (hence prior to growth). z_m was determined from the equation describing exponential attenuation of $\bar{I}_o'$ with depth:

$$I_z = I_o' e^{-K_d . z_m} \qquad \text{Lambert-Beer relationship} \quad (3)$$

For the purposes of determining I_{ini}, $\bar{I}_o'$ was assumed to be 600 µmol m^{-2} s^{-1} and K_d values were 6, 12 and 24 (Table 7.2).

Photosynthesis-irradiance data determined from laboratory oxygen production experiments indicated light-saturated photosynthesis occurred at approximately 450 µmol $m^{-2}s^{-1}$, and that photosynthesis equalled respiration at 20-25 µmol $m^{-2}s^{-1}$ (Chapter 8). Therefore plants in the 5 and 0.1 µmol m^{-2} s^{-1} treatments initially received insufficient light for net photosynthesis.

Solar irradiance I_o was recorded every 60 seconds and averaged over an hour throughout the experiment with a LiCor aerial quantum sensor and logged on a LiCor Li1000

Table 7.2. Average irradiance $\bar{I}$ occurring between the water surface and sediments. K_d treatments were maintained with clay suspensions of varying turbidity, measured in nephelometric turbidity units (NTU). z_m (cm) is the depth to the sediments. I_{ini} is the initial irradiance at the tips of 10 cm-long leaves prior to growth, which was used to determine $\bar{I}$ and z_m. The standard errors associated with the mean K_d and turbidity levels are given (n=26). Units of $\bar{I}$ and I_{ini} are μmol photons $m^{-2}s^{-1}$.

K_d (m^{-1}):	6.48±0.17		12.59±0.34		21.92±0.33	
Turbidity (NTU):	90±2		209±6		504±8	
Secchi depth (cm):	21		13		7	
I_{ini}	$\bar{I}$	z_m	$\bar{I}$	z_m	$\bar{I}$	z_m
450	141.3	14	*110.9	12	67.6	11
100	78.3	39	67.7	24	46.9	17
20	49.6	66	43.5	39	33.8	24
5	36.8	90	34.8	49	26.3	31
0.5	NA	NA	NA	NA	20.4	39
0.1	18.3	†145	20.8	82	17.8	46

† Effects of depth simulated using shade cloth to reduce irradiance. This was necessary as the pond was of insufficient depth to attain this I_{ini}. Comparison of measured and calculated irradiances indicate this method accurately created the required $\bar{I}$.
* Most plants in this treatment were grazed by ducks and are excluded from most data analyses.
NA not available.

datalogger. Daily $\bar{I}_o'$ from mid May to late August 1996 was calculated as incoming irradiance I_o corrected for surface reflection. Reflectance was measured over a range of I_o for each K_d. I_o and I_o' were measured with aerial and underwater (cosine-corrected) LiCor quantum sensors respectively. The mean daily I_o' value, $\bar{I}_o'$, for each K_d treatment was calculated as the mean I_o' over 10 hours of daylight (8 am-6 pm).

Plants were randomly allocated to treatments and placed on racks in the turbid water on 16 May so that the sediment surfaces were at the depths shown in Table 7.2. Six replicates were allocated to each treatment. Plants were allocated randomly to turbidity treatments, but within each pond racks were positioned so as to reduce shading, with plants on the northern side being lower. The experiment lasted 102 days which is comparable with the duration of the medium-longest flood events.

7.3.4 Measurements of growth and recruitment

Leaf recruitment and senescence, width and extension rate were recorded on 15 May, 5 and 25 June and 25 August in the K_d 12.59 treatments. On 15 May the youngest leaf in one randomly selected shoot per pot was marked with two small holes using a dissecting probe as close to the sediment surface as possible. Length to the mark was measured subsequently to determine extension rates. Leaves were re-marked lower down as the tip sensesced. New leaves are produced in the middle of the plant, with older leaves pushed alternately to either side (Fig. 7.2), allowing relative leaf ages to be inferred. In this way numbers of old and new leaves were determined relative to the marked leaf.

Plants were harvested on 26-29 August after 102 days' growth. Sediments were removed by washing over a 1 mm mesh sieve, and leaves (including leaf bases and the few female peduncles), roots and stolons separated by flotation. Root loss was considered <1% by weight. Plants were oven dried at 80°C to constant weight (72 h).

7.3.5 Light extinction coefficient for Vallisneria

The specific spectral absorption coefficient for *Vallisneria* was measured according to the procedure of Westlake (1964). Shoots with leaves 10-60 cm long were secured to a circular wire frame of the same diameter as the experimental pots. Shoots were positioned around the frame's circumference and on crosswires in a stratified random distribution. Four densities of shoots were used. Approximately 20% of leaves at each density reached the surface. At each density, 25 measurements of irradiance were made at the base of the shoots (depth 0.30 m) with a LiCor underwater quantum sensor. Light readings I_z were taken at positions throughout the plant in a stratified random pattern. Measurements were made between 12 and 2 pm on a cloudless day. I_o' was recorded simultaneously with I_z, and the light attenuation due to the canopy assumed to be linear through the canopy. The specific spectral absorption coefficient K_s was calculated as the slope of the relationship between K_d and B, the leaf biomass (m^3 over a z_m of 0.30 m). Values of B used in Eq (2) were the leaf dry weight expressed as per m^3 over z_m.

7.3.6 *Proportion of the canopy biomass* B$_e$ *receiving irradiances exceeding light compensation levels*

The proportion of the canopy (g dry wt) receiving more-than light compensation level irradiances I_c, averaged over the daylight hours, was estimated. An I_c of 20 µmol m^{-2}s^{-1} was used as an average of measured values across leaves of varying ages at different depths (cf. Chapter 8). The mean depth of $\bar{I}_c$-level irradiance over the day was calculated using the mean daily $\bar{I}_o'$ values and Eq (3) for each K_d. At the end of the experiment the length of each leaf occurring above the mean daily $\bar{I}_c$-depth was estimated as the total leaf length minus the length below that depth. In leaves reaching the surface, curvature away from vertical was minimal below depth 10 cm (cf. Chapter 9). As this was the shallowest mean daily $\bar{I}_c$ depth (for a K_d of 21.92), the calculations assumed leaves were vertical below 10 cm.

The depth corresponding to the penetration of mean daily compensating irradiances was determined, rather than the depth to saturating irradiances, for two reasons (cf. Dennison and Alberte, 1982; Dennison, 1987). The range in laboratory-determined compensating irradiances was smaller (I_c; 2-35 µmol m^{-2} s^{-1}, Chapter 8) than that of the onset of photosaturation (I_k; 19-144 µmol m^{-2} s^{-1}). Also, I_k values were high relative to the maximum *in situ* irradiances due to the high turbidities. A large proportion of the canopy's photosynthesis thus occurred at irradiances less than I_k.

The relationships between leaf length and dry weight was determined in plants from three ranges in z_m (11-24 cm, 31-49 cm and 60-90 cm). Plants from several rooting depths within each z_m range were selected. Twenty to thirty leaves of varying ages in each z_m range were measured and the leaf projected area measured with a Delta T leaf area meter. Leaves were then dried at 80°C to constant weight (72 h).

7.3.7 *Modelling*

Nonlinear estimation was employed to fit the Jassby and Platt (1976) hyperbolic tangent model to RGR and NAR data as functions of $\bar{I}$ (Statistica, 1994). Quasi-simplex estimation was most effective, and the loss function minimised the squared difference between observed and expected values. Models were accepted upon the condition of normality of residuals.

The modified Jassby and Platt model was employed to describe RGR as a function of RGR_{max}, α, $\bar{I}$ and R:

$$RGR = RGR_{\max} \tanh(\frac{\alpha \bar{I}}{RGR_{\max}}) - R \qquad (4)$$

where RGR_{max} = Estimated maximum RGR (mg $g^{-1}d^{-1}$)

α = slope of the initial linear section of the curve, and reflects photosynthetic efficiency (units mg $g^{-1}d^{-1}(\mu mol\ m^{-2}s^{-1})^{-1}$)

R = constant to adjust for respiration (van der Bijl *et al.*, 1989; Olesen and Sand-Jensen, 1993)

The calculated onset of $\bar{I}$-saturated RGR, $\bar{I}_k$, equals P_{max}/α (Bannister, 1979).

7.3.8 *Modelled changes in plant biomass under varying flooding regimes in the Murray*

The relationship between RGR and $\bar{I}$ established for plants in the pond experiment was used to predict the effects of flooding of various depths, durations and K_d on *Vallisneria americana* populations the Lower Murray. $\bar{I}$ was calculated from Eq (1) for each combination of z_m and K_d. K_d values spanned the range in observed values for the Lower Murray (2-25 m^{-1}). Flooding depths were 0.5, 1.0, 1.5 and 2.0 m. For each $\bar{I}$, RGR was determined from the RGR-$\bar{I}$ model (Fig. 7.5a).

The effect of flood duration on plant biomass was calculated by solving the equation for RGR as the proportional change in biomass W_f / W_i (final and initial plant dry weights):

$$\%\ change\ in\ plant\ biomass = \frac{W_f}{W_i} = e^{RGR*t} \qquad (5)$$

where RGR is in mg g^{-1} d^{-1} and time t in days. It assumes RGR is constant over t (hence exponential, density-independent growth) and is strictly applicable only for similar temperature, photoperiod, carbon supply and nutrient conditions. Plants are assumed to be mature and in shallow water (c. 10-30 cm depth) with leaves c. 10 cm long from natural exposure to waves and air.

7.4 Results

7.4.1 Solar irradiance and water temperature

Mean solar irradiance $\overline{I}_o$ peaked at 589 µmol $m^{-2}s^{-1}$ from 1-2 pm (Fig. 7.4). Mean daily $\overline{I}_o$ over the experiment was 303 µmol $m^{-2}s^{-1}$, calculated as the mean integrated I_o over 10 h per day over 102 days. Surface reflectance was 29% for the two lower K_ds and 41% for K_d 21.92. These values are much higher than those reported for less turbid water (c. 2-10% for much lower turbidities) due to high scatterance (Kirk, 1983). Hence mean daily subsurface irradiance $\overline{I}_o'$ for K_d 6.48 and 12.59 was 0.71 x 303 = 215 µmol m^{-2} s^{-1}, and 0.59 x 303=179 µmol m^{-2} s^{-1} for K_d 21.92. These values were used in Eq (1), (2) and (3) to calculate $\overline{I}$ and I_z. Mean minimum and maximum water temperatures were 12°C and 13.5°C, and ranged from 10-14°C (min.) and 11-17°C (max.).

7.4.2 Survival

Survival was 100% for all treatments. Even plants in the deepest treatments survived 3 months with irradiances insufficient or barely sufficient for photosynthesis (according to laboratory-determined P-I data). This indicates that *Vallisneria* can tolerate extended periods when photosynthesis is minimal, as determined by Meyer *et al.* (1943), Titus and Adams (1979), Madsen *et al.* (1991) and Harley and Findlay (1994).

7.4.3 Effect of turbidity on growth, biomass accumulation and recruitment at constant z_m

Data in Table 7.3 show that plant performance diminishes under high turbidity for a given depth. The ecophysiological mechanisms underlying this relationship between growth and light are then investigated below by examining the RGR-$\overline{I}$ response (see Section 7.4.4).

Growth was negatively correlated with increasing turbidity at rooting depth 39 cm (Table 7.3). RGR and NAR declined as turbidity increased. The relationship between RGR and turbidity is

$$\text{RGR (mg g}^{-1}\text{ d}^{-1}) = 21 - 0.047^{*}(\text{turbidity, NTU}) \qquad (r^2=0.933, P<0.0001, n=17)$$

Table 7.3. Reduction in growth and recruitment with increasing turbidity. Depth z_m is 39 cm. $\bar{I}$ is the average daily irradiance between the surface and sediment (Eq 1)). One-way analysis of variance was conducted on ln-transformed data, except for root dry weights (arcsin transformed), and RGR, NAR and LAR (untransformed). Values with the same letter are not significantly different at P=0.05 (Tukey's HSD). Data are mean and standard deviations (n=5-6).

Turbidity (NTU)	$\bar{I}$ (µmol m^{-2}s^{-1})	K_d (m^{-1})	RGR (mg g^{-1}d^{-1})	NAR (x 10^{-6} g cm^{-2} d^{-1})	LAR (cm^{2}g^{-1})
90	78.3	6.48	17.45 ± 1.39^a	77.0 ± 14.4^a	231.1 ± 29.8^a
209	43.5	12.59	10.85 ± 3.07^b	35.8 ± 11.3^b	309.4 ± 51.3^b
504	20.4	21.92	2.36 ± 2.15^c	-8.4 ± 7.4^c	294.4 ± 42.2^{ab}

Turbidity (NTU)	Dry weight (g)					
	Total	Leaves	Stolons	Roots	Below-gr.	Above:below
90	7.72 ± 2.21^a	6.90 ± 1.98^a	0.29 ± 0.12^a	0.53 ± 0.15^a	0.82 ± 0.25^a	8.41 ± 1.11^a
209	4.04 ± 1.42^b	3.58 ± 1.23^b	0.12 ± 0.08^a	0.34 ± 0.15^b	0.46 ± 0.22^a	7.78 ± 1.60^a
504	0.94 ± 0.22^c	0.74 ± 0.20^c	0.05 ± 0.01^b	0.15 ± 0.03^c	0.20 ± 0.04^b	3.70 ± 1.16^b

Turbidity (NTU)	Number of new shoots	Total number of leaves	Cumulative leaf length (m)
90	5.83 ± 2.48^a	69.3 ± 20.24^a	22.40 ± 7.1^a
209	1.33 ± 1.21^b	37.2 ± 9.04^b	12.48 ± 3.1^b
504	0	15.6 ± 4.04^c	3.05 ± 0.9^c

LAR remained fairly constant, even slightly increasing, over the turbidity range compared with NAR. This was despite a four-fold decrease in $\bar{I}$, from 78.3 to 20.4 µmol m^{-2} s^{-1} (Table 7.3).

The monotonic decrease in RGR with NAR indicates the poor performance of *Vallisneria* in highly turbid water is due to a reduced capacity to assimilate carbon under lower irradiances. This was observed in a reduction in total biomass from 7.72 to 0.94 g under low and high turbidities. Leaf biomass fell 10-fold (6.90 to 0.74 g) but below-ground biomass fell only 4-fold (0.82 to 0.20 g) as turbidity increased. This suggests a survival strategy of *Vallisneria* in highly turbid water is to maintain root and stolon biomass in preference to leaves. A strong below-ground structure provides for anchoring in the sediments of the littoral where wave action maybe strong. When floods recede or turbidity declines regrowth can occur from the protected meristems. Shoot recruitment was significantly lower at the medium turbidity treatment (209 NTU), and was zero at 504 NTU.

Numbers of leaves, total leaf length and surface area declined at higher turbidities. The increase in LAR under the two higher turbidities, from 231 to c. 309 cm^2 g^{-1}, occurred despite this decrease in allocation to leaves. Leaves produced in these treatments were generally thinner and narrower than at a turbidity of 90 NTU. This may allow greater interception of light by chlorophyll due to a higher surface area to volume ratio. Enriquez *et al.* (1995) found a significant negative correlation between maximum rates of light-saturated photosynthesis and lamina thickness in marine macrophytes, and concluded that thin leaves were an adaptation to growth under low light.

7.4.4 Effects of $\bar{I}$ over varying z_m on plant performance

Plant performance over a range of z_m for the three turbidity regimes was examined to determine the combined effects of flooding depth and rate of downwelling extinction. The mechanisms producing the growth patterns are investigated using $\bar{I}$. As growth responses are due to the depth distribution of the canopy relative to the strong vertical light gradient, the relationship between plant performance and B_e, the proportion of the canopy receiving irradiances greater than compensation irradiances, is then investigated.

Relative Growth Rate, Net Assimilation Rate and Leaf Area Ratio

The relationship between RGR and $\bar{I}$ follows the theoretically predicted P-I response of Eq (4) (r^2=0.893, Fig. 7.5a). The fact that data for all turbidity regimes were adequately described by a single curve indicates $\bar{I}$ is biologically meaningful. Regardless of the depth distribution of photosynthetic tissues and depth to the sediment, growth is highly correlated with $\bar{I}$.

Interestingly, the $\bar{I}$ at which RGR is zero ($\bar{I}_c$=26 μmol m^{-2} s^{-1}, Table 7.4) is very similar to the laboratory determined mean compensation irradiances in leaf pieces (20-25 μmol m^{-2} s^{-1}) (Table 7.4). This seems remarkable given the wide range in oxygen production rates in the various tissues at any instant; from highly positive in surface leaves over the day to highly negative in roots (Chapter 8). It seems unlikely that this result is an artefact of the formulation of $\bar{I}$.

RGR increases linearly with $\bar{I}$ at low $\bar{I}$, as the majority of the canopy is not photosaturating. Growth efficiency, α, is 0.33 mg g^{-1} d^{-1}(μmol m^{-2} $s^{-1})^{-1}$ at low $\bar{I}$. With increasing $\bar{I}$, a greater proportion of the canopy will receive irradiances sufficient for net photosynthesis, causing an increase in RGR. At values of $\bar{I}$ greater than $\bar{I}_k$ (58 μmol m^{-2} s^{-1}) a significant proportion of the canopy photosaturates during the day, and the rate of increase in RGR with increasing $\bar{I}$ approaches a maximum asymptotic value of 19.1 mg g^{-1} d^{-1}.

Reported maximum RGR values for other macrophytes include 40 mg g^{-1} d^{-1} for *Egeria densa* in turbid water (Tanner *et al.*, 1993) and 30-70 mg g^{-1} d^{-1} for *Elodea canadensis* and *Callitriche cophocarpa* (Madsen and Sand-Jensen, 1994). Note that $\bar{I}$ is calculated over the light period but RGR over 24 h.

For a given $\bar{I}$, z_m becomes very shallow as turbidity increases (Eq (1)), causing a dense surface canopy to form. For example, the mean maximum leaf length is 50 cm in plants at 11 cm (see Fig. 7.13), which places approximately three quarters of the leaf biomass B at the surface. Development of a dense surface canopy reduces the actual $\bar{I}$ experienced over z_m (Eq (2)).

Table 7.4. Parameters describing the relationships between RGR and NAR and the average irradiance $\bar{I}$ between the water surface and sediment. The effect of absorption by the canopy on parametres in the RGR-$\bar{I}$ response is shown (canopy extinction coefficient, K_s, included). All parameters were determined from the graphs and compared with model predictions for accuracy. NAR_{max} was determined from the NAR-$\bar{I}$ model.

Term	maximum rate	α (rate per µmol m^{-2} s^{-1})	$\bar{I}_c$ (µmol m^{-2} s^{-1})	$\bar{I}_k$ (µmol m^{-2} s^{-1})
RGR (mg g^{-1} d^{-1})				
a. Without K_s (Eq (1))	19.1	0.33	26	58
b. With K_s (Eq (2))	19.6	0.36	24	54
NAR (10^{-5} g cm^{-2} d^{-1})	15	0.14	26	107

The specific absorption coefficient, K_s, was 0.0051 m^2 g^{-1}. When absorption by the canopy was considered (Eq (2)), calculated $\bar{I}$ fell by up to 27% for plants in shallow water. At low $\bar{I}$ the reduction was 1-5%, due to a much smaller leaf biomass *B*. $\bar{I}_k$ and $\bar{I}_c$ were lower (54 and 24 µmol m^{-2} s^{-1}, respectively) and α slightly higher (0.36 mg g^{-1} d^{-1} (µmol m^{-2} s^{-1})$^{-1}$) when absorption by the canopy is included. Lower saturation and compensation points, and higher growth efficiency, calculated using Eq (2), reflect a greater adaptation to shading than suggested by Eq (1). Whilst light penetration to lower strata is reduced by *B*, light interception by surface leaves increases the effective $\bar{I}$ over the whole canopy due to a much higher carbon assimilation rate (cf. Chapter 9). Hence RGR is influenced more so by the depth distribution of *B* than the value of *B* itself (see below). The value of K_s in this study is lower than that reported for *Vallisneria* in Wisconsin lakes by Titus and Adams (1979; 0.013-0.024 m^2 g^{-1}), and for *Potamogeton pectinatus* (0.024 m^2 g^{-1}; van der Bijl *et al.*, 1989).

The RGR-$\bar{I}$ response was due mainly to the influence of $\bar{I}$ on the rate of biomass production per unit leaf area and time, NAR (Fig. 7.6). The NAR-$\bar{I}$ relationship fits the theoretical P-I curve, with 93% of the variance explained by Jassby and Platt's (1976) model. The predicted NAR_{max} value of 15 x 10^{-5} g cm^{-2} d^{-1} occurs at considerably higher $\bar{I}$ than used in this study. The $\bar{I}_k$ value for this response is nearly twice that for RGR (107 *v* 58 μmol m^{-2} s^{-1}, Table 7.4). This suggests that changes not in assimilation efficiency but in the canopy's leafiness, *i.e.* LAR (Hunt, 1982; p24) are responsible for the plateau in RGR at high $\bar{I}$.

In comparison with NAR, the variation in LAR with $\bar{I}$ was small (Fig. 7.7). Values of LAR ranged nearly 3-fold, between 146 and 406 cm^2 g^{-1}, whereas NAR varied 17-fold, between -3 and 13 x 10^{-5} g^{-1} cm^2 d^{-1}. The large reduction in NAR at low $\bar{I}$ was not offset by a concomitant increase in LAR - with the result being a lower RGR. Considering the very large reduction in $\bar{I}$ with depth, this is not surprising. However, the changes in LAR with $\bar{I}$ reflect the morphological adaptation of *Vallisneria* to growth in turbid water. Unit leaf area per unit dry weight is at its lowest under the highest $\bar{I}$ as leaves were thicker. At low $\bar{I}$ thinner leaves were produced. This appeared to serve two purposes - by maximising the leaf length per unit dry weight it is able to reach the surface sooner, and its thin leaves are likely to intercept more photons (Enríquez *et al.*, 1995). LAR peaked within a narrow range in $\bar{I}$ regardless of K_d (25-40 μmol m^{-2} s^{-1}), confirming *Vallisneria* is well adapted to adjust the morphology of its canopy in response to fluctuations in turbidity in the River Murray. At values of $\bar{I}$ less than $\bar{I}_c$, the production of morphologically plastic young leaves is negligible (see Table 7.6). The lower LAR is due to the presence of mainly thick leaves initiated prior to flooding with turbid water.

NAR and LAR as functions of RGR

RGR increased linearly with NAR over the range in RGR from -5 to 10 mg g^{-1} d^{-1} (Fig. 7.8a). Growth was light-limited over the range in $\bar{I}$ corresponding to these values, evident in the RGR-$\bar{I}$ relationship in Fig. 7.5a. In comparison, LAR changed little (two to three fold; Fig. 7.8b). K_d had little influence on the relationships between RGR and NAR, and RGR and LAR, except at the highest K_d values.

Growth as a function of zm and K_d

The influence of z_m on RGR, NAR and LAR in plants grown in water of varying rates of downwelling extinction is shown in Fig. 7.9. RGR was maximum at the shallowest depth in the least turbid water and decreased with z_m. The rate of decrease was greater at higher rates of downwelling irradiance. RGR decreased in a sigmoidal fashion with z_m owing to changes in NAR and LAR (Fig. 7.9 c and d). The effect of high assimilation rates (NAR) on RGR in shallow water is to some extent countered by a reduction in the leaf area per unit weight, LAR. The slope of the RGR *v.* z_m curve is maximal over the medium depths for each K_d due to an increasing NAR with z_m and high LAR. The decrease in NAR with z_m reflects downwelling light extinction. LAR increases with z_m due to morphological changes in the canopy under low light (see above).

Interpolation from Fig. 7.9a indicates the depths at which no net growth occurred were c. 130, 68 and 32 cm for K_d 6.48, 12.59 and 21.92, respectively. From these data the relationship between estimated z_c, the maximum depth of colonisation (estimated here as the depth at which RGR is zero, cf. Schwarz *et al.,* 1996) and K_d is

$$z_c\,(\mathrm{m}) = 8.89/K_d - 0.06 \qquad (r^2=0.99,\ n=3)$$

The relationship is based on a limited data set and should be tested under field conditions. Expressions relating z_c to K_d or Secchi depth have been documented for bryophytes, charophytes and angiosperms in a wide range of lakes throughout the world (Spence, 1982; Chambers and Kalff, 1985; Vant *et al.,* 1986; Schwarz *et al.*, 1996; Middelboe and Markager, 1997). However, the expression presented here predicts much deeper z_c than observed for low K_d, *e.g.* z_c of 4.4 m for a K_d of 2 m^{-1}, whilst *Vallisneria* appears not to grow below 2 m depth in the Lower Murray. This overprediction of z_c is presumably due to the higher light requirements of seedlings (though this was not tested), and their greater susceptibility to grazing and dislodgement by turbulence.

The expression does not permit predictions of growth at depths shallower than z_c. Accordingly a logistic model was constructed to describe RGR as a function of z_m and K_d (Fig. 7.9b). The expression modelled the observed patterns reasonably well, and explained 86% of the variance. Observed reductions in RGR at higher K_d for a given z_m is produced by including K_d, raised to a negative constant, in the denominator. When water clarity is high ($K_d = 1$), RGR is predicted to occur at maximum rates to a depth of 1 m. As turbidity increases RGR declines more rapidly to zero. A minimum RGR of -5 mg g^{-1} d^{-1} is predicted regardless of K_d.

Shoot and leaf production

Shoot and leaf production increased with $\bar{I}$ (Fig. 7.10). Similar results have been reported for a range of macrophytes (*Zostera marina*; Dennison and Alberte, 1982; *Hydrilla verticillata, Myriophyllum spicatum* and *Egeria densa*; Barko and Smart, 1981; *Potamogeton perfoliatus*; Goldsborough and Kemp, 1988). An apparent $\bar{I}$ threshold of c. 35 μmol m^{-2} s^{-1} exists below which shoot and leaf recruitment does not occur.

Recruitment increases linearly with $\bar{I}$ up to c. 80 μmol m^{-2} s^{-1}, which corresponds to the $\bar{I}_k$ value for the NAR-$\bar{I}$ response, then plateaus. This is ascribed to the increasing proportion of the canopy experiencing light-saturated levels of photosynthesis. A similar plateau in recruitment was reported for *Hydrilla verticillata* at high irradiances (Barko and Smart, 1981). Shoot and leaf recruitment declined linearly with depth until the depth corresponding to an $\bar{I}$ of 35 μmol m^{-2} s^{-1} was reached (Fig. 7.11). At lower depths recruitment was negligible.

Cumulative plant leaf length was highest in the shallowest depths, in the least-turbid water (Fig. 7.12). Self-shading may have reduced lengths in the shallowest depth for K_d 6.48. The longest leaves were produced at the greatest depth, though few in number, typically 1-2 per plant. These leaves had only recently been initiated when plants were flooded with turbid water, with their responsiveness being due to age. Apart from the second youngest leaf, which occasionally also responded, older extant leaves at the time of inundation with turbid water did not grow. These were produced in shallow clear water during the establishment phase when $\bar{I}$ was high, and were physiologically unable to extend when $\bar{I}$ markedly declined. Irrespective of depth or K_d, once one leaf had reached the surface, new leaves were produced, though more slowly in deeper plants. Thus the majority of leaves at the surface, particularly in deeper water, were initiated after inundation with turbid water. The

Table 7.5. Mean percent tissue dry weights across depth gradients in 3 K_d treatments. Data are tabled by depth, and can not be directly compared between K_d levels. Data are the means of 4-6 plants.

% of total dry weight											
$K_d = 6.48$				$K_d = 12.59$				$K_d = 21.92$			
Depth (cm)	Leaves	Stolon	Root	Depth (cm)	Leaves	Stolon	Root	Depth (cm)	Leaves	Stolon	Root
14	86.2	5.5	8.3	-	-	-	-	11	87.9	4.4	7.7
39	89.4	3.7	6.9	24	90.5	2.7	6.8	17	91.4	1.2	7.4
66	89.3	2.7	8.0	39	88.6	3.1	8.3	24	88.1	2.1	9.2
90	89.3	1.4	9.3	49	85.6	3.1	11.3	31	83.1	3.2	13.7
†145	80.3	4.2	15.5	82	78.7	9.2	12.1	46	77.2	6.6	16.2

† Effects of depth simulated using shade cloth above the pond surface.
- grazed by ducks.

relationship between maximum leaf length per plant and depth is independent of K_d (P>0.22 for K_d, Fig. 7.13). Maximum length at depth 14 cm was c. 0.5 m, increasing linearly to c. 1.1 m at 90 cm depth. The ratio of maximum leaf length to depth is c. 1.3 at 90 cm, increasing to c. 3.0 at 14 cm.

Biomass distribution between tissues

Total, leaf, root and stolon dry weights decreased with depth and were lowest in the most turbid water (Fig. 7.14). Total and leaf dry weights decreased sigmoidally with depth. Exponential reduction in irradiance with depth diminishes the effect of depth on growth in deeper water, producing the long 'tail'. In general, root dry weight declined linearly with depth, at similar rates for each K_d. Above:below ground dry weight ranged between 3.8 and 11, and was highest in the mid-depth range. Allocation above-ground peaked at 17 cm in the K_d 21.92 treatment. As light penetration increased, the ratio peaked at a greater depth.

Leaves and leaf bases constituted 86-91% of total plant dry weight in shallow water, declining to 77-80% with depth (Table 7.5). In contrast, percent root dry weight rose from 7-8% to 13-16%. Below-ground tissues formed a greater proportion of total plant dry

Table 7.6. Leaf recruitment and senescence across a depth gradient in water with a light attenuation coefficient of 12.59 (turbidity, 209 NTU). Rates with the same letters are not significantly different at P=0.01 (one-way analysis of variance, followed by Tukey's HSD test). Data are mean ± standard errors (n=4-6).

Depth (cm)	$\bar{I}$ (μmol m^{-2}s^{-1})	Recruitment rate (week^{-1})	Senescence rate (week^{-1})
12	110.9	0.55 ± 0.03^{a}	0.38 ± 0.12^{a}
24	67.7	0.53 ± 0.03^{a}	0.42 ± 0.05^{a}
39	43.4	0.34 ± 0.05^{b}	0.32 ± 0.05^{a}
49	34.8	0.18 ± 0.05^{c}	0.25 ± 0.08^{a}
82	20.8	0.03 ± 0.01^{c}	0.33 ± 0.10^{a}

weight at depth as leaf production slowed, with only 1-2 thin, structurally weak leaves being produced. Stolon dry weight varied between 1 and 9%, being highest at the extremes.

Senescence of most old leaves reduced the respiratory drain on the plant. One or two young leaves were maintained which grew slowly or not at all. Several old leaf bases per shoot appear to be retained, which have much lower light compensation points than new leaves (5 *v. c.* 35 μmol m^{-2} s^{-1}; Chapter 8). This seems to be a strategy to harvest light in old leaves at very low $\bar{I}$ to support extension in young leaves.

Leaf turnover, extension and width

Leaf recruitment was significantly higher in shallower water (0.53-0.55 week^{-1}), and fell to 0.03 week^{-1} at depth 82 cm, K_d 12.59 (Table 7.6). Senescence rates did not differ significantly with depth (P=0.64), varying between 0.25 and 0.42 week^{-1}. Recruitment equalled senescence in the depth range 39-49 cm.

Maximum extension rate in K_d 12.59 treatments was 1.1 cm day^{-1}. Peak rates occurred earlier in plants in shallow water (12, 24 and 39 cm depths, from 5 May to 5 June), but slowed when the length of leaf on the surface was equivalent to one to two times the water depth (25 June to 25 August). Plants at 49 cm exhibited slower growth of 0.3 cm day^{-1}

Table 7.7. Mean widths of leaves down a depth gradient (K_d 12.59). Only mature leaves, initiated following inundation with turbid water, and that had reached the surface, were included. Widths were measured 15 cm above the sediment surface. Numbers with the same letters are not significantly different at P=0.01 (one-way analysis of variance, followed by Tukey's HSD). Data are mean ± standard deviation (n=4-6).

Depth (cm)	Width (mm)	*n*
12	19.3 ± 0.6^a	28
24	16.2 ± 0.5^a	69
39	10.6 ± 0.6^b	33
49	9.5 ± 0.5^b	38
82	9.8 ± 0.5^b	6

initially, increasing to 0.95 cm day^{-1} as exposure to light increased, then slowing again upon reaching the surface (0.36 cm day^{-1}). No marked leaves at 82 cm grew. These were initiated prior to flooding with turbid water. Leaves produced immediately prior to these did grow however, whilst the third-youngest leaves did not.

Leaf width decreased with depth, from 19.3 mm at 12 cm, to 9.5 mm at depth 49 cm (Table 7.7). Widths did not decrease significantly below 39 cm.

7.4.6 Relationship between plant performance and the effective photosynthetic leaf biomass B_e

The depths calculated as receiving an average of 20 µmol m^{-2} s^{-1} over the day were 37, 19 and 10 cm for K_d 6.48, 12.59 and 21.92, respectively. These are compared to the calculated depth-time plots of the penetration of 20 µmol m^{-2} s^{-1} into the water column over the day in Fig. 7.15.

RGR was significantly correlated with B_e (Fig. 7.16a). This relationship produces the NAR-$\bar{I}$ response which underlies the hyperbolic tangential increase in RGR with $\bar{I}$. Plants with a greater proportion of their canopy receiving light sufficient for net photosynthesis will assimilate more biomass. The linear model suggests a threshold value of B_e of c. 22% below which growth does not occur. The plateau in RGR at high B_e reflects the increasing incidence of photosaturation and decreasing LAR. The similarity between the RGR-$\bar{I}$ response and the RGR-B_e relationship indicates the biological basis for $\bar{I}$ is its relationship with B_e (Fig. 7.17). B_e is positively correlated with $\bar{I}$ (r^2=0.66, P<0.0001). For low mean irradiances $\bar{I}$, light penetration through the water column z_m is low. Leaves rising from z_m must grow a greater distance to reach depths experiencing irradiances exceeding compensation levels than when $\bar{I}$ is high. Thus at low $\bar{I}$ a smaller proportion of the canopy will receive irradiances exceeding compensation levels.

Shoot and leaf recruitment increased with B_e and were maximum when B_e was 100% (Fig. 7.16 b and c). However, zero recruitment occurred at B_e values of up to 80%. In these plants the high RGR at this B_e value was due to the allocation of resources to growing longer leaves rather than more leaves.

7.5 Discussion

7.5.1 Growth and recruitment as functions of $\bar{I}$

Relative growth rate in *Vallisneria* is highly correlated with the average irradiance $\bar{I}$ between the water surface and sediment. The RGR-$\bar{I}$ relationship followed the theoretical photosynthesis-irradiance curve of Jassby and Platt (1976). This was due to the high correlation between net assimilation rate and $\bar{I}$ according to the Jassby and Platt model (r^2=0.934, and 0.893 for RGR-$\bar{I}$, Fig. 7.5). Leaf and shoot recruitment and the biomass of all tissues increased with $\bar{I}$. Similar growth-irradiance responses have been determined for a range of angiosperms and charophytes by Sand-Jensen and Madsen (1991), Olesen and Sand-Jensen (1993), and Madsen and Sand-Jensen (1994).

The NAR-$\bar{I}$ curve is the long-term integration of the P-I relations of all leaf tissues over a wide range of irradiances (including night time) over the experiment. In comparison, LAR changed less with $\bar{I}$. Whilst *Vallisneria* was unable to maintain a high RGR under low $\bar{I}$ (by increasing its LAR sufficiently to offset the reduced NAR), the changes in LAR with $\bar{I}$ indicate morphological plasticity at low light is an important component of *Vallisneria's* suite of adaptations to growth in the turbid Lower Murray. Plasticity in leaf morphology has been recognised as an important adaptation to variable light and flow conditions in submersed macrophytes (Madsen, 1991).

The biological basis for the RGR-$\bar{I}$ relationship is the relationship between $\bar{I}$ and B_e. $\bar{I}$ was significantly correlated with the estimated proportion of the canopy achieving net photosynthesis over the day, B_e (Fig. 7.17). When B_e was high, $\bar{I}$ was high and plant performance was high (Fig. 7.16). As less of the canopy achieved net photosynthesis over the day (lower B_e and $\bar{I}$), growth declined. The threshold value of B_e for growth was 22%, indicating *Vallisneria* can survive with up to four fifths its canopy below the depth of mean daily penetration of compensating irradiance.

The relationship between B_e and growth is analagous to that developed by Dennison and Alberte (1982) and Dennison (1987) for seagrass *Zostera marina,* between the time exposed to greater-than compensating irradiances and growth. Both involve the determination of a relationship between light availability and plant performance. However, the proportion of the canopy achieving net photosynthesis is the critical determinant of growth rather than the quantum flux reaching the leaf tips, particularly in highly turbid, shallow water such as in the littoral zone of floodplain rivers. This is due to the differential between the quantum flux received at the leaf tip and the leaf base, which is determined by z_m, K_d and leaf length. This differential can be considerable for long leaved submersed species in floodplain rivers and wetlands, as shown for *Vallisneria.* In deeper, less turbid water *e.g.* estuaries, the differential is generally likely to be much less, and the quantum flux at the leaf tips is an appropriate estimate of available light. In such cases, the approach of Dennison is more appropriate.

The specific absorption coefficient K_s for *Vallisneria* was 0.0051 $m^2\ g^{-1}$. The effect of light extinction by the canopy was to reduce $\bar{I}$ by 1% (low canopy biomass *B*) to 27% (high *B*) (see Eq (2)). The true effect of *B* on RGR was dependent on the depth distribution of *B* relative to the vertical light gradient rather than its absolute size (as shown above). When a high proportion of *B* is at the surface, light interception is maximised. In contrast a plant in deeper water with most of the canopy close to the sediments will experience an effective $\bar{I}$ lower than that predicted by Eq (1) (Titus and Adams, 1979). K_s in *Vallisneria* in this study was two to four times lower than reported for *Vallisneria* by Titus and Adams. The difference is probably due to methodology rather than leaf morphology. In determining K_s, minor changes in the position of the quantum sensor beneath the constructed canopy greatly alters the measured flux density due to the highly heterogeneous nature of the light field in the canopy. A lower K_s would confer an adaptive advantage over species with higher canopy extinction coefficients in highly turbid water by permitting greater light penetration to young leaves.

The $\bar{I}_c$ value for the RGR-$\bar{I}$ curve and P-I responses for leaf pieces were similar (respectively 26 μmol m^{-2} s^{-1} and a mean of 20-25 μmol m^{-2} s^{-1} across leaves of different ages and depths at 12°C). This is remarkable as P-I measurements do not account for night time leaf and 24 h below-ground respiration (Bowes and Salvucci, 1989). Hence one may expect photosynthesis to balance respiration over 24 h at a higher $\bar{I}$. That this is not the case seems to be due to the high rates of carbon assimilation at the surface where most of the biomass is concentrated. Canopy photosynthesis is thus higher than expected from an homogeneous canopy profile, which would cause total photosynthesis and respiration to balance at a lower $\bar{I}$. I_c values for growth ranging from 3.5-47.3 μmol m^{-2} s^{-1} have been reported for charophytes (*Chara vulgaris* and *Nitella translucens*) and angiosperms (*Callitriche cophocarpa, Elodea canadensis, Fontinalis antipyretica, Littorella uniflora, Ranunculus peltatus* and *Zostera marina*) (Sand-Jensen and Madsen, 1991; Olesen and Sand-Jensen, 1993; Madsen and Sand-Jensen, 1994). These I_c values refer to the ambient irradiance reaching the surface, but can be assumed to approximate $\bar{I}_c$ as plants were grown in clear water.

Canopy-forming macrophytes have an optimal plant architecture for light interception and light competition in turbid water (Titus *et al.*, 1975; Titus and Adams, 1979). *Vallisneria* often forms dense monospecific beds with a semi-continuous surface canopy. Its ribbon-shaped leaves are quite resilient to wave motion, and its basal meristem permits the development of young leaves close to the sediment where wave energy is lower. *Vallisneria* occurs in areas of the littoral exposed to strong wave action. Common dicots of the Lower Murray, such as *Potamogeton crispus, P. tricarinatus* and some *Myriophyllum* spp, favour more protected areas, perhaps due to a less robust structure.

Vallisneria allocated the majority of its biomass to leaves - 77% in deep water rising to 91% in shallow water (Table 7.5). Allocation to stolons was <10%, and maximum when growth was very high (hence high vegetative reproduction) or very low (negligible leaf recruitment). As turbidity increased, leaf biomass declined more rapidly than in roots and stolon (Table 7.3). This suggests a survival strategy of *Vallisneria* in very low light is to retain a comparatively strong below-ground structure to anchor the basal meristems. The canopy consists of mainly moribund leaves with 1-2 young leaves under low light conditions. Old leaves have a low I_c and low respiration rate. Their function seems to be to harvest photons at very low flux densities to support extension in the youngest leaves, which have a high I_c and I_k.

7.5.2 Value of $\bar{I}$ in studies of submersed macrophytes

$\bar{I}$ averages the very large differences in instantaneous irradiance occurring between the water surface and the sediments. In addition, it is calculated using a mean daily subsurface irradiance estimate $\bar{I}_o{}'$, of 303 μmol m^{-2} s^{-1} which averaged daily irradiances ranging between 40 and >1600 μmol m^{-2} s^{-1}. In spite of being such a gross estimate of the light environment of *Vallisneria*, $\bar{I}$ was highly correlated with growth and recruitment.

The utility of $\bar{I}$ as a measure of a plants' total light environment is enhanced by it being a single number, calculated from simple parameters which can be determined rapidly and cheaply. Whilst RGR could be expressed as a function of z_m and K_d (Fig. 7.9.b), this expression does not permit as great an insight into the dependence of growth on light. An interesting study would be to determine if leaf and whole plant light compensation points coincide for other species. If this is the case predictions of plant growth could be made by assuming RGR is zero at an $\bar{I}$ corresponding to the I_c of leaf pieces, with the latter being much more simple to determine.

The potential of growth-$\bar{I}$ relationships in researching and managing submersed macrophytes is considerable. Once the RGR-$\bar{I}$ relationship for a species is known, predictions of relative performance can be easily made by simply determining $\bar{I}$ from the mean subsurface irradiance $\bar{I}_o{}'$, z_m and K_d. This relationship will depend on inorganic carbon concentration (Hough and Fornwall, 1988; Madsen and Maberly, 1991; Madsen and

Sand-Jensen, 1991; Vadstrup and Madsen, 1995), temperature (Barko and Filbin, 1983) and nutrients (Chambers and Kalff, 1987). $\bar{I}$ may only be an appropriate estimate of a plant's average light environment if photosynthetic tissues reach the surface. Shorter plants will experience a lower $\bar{I}$ than suggested by Eq (1). It is suggested $\bar{I}$ may be most useful in studying turbid waterbodies, where plants experience a wide range of light conditions. Future studies could determine RGR as a function of $\bar{I}$ and one or more of these factors. For example, Madsen and Sand-Jensen (1994) determined the relationship between RGR, irradiance and inorganic carbon supply for *Elodea canadensis* and *Callitriche cophocarpa*. Such relationships are central to understanding the biology of submersed macrophytes and would allow the formulation of simple testable empirical models (Peters, 1990).

7.5.3 Modelled growth in field populations of Vallisneria *in the Lower Murray under varying flooding regimes*

The RGR-$\bar{I}$ relationship established for plants in the pond experiment (Fig. 7.5a) was then used to model growth under a range of z_m, K_d and flood durations in the Lower Murray (Table 7.8). z_m and K_d are assumed constant over time, though the relationship could easily be used to model varying combinations of z_m and K_d over time. The percent change in biomass in assumed independent of pre-flood biomass.

The model predicts growth (positive RGR) for flooding depths up to 2 m for values of K_d up to 5 m^{-1}. This coincides with the observed maximum colonised depth of *Vallisneria* in the Lower Murray during periods when K_d is in the range 2-5 m^{-1}. A 14% increase in plant biomass is predicted when water levels rise 0.5 m for 1 week when K_d is 2 m^{-1}. This value falls to 11% when flooding depth is 2 m, due to a reduction in RGR from 19.0 to 15.0 mg g^{-1} d^{-1} as $\bar{I}$ falls from 172.4 to 66.9 μmol m^{-2} s^{-1}. Plant biomass is predicted to double in c. 5 weeks and quadruple in 12 weeks when flooded to 0.5 m (K_d, 2 m^{-1}).

As K_d or z_m increases, $\bar{I}$ decreases causing a lower RGR. Plants flooded to 2 m with water of K_d 5 m^{-1} are predicted to show essentially no growth (only a 2% increase in biomass over 12 weeks), as $\bar{I}$ equals 24.2 μmol m^{-2} s^{-1}, the minimum light requirement for growth (Table 7.4). A reduction in plant biomass is predicted for plants flooded to 1.5 m when K_d is 8 m^{-1} as $\bar{I}$ is below the $\bar{I}_c$ for growth (17.7 μmol m^{-2} s^{-1}, Table 7.8). A 3% loss in biomass after 1 week is predicted, rising to 27% after 12 weeks. With increasing K_d the

Table 7.8. Modelled growth in field populations of *Vallisneria* under a range of flooding regimes in the Lower Murray. Growth is expressed as the percent change in whole plant dry weight. RGR was calculated from the RGR-$\overline{I}$ model in Fig. 7.5a, and $\overline{I}$ was calculated for a range of flooding depths z_m and downwelling extinction coefficients K_d (see Eq (1)). For each combination of K_d and z_m, percent change in biomass for varying flood duration was determined as e^{RGR*t}, where time t is in days (see Eq (5)).

K_d	Flooding depth	$\overline{I}$ [a,b]	RGR	% change in plant dry weight						
				Flood duration (weeks)						
(m^{-1})	(m)	($\mu mol\ m^{-2}\ s^{-1}$)	($mg\ g^{-1}\ d^{-1}$)	**1**	**2**	**3**	**4**	**6**	**8**	**12**
2	0.5	172.4	19.0	14	31	49	70	122	190	394
	1.0	117.9	18.6	14	30	48	68	118	183	375
	1.5	86.4	17.2	13	27	43	62	106	162	324
	2.0	66.9	15.0	11	23	37	52	88	131	252
5	0.5	89.0	17.4	13	28	44	63	108	165	331
	1.0	48.2	10.7	8	16	25	35	57	82	146
	1.5	32.3	4.5	3	7	10	14	21	29	46
	2.0	24.2	0.3	0	0	1	1	1	2	2
8	0.5	52.1	11.8	9	18	28	39	64	94	170
	1.0	26.5	1.6	1	2	3	4	7	9	14
	1.5	17.7	-3.7	-3	-5	-7	-10	-14	-19	-27
	2.0	13.3	-6.6	-5	-9	-13	-17	-24	-31	-43
11	0.5	38.4	7.2	5	11	16	22	36	50	84
	1.0	19.3	-2.7	-2	-4	-5	-7	-11	-14	-20
	1.5	12.9	-6.9	-5	-9	-13	-18	-25	-32	-44
	2.0	9.6	-9.1	-6	-12	-17	-23	-32	-40	-53
15	0.5	28.3	2.5	2	4	5	7	11	15	23
	1.0	14.1	-6.0	-4	-8	-12	-15	-22	-29	-40
	1.5	9.4	-9.3	-6	-12	-18	-23	-32	-40	-54
	2.0	7.1	-10.9	-7	-14	-21	-26	-37	-46	-60
20	0.5	19.7	-2.4	-2	-3	-5	-7	-10	-13	-18
	1.0	9.9	-9.0	-6	-12	-17	-22	-31	-39	-53
	1.5	6.6	-11.3	-8	-15	-21	-27	-38	-47	-61
	2.0	4.9	-12.5	-8	-16	-23	-29	-41	-50	-65
25	0.5	14.5	-5.7	-4	-8	-11	-15	-21	-28	-38
	1.0	7.3	-10.8	-7	-14	-20	-26	-36	-45	-60
	1.5	4.9	-12.5	-8	-16	-23	-30	-41	-50	-65
	2.0	3.6	-13.4	-9	-17	-25	-31	-43	-53	-68

[a] Estimated % surface reflectance for K_d 2, 5, 8, 11, 15, 20 and 25 m^{-1} are 10, 20, 30, 30, 30, 35 and 40 % respectively.

[b] Mean daily subsurface irradiance $\overline{I}_o'$ is 303 $\mu mol\ m^{-2}\ s^{-1}$.

depth at which no net growth occurs becomes shallower. Hence a net loss in biomass is predicted at a z_m of 1.0 m when K_d is 11 m^{-1}, but at 0.5 m when K_d is 20 m^{-1}. In the mid-late 1980's, significant natural declines in the abundance and distribution of submersed macrophytes were observed, particularly *Vallisneria*, in the Lower Murray due to highly-turbid inflows from the Darling River (Walker *et al.*, 1994). Turbidity was frequently in the range 30-160 NTU and occasionally reached 450 NTU (Mackay *et al.,* 1988). Few data exist for K_d in this period. However, from turbidity and K_d data presented in Oliver (1990) for the River Murray and Darling River, and the turbidity-K_d relationship in the present study, K_d was probably in the range c. 3-20 m^{-1} during this period. Submersed macrophytes did not occur below 1 m, and were largely excluded from river reaches below weirs where water level fluctuations equivalent to the photic depth occurred regularly. The RGR-$\bar{I}$ response fairly accurately predicts these general declines in growth at high K_d.

Kimber *et al.* (1995b) found *Vallisneria* produces tubers at depths equal to or less than 0.8 m for a mean K_d of 4.64 m^{-1} in Lake Onalaska, USA. From their data, the minimum $\bar{I}$ for tuber production is 225 μmol m^{-2} s^{-1} (using an $\bar{I}_o'$ of 912 μmol m^{-2} s^{-1} from the given mean daily incoming irradiance of 39.4 mol m^{-2}, a daylength of 12 h and 6% surface reflectance). This value is much higher than the $\bar{I}_c$ for growth in the present study (26 μmol m^{-2} s^{-1}). The difference in $\bar{I}_c$ may be largely due to the high energetic costs of tuber production. Tuber production in Lower Murray *Vallisneria* has not been observed, presumably due to much milder winters.

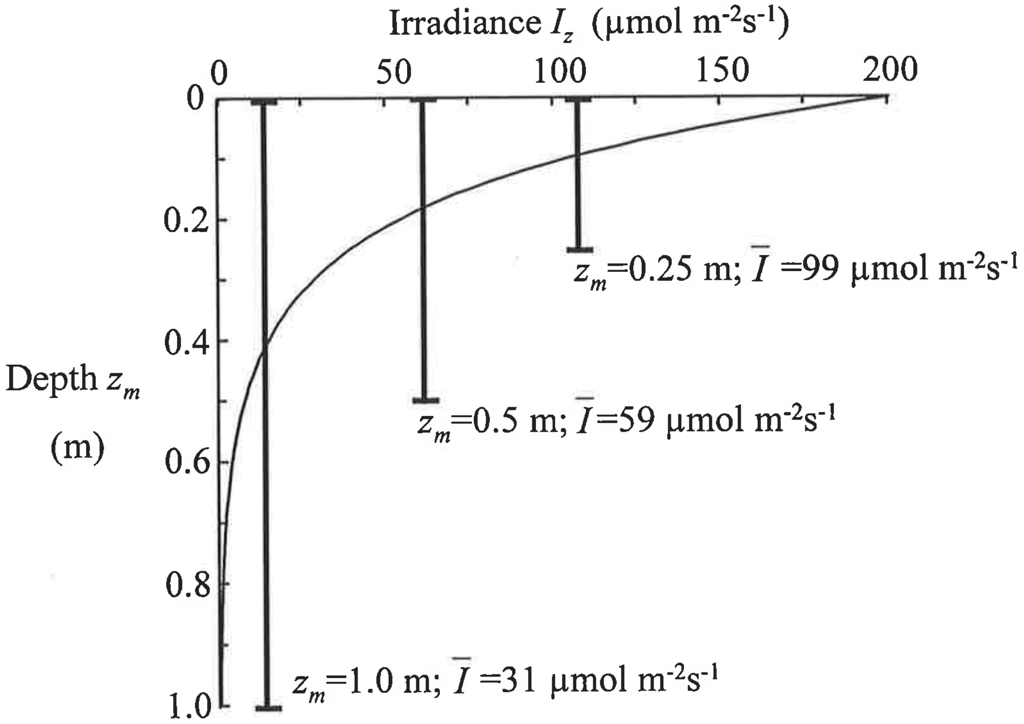
Caution must be observed when applying this growth model to predict the effects of flooding on field populations of *Vallisneria.* Losses in biomass to grazing and turbulence/waves are likely for all z_m and K_d, and would reduce actual biomass accrual below predicted levels. This is probably more likely at low $\bar{I}$ as leaves are thinner and narrower, and thus more prone to ripping. Preliminary results suggest the sandy littoral sediments of the Lower Murray are nutrient poor (G. Ganf, pers. obs). Nitrogen was supplied at a relatively high rate in this study to ensure a rapid response over winter (100 g N m^{-2} y^{-1}), and the growth model may therefore overpredict biomass gain under field conditions. Given these constraints, growth estimates presented here must be viewed as maximum winter values.

7.6 Conclusion

This study confirms observations that light limitation during flooding with highly turbid water constrains growth in *Vallisneria americana* in the Lower Murray. The depth at which growth was zero in *Vallisneria* decreased as turbidity increased, and plant performance declined at all depths. Growth is highly correlated with the average irradiance over the water column $\bar{I}$, with the RGR-$\bar{I}$ response describing the classic P-I curve of Jassby and Platt (1976). This was due to the high correlation between NAR and $\bar{I}$. LAR changed much less with $\bar{I}$, but indicated substantial morphological plasticity in response to low light. Shoot and leaf production was highest at high $\bar{I}$, but the rate of leaf senescence was independent of $\bar{I}$. The biological validity of $\bar{I}$ is its relationship with B_e, the photosynthetically effective proportion of the canopy biomass B. $\bar{I}$ was significantly correlated with the proportion of B estimated to receive greater-than compensation level irradiances, averaged over the day. RGR, and shoot and leaf recruitment increased with $\bar{I}$ due to an increasing B_e. The RGR-$\bar{I}$ relationship adequately predicted the observed changes in growth in *Vallisneria* plants in the Lower Murray under a range of flooding depths and K_d. The simple model accurately predicted the colonised depth and general performance of *Vallisneria* under a typical turbidity regime, and the reduction in vigour at high turbidities.

Figure 7.1. Relationship between average irradiance $\bar{I}$, depth z_m and the rate of downwelling extinction K_d (see Eq (1)). The effect of increasing z_m or K_d is to reduce $\bar{I}$. a. Increasing z_m with constant K_d (K_d equals 6.48 $\mathrm{m^{-1}}$). b. Increasing K_d with constant z_m. For both examples subsurface irradiance $\bar{I}$ equals 200 µmol $\mathrm{m^{-2}s^{-1}}$. Values of K_d are those used in the study.

a. Increasing z_m, constant K_d



b. Increasing K_d, constant z_m

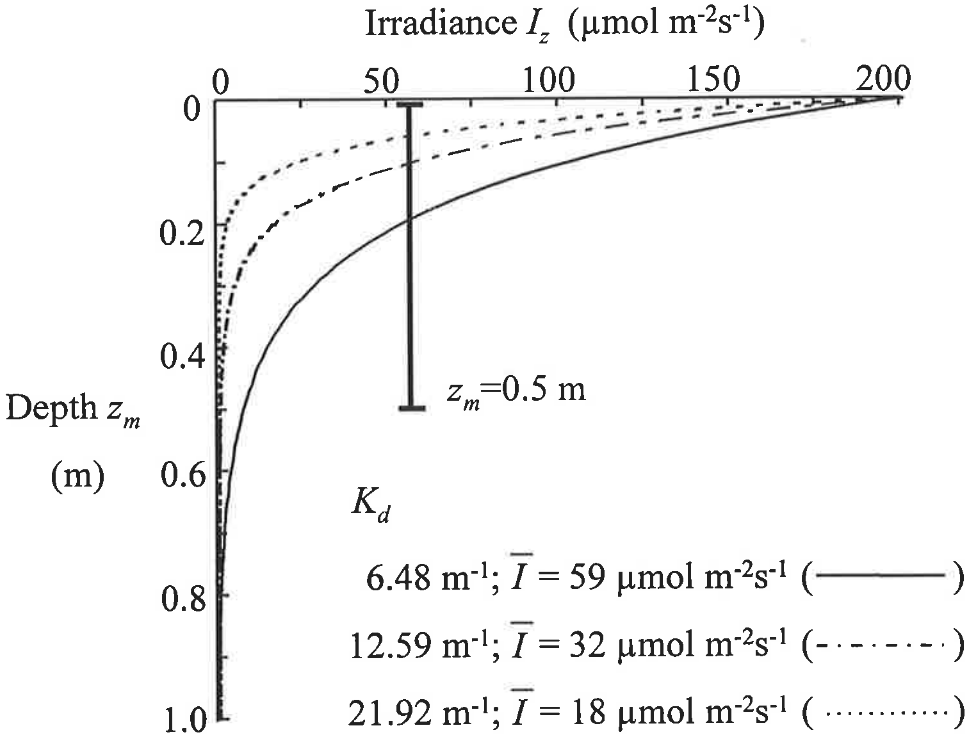


Figure 7.2. Habit of *Vallisneria americana* Michx. var. a*mericana*. Female flowers are placed on the surface for pollination by spiralled peduncles. Clonal growth is *via* spongy stolons.


5 cm

Plate 7.1. *Vallisneria americana* plants in water of turbidity 209 NTU.

Figure 7.3. Relationship between the rate of downwelling extinction, K_d, and turbidity (measured as nephelometric turbidity units, NTU) in three experimental ponds (n=78).

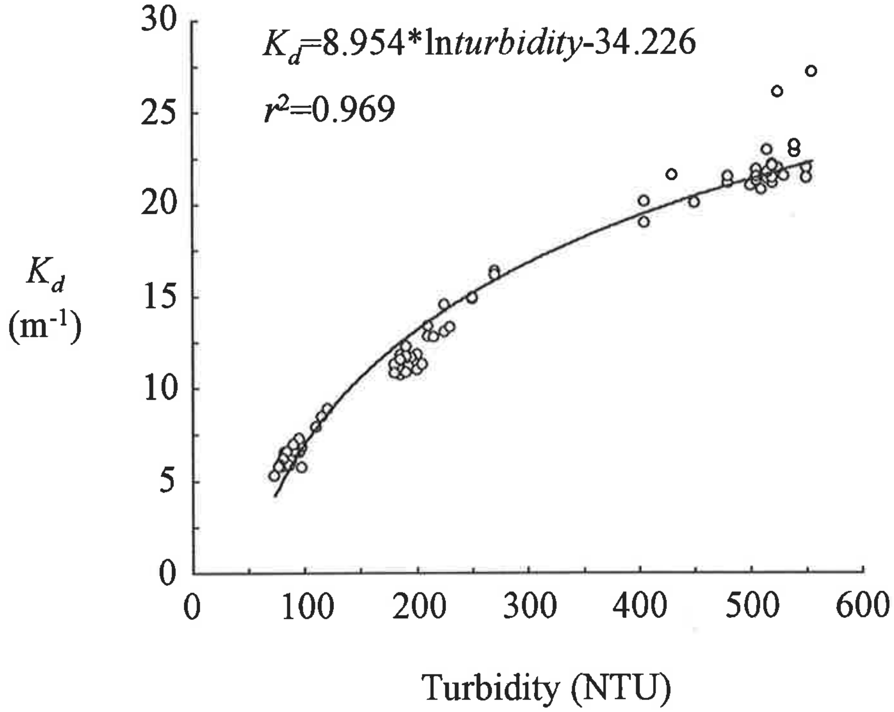

K_d=8.954*ln*turbidity*-34.226
r^2=0.969
30
25
20
15
10
5
0
K_d (m^{-1})
0
100
200
300
400
500
600
Turbidity (NTU)

Figure 7.4. Mean hourly solar incoming irradiance over the experimental period (16 May to 28 August 1997). Daylength declined from 10 h in mid May to 9 h in mid June (mean±SD, *n*=102 days).

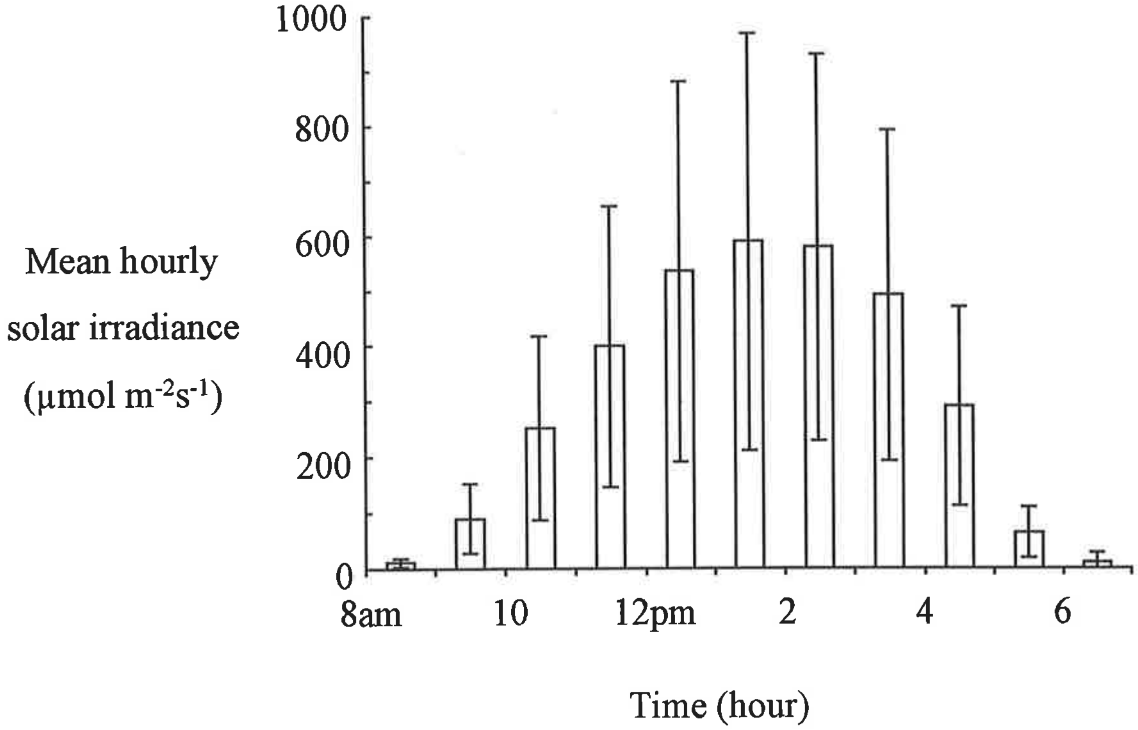
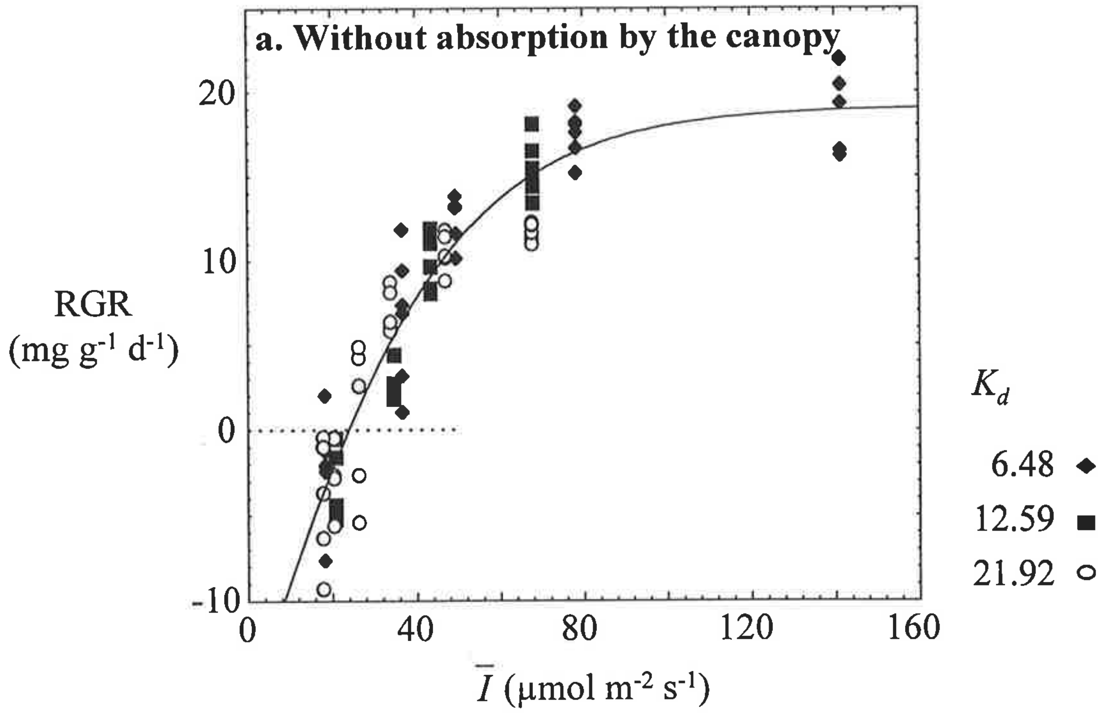

Mean hourly
solar irradiance
(µmol m-2s-1)
1000
800
600
400
200
0
8am
10
12pm
2
4
6
Time (hour)

Figure 7.5. Relationship between relative growth rate (RGR) in *Vallisneria* and the average irradiance $\bar{I}$ between the water surface and the sediments. $\bar{I}$ is calculated by a. excluding and b. including the effects of absorption by the canopy (see Eqs (1) and (2) respectively). The fitted model is the P-I relationship of Jassby and Platt (1976). Parameters are given in Table 7.4. Different $\bar{I}$ levels were created by maintaining different rates of downwelling extinction in experimental ponds. Models are: (a) RGR (mg g^{-1} d^{-1}) = 35.13*tanh(0.73* $\bar{I}$ /35.13)-16.05 (r^2=0.893, n=81); (b) RGR (mg g^{-1} d^{-1}) = 38.01*tanh(0.83* $\bar{I}$ /38.01)-18.43 (r^2=0.896, n=81).


a. Without absorption by the canopy
RGR
(mg g^{-1} d^{-1})
20
10
0
-10
0
40
80
120
160
$\overline{I}$ (μmol m^{-2} s^{-1})
K_d
6.48 ◆
12.59 ■
21.92 ○

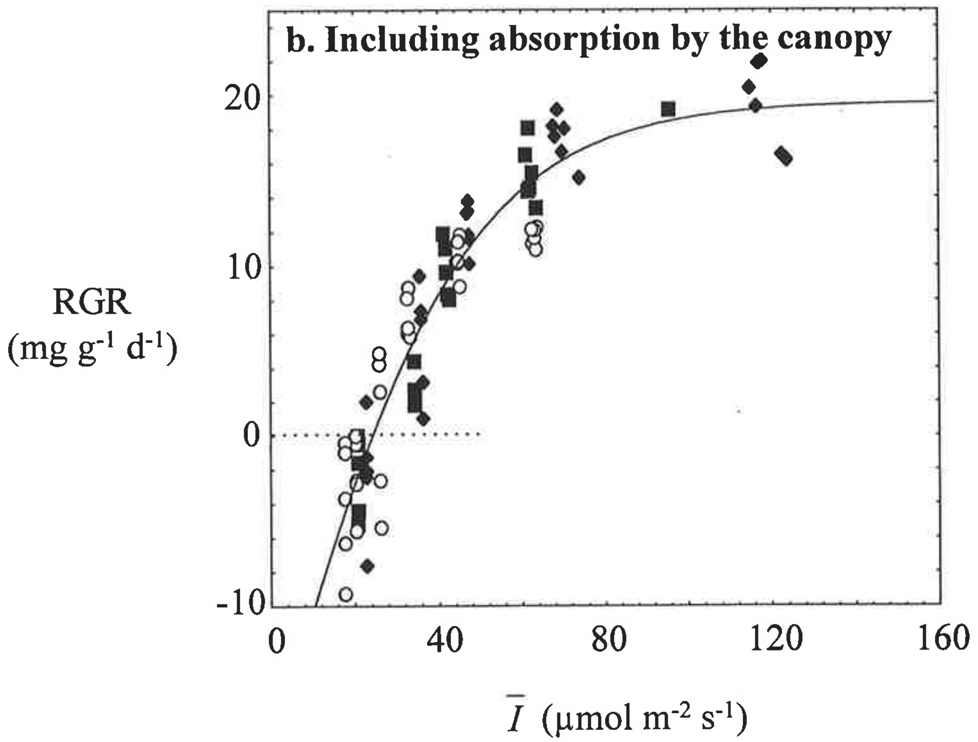

b. Including absorption by the canopy
RGR
(mg g^{-1} d^{-1})
20
10
0
-10
0
40
80
120
160
$\overline{I}$ (μmol m^{-2} s^{-1})

Figure 7.6. Relationship between net assimilation rate (NAR) in *Vallisneria* and the average irradiance $\bar{I}$ between the water surface and sediments. The fitted model is the P-I relationship of Jassby and Platt (1976). Parametres are given in Table 7.4. Model is: NAR (cm^{2} g^{-1} d^{-1}) = 0.000191*tanh(0.000002* $\bar{I}$ /0.000191)-0.000042 (r^{2}=0.934, n=81).

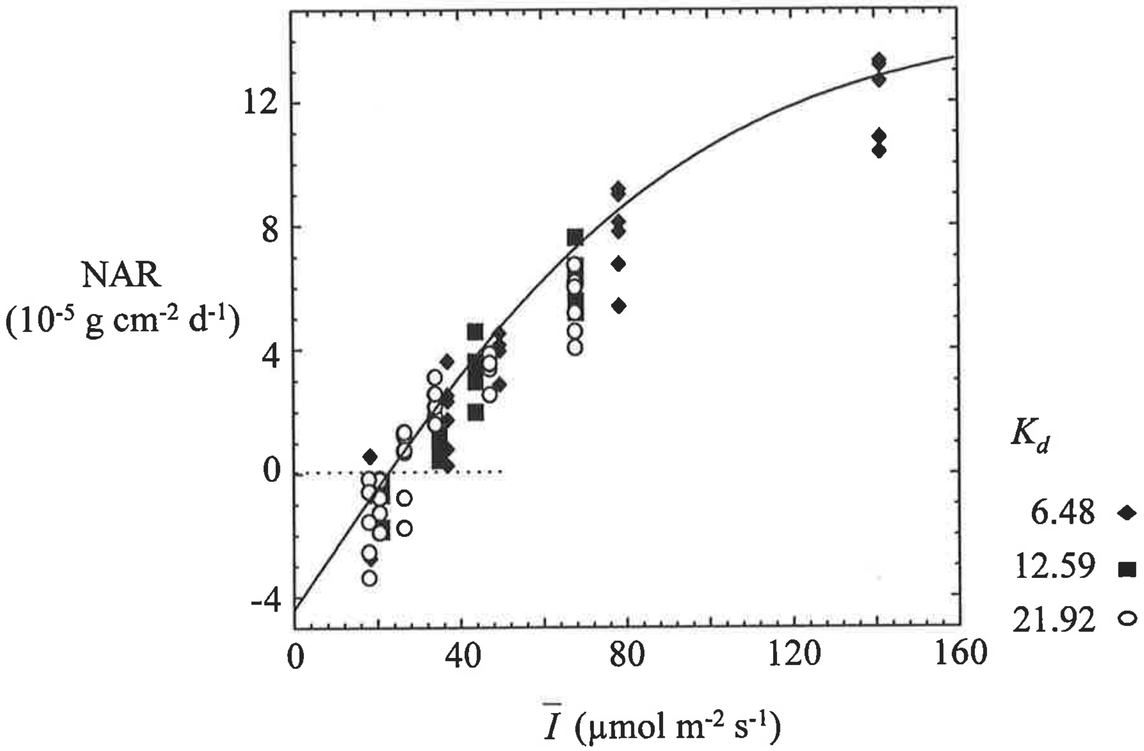

NAR
(10⁻⁵ g cm⁻² d⁻¹)
12
8
4
0
-4
0
40
80
120
160
Ī (μmol m⁻² s⁻¹)
K_d
6.48 ◆
12.59 ■
21.92 ○

Figure 7.7. Relationship between leaf area ratio (LAR) in *Vallisneria* and the average irradiance $\bar{I}$ between the water surface and the sediment. Data are mean±standard deviation (n=4-6).

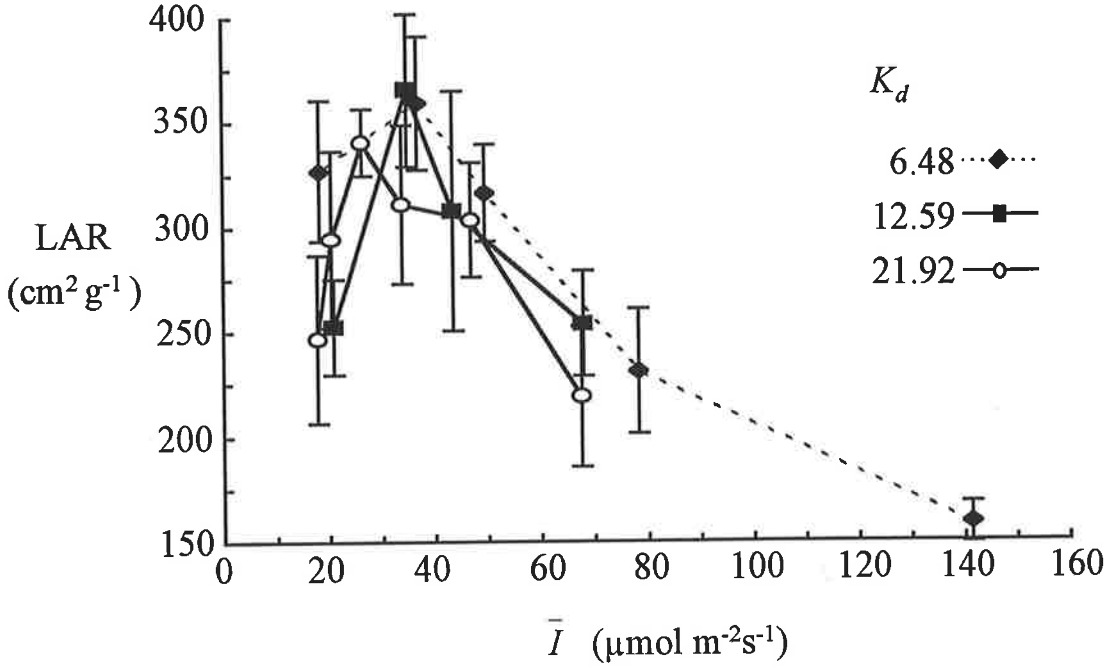

LAR
(cm^2 g^{-1})
400
350
300
250
200
150
0
20
40
60
80
100
120
140
160
$\bar{I}$ (µmol m^{-2}s^{-1})
K_d
6.48
12.59
21.92

Figure 7.8. a. NAR and b. LAR as functions of RGR in *Vallisneria.* Plants were grown over a range in $\bar{I}$, indicated by the arrow showing the direction of increasing $\bar{I}$ (see Fig. 7.5) (mean±standard deviation, n=4-6).

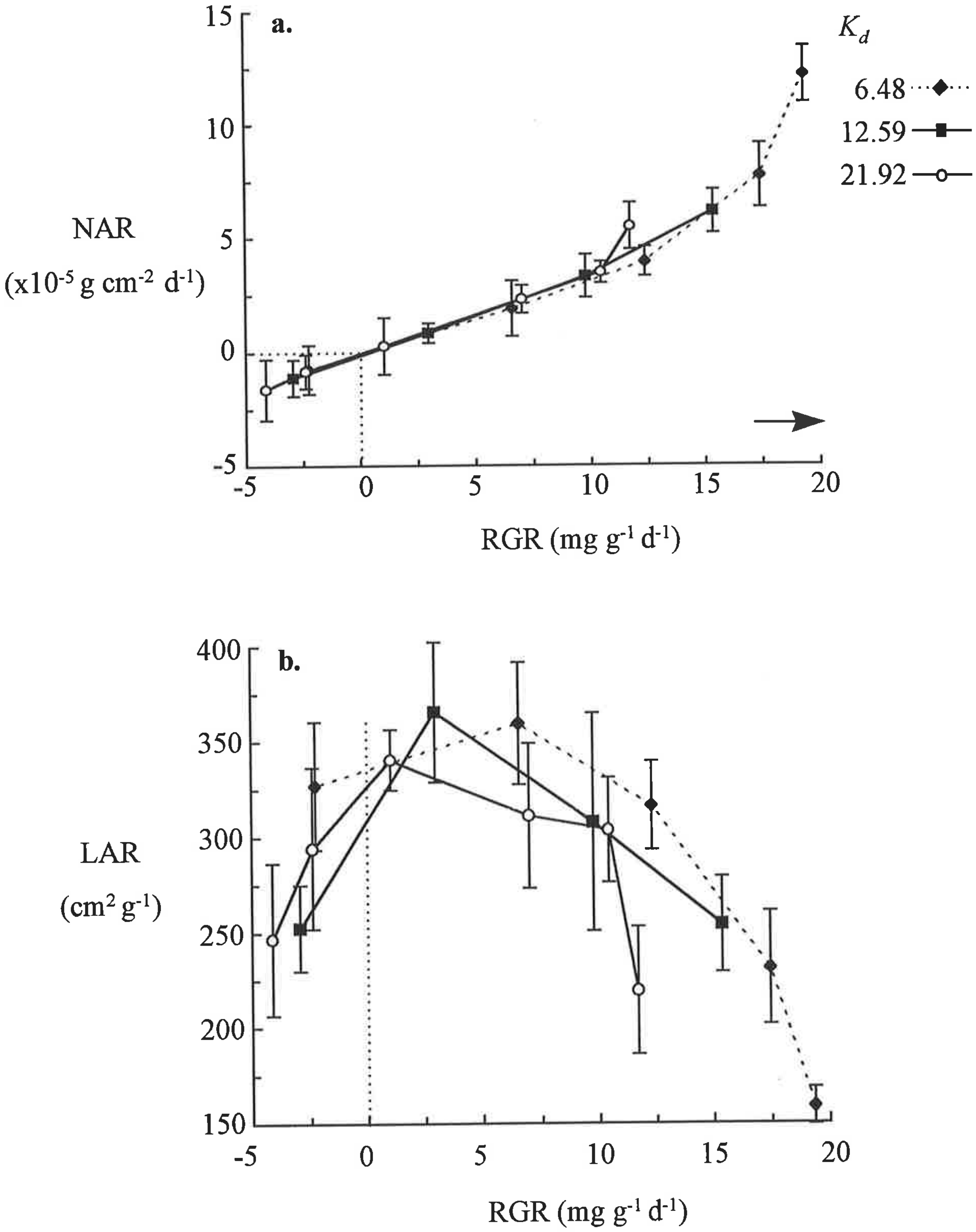

a.
NAR
(x10^{-5} g cm^{-2} d^{-1})
15
10
5
0
-5
-5
0
5
10
15
20
RGR (mg g^{-1} d^{-1})
K_d
6.48
12.59
21.92
b.
LAR
(cm^{2} g^{-1})
400
350
300
250
200
150
-5
0
5
10
15
20
RGR (mg g^{-1} d^{-1})

Figure 7.9. a. RGR c. NAR and d. LAR in *Vallisneria* across a depth gradient. Experimental ponds were maintained at three levels of turbidity, indicated by the rate of downwelling extinction K_d. Data are mean and standard deviation (n=4-6). b. RGR data was modelled using the logistic expression

$$RGR\ (mg\ g^{-1}\ d^{-1}) = 21.0 - \frac{25.8}{1 + K_d^{\ -3.34} e^{11.43-6.52*z_m}}\ (r^2=0.861,\ n=81).$$

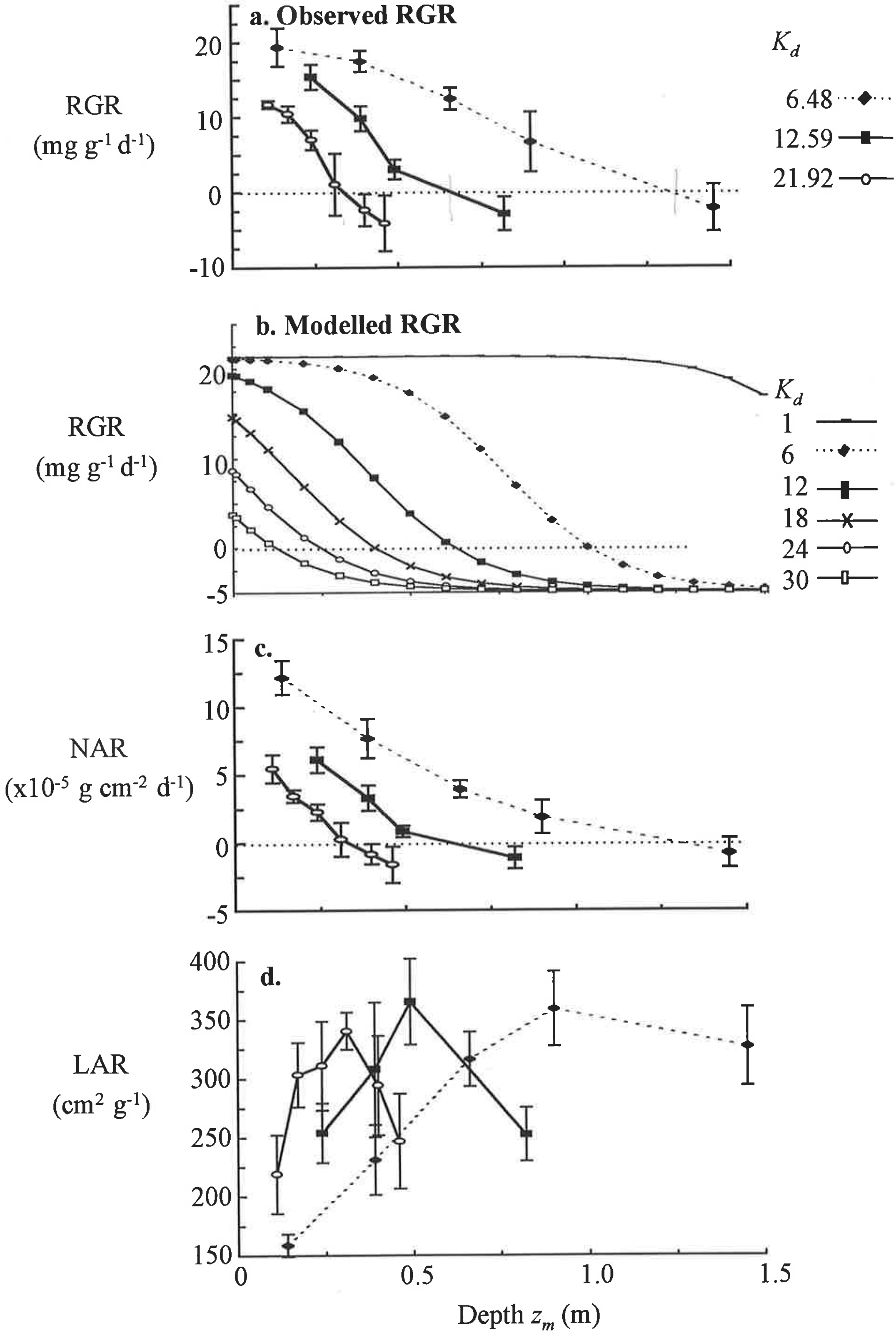
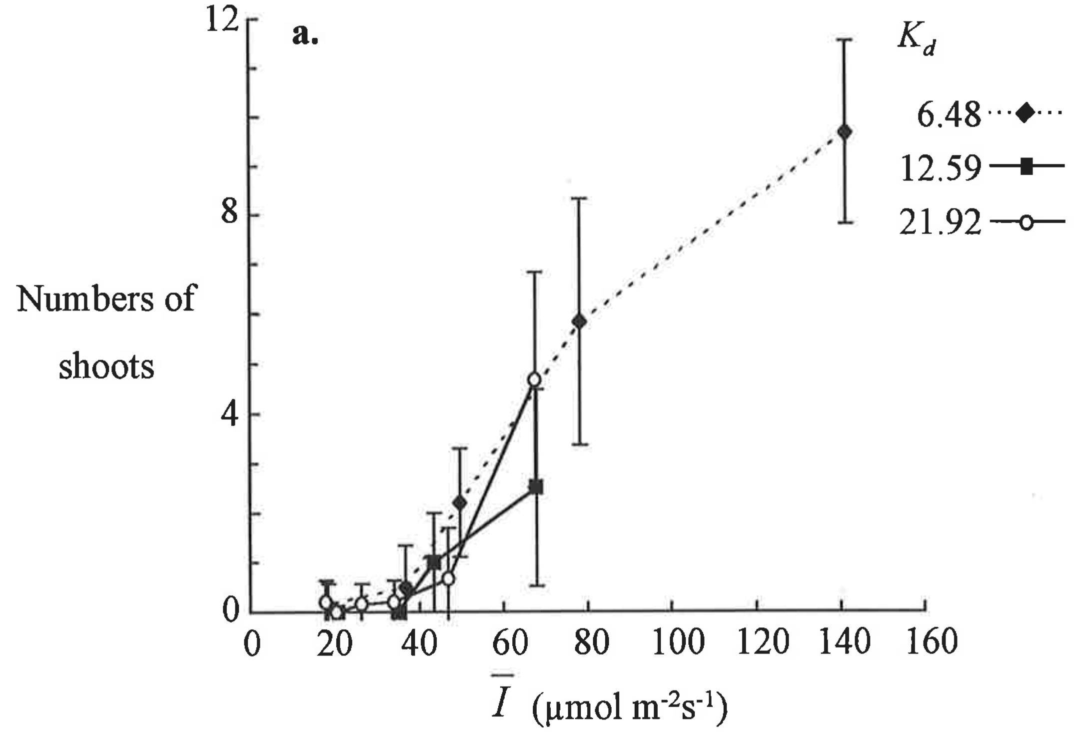
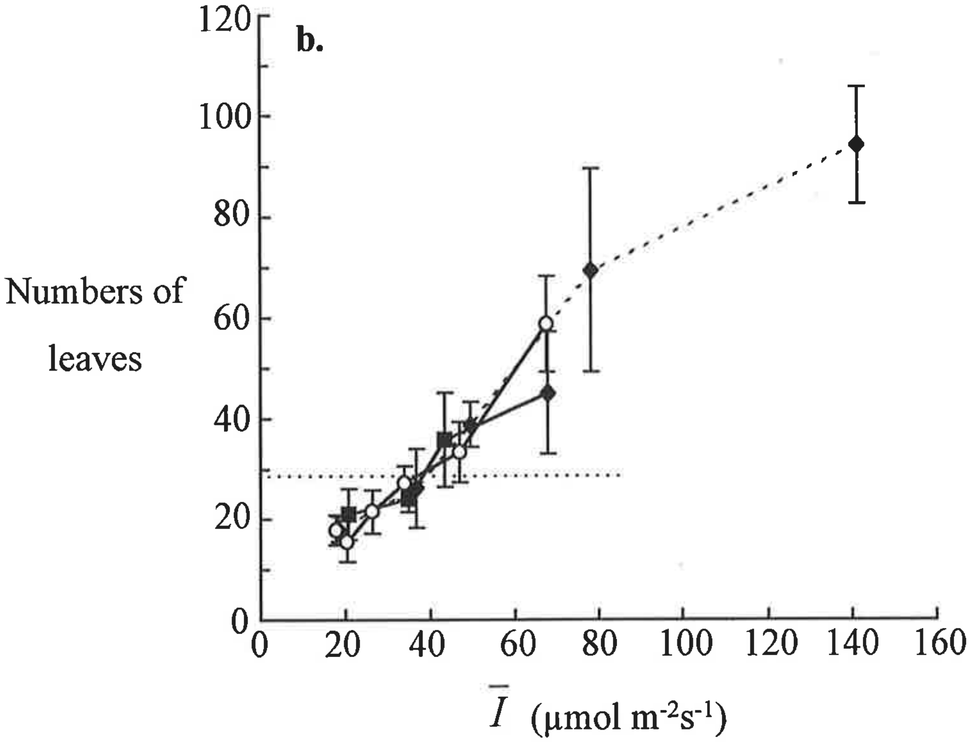

a. Observed RGR
RGR
(mg g-1 d-1)
20
10
0
-10
Kd
6.48
12.59
21.92
b. Modelled RGR
RGR
(mg g-1 d-1)
20
10
0
-5
Kd
1
6
12
18
24
30
c.
NAR
(x10-5 g cm-2 d-1)
15
10
5
0
-5
d.
LAR
(cm2 g-1)
400
350
300
250
200
150
0
0.5
1.0
1.5
Depth zm (m)

Figure 7.10. a. Shoot and b. leaf recruitment as functions of the average irradiance $\overline{I}$ in *Vallisneria*. The mean number of leaves in plants at the commencement of the experiment was 29, indicated by a dashed line (see Fig. 7.5) (mean±standard deviation, *n*=4-6).

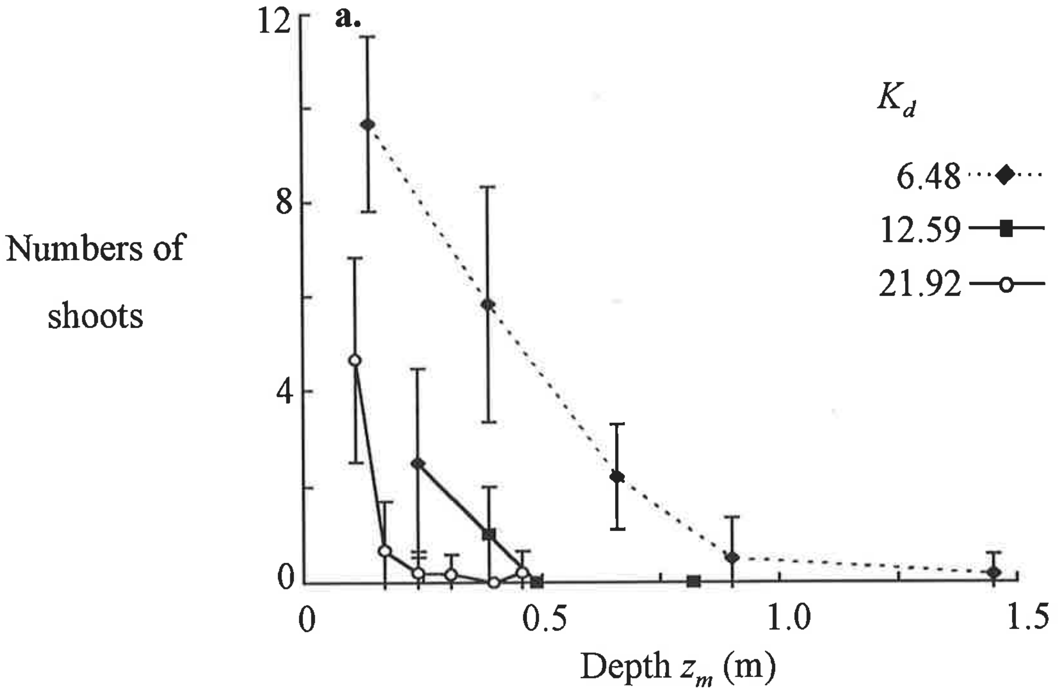


a.
Numbers of shoots
0
4
8
12
0
20
40
60
80
100
120
140
160
$\bar{I}$ (μmol $m^{-2}s^{-1}$)
K_d
6.48
12.59
21.92



b.
Numbers of leaves
0
20
40
60
80
100
120
0
20
40
60
80
100
120
140
160
$\bar{I}$ (μmol $m^{-2}s^{-1}$)

Figure 7.11. a. Shoot and b. leaf recruitment as functions of depth in *Vallisneria*. Plants were grown in experimental ponds at varying levels of turbidity, indicated by the rates of downwelling extinction K_d. The mean number of leaves in plants at the commencement of the experiment was 29, indicated by a dashed line (mean±standard deviation, n=4-6).


a.
Numbers of shoots
0
4
8
12
0
0.5
1.0
1.5
Depth z_m (m)
K_d
6.48
12.59
21.92

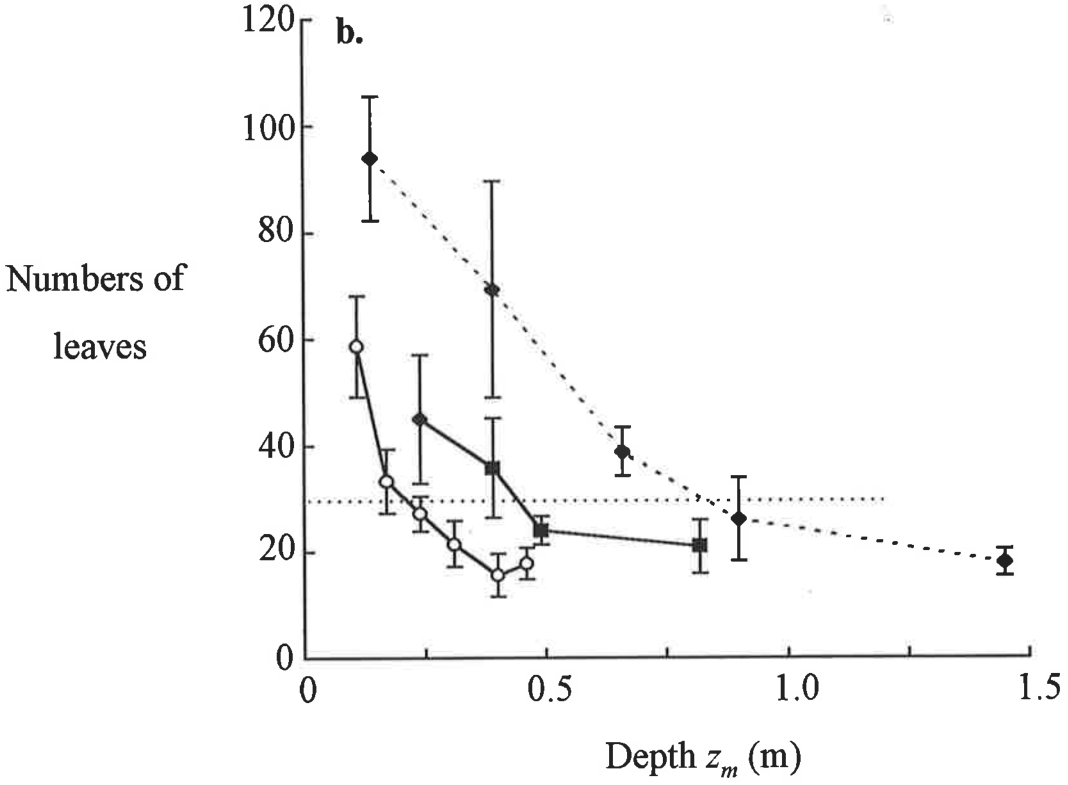

b.
Numbers of leaves
0
20
40
60
80
100
120
0
0.5
1.0
1.5
Depth z_m (m)

Figure 7.12. Total leaf length per plant in *Vallisneria* plants across an elevation gradient at three rates of downwelling extinction K_d (mean±standard deviation, n=4-6).

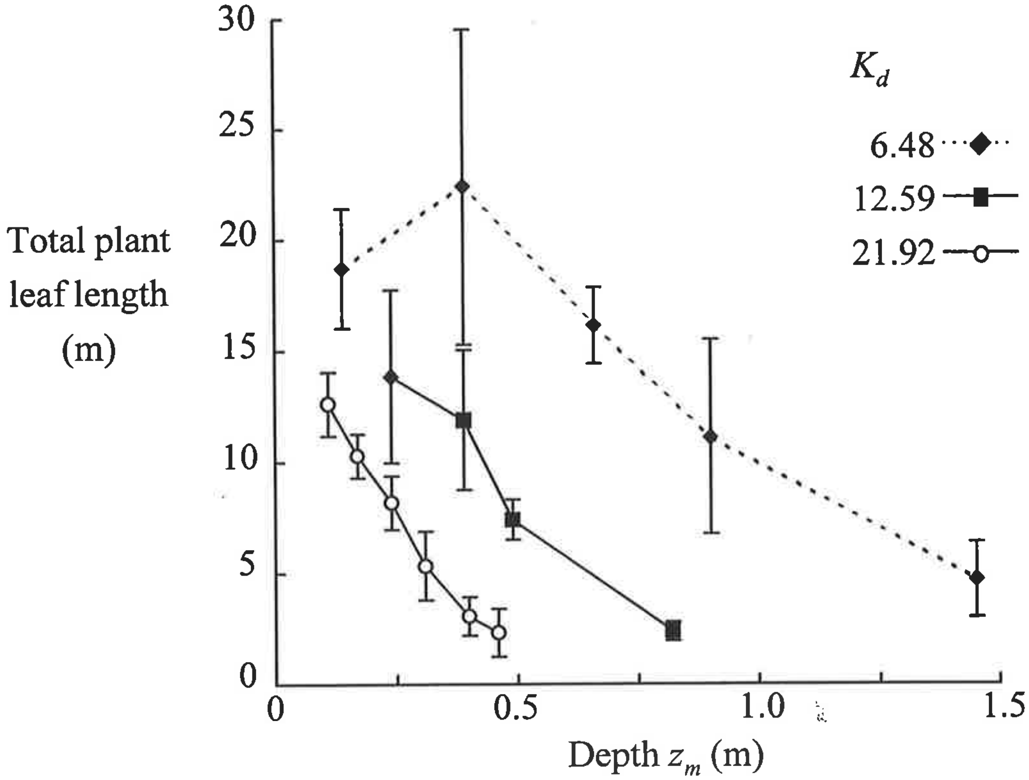

Total plant leaf length (m)
30
25
20
15
10
5
0
0
0.5
1.0
1.5
Depth z_m (m)
K_d
6.48
12.59
21.92

Figure 7.13. Relationship between the maximum leaf length per plant and depth to sediment in *Vallisneria* (r^2=0.819, P<0.0001). The rate of downwelling extinction K_d did not influence the relationship (P=0.23).

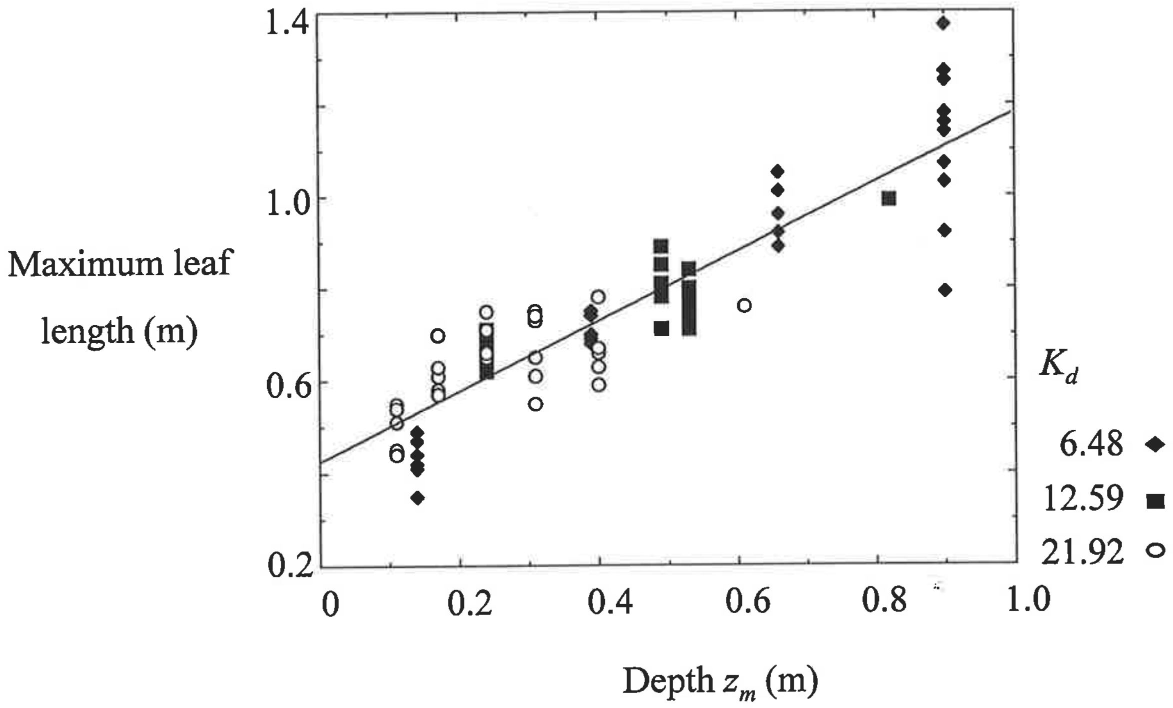

1.4
1.0
0.6
0.2
Maximum leaf length (m)
0
0.2
0.4
0.6
0.8
1.0
Depth z_m (m)
K_d
6.48 ◆
12.59 ■
21.92 ○

Figure 7.14. Biomass allocation to tissues in *Vallisneria* plants grown across a depth gradient. Experimental ponds were maintained at three turbidity levels, indicated by the rate of downwelling extinction, K_d. Data are means and standard deviations (n=4-6).

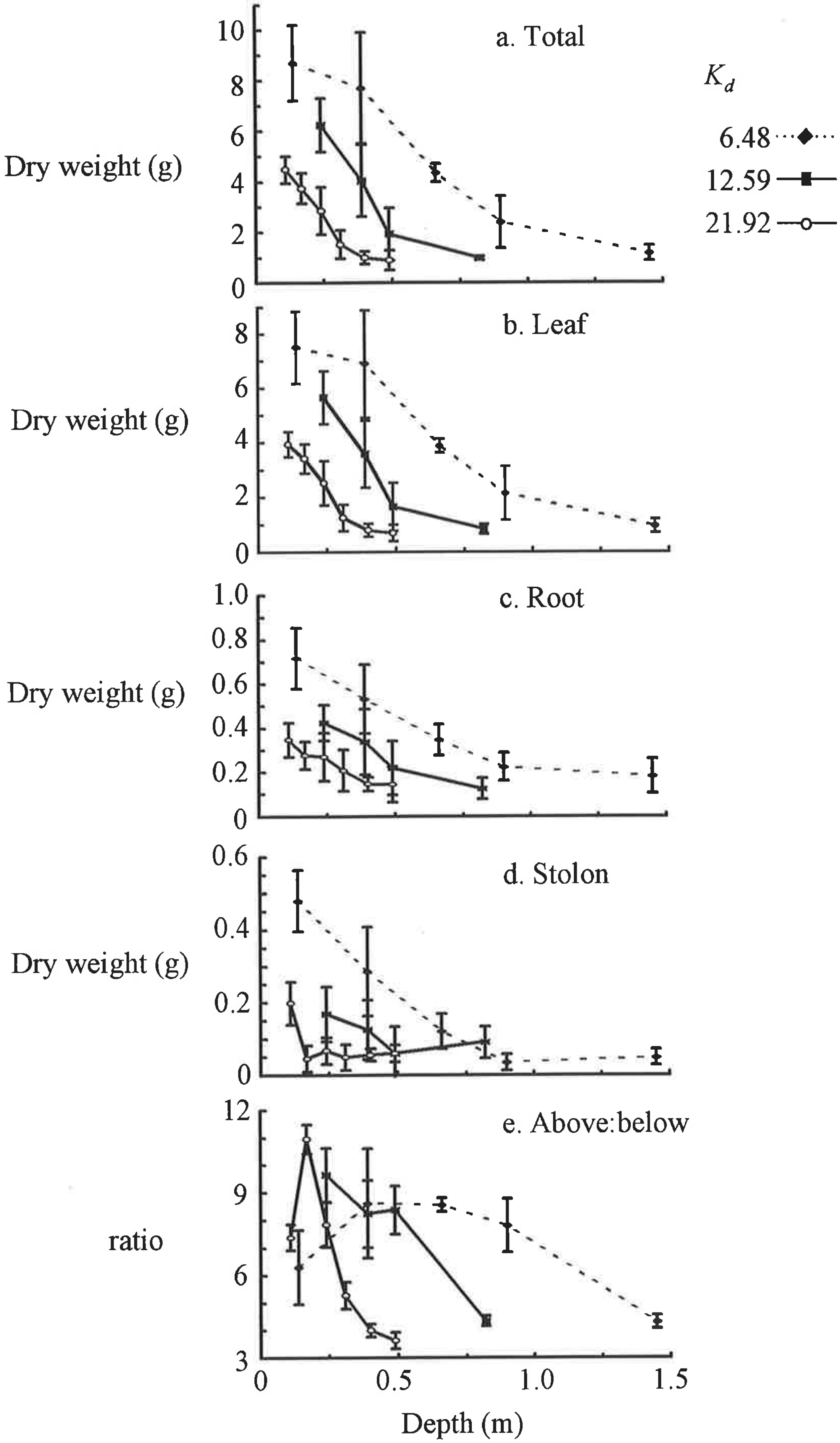

a. Total
b. Leaf
c. Root
d. Stolon
e. Above:below
Dry weight (g)
Dry weight (g)
Dry weight (g)
Dry weight (g)
ratio
10
8
6
4
2
0
8
6
4
2
0
1.0
0.8
0.6
0.4
0.2
0
0.6
0.4
0.2
0
12
9
6
3
0
0.5
1.0
1.5
Depth (m)
K_d
6.48
12.59
21.92

Figure 7.15. Depths to which the mean compensating irradiance (mean I_c=20 µmol m^{-2} s^{-1}) penetrated into experimental ponds with three turbidity levels. Mean daily depth of $\bar{I}_c$ was 0.10, 0.19 and 0.37 m for K_d 21.92, 12.59 and 6.48 m^{-1}, respectively (indicated by horizontal dashed lines). Depth-time plots were determined using a mean subsurface irradiance over the experiment of 303 µmol m^{-2} s^{-1} and the sin relationship between irradiance and time (e.g. Zimmerman *et al.*, 1994). Irradiance at depth z_m was calculated from the Lambert-Beer relationship.

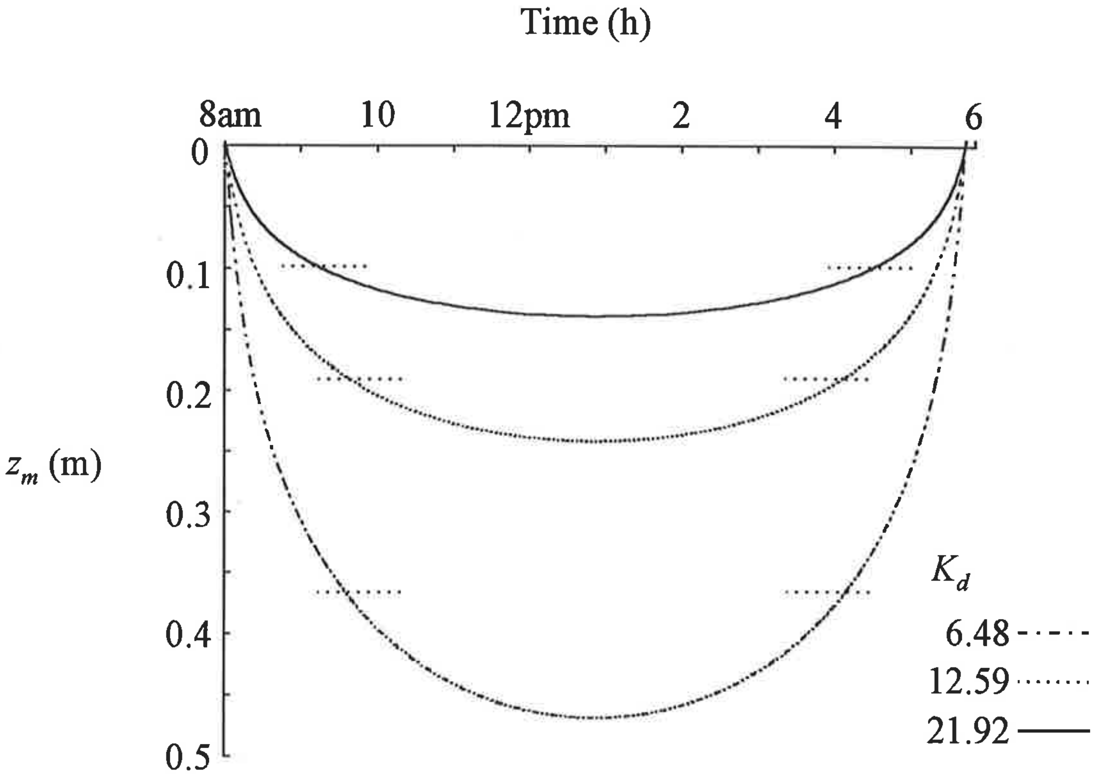

Time (h)
8am
10
12pm
2
4
6
0
0.1
0.2
0.3
0.4
0.5
z_m (m)
K_d
6.48
12.59
21.92

Figure 7.16. a. RGR and b. shoot and c. leaf recruitment as functions of B_e, the photosynthetically effective canopy biomass. B_e was estimated as the proportion of the leaf biomass experiencing irradiances exceeding compensating levels over the day (calculated as being shallower than the depths shown in Fig. 7.14). The linear relationship between RGR and B_e was highly significant (r^2=0.830, P<0.0001). The mean number of leaves at the commencement of the experiment was 29 per pot, indicated by a dashed line in (c).

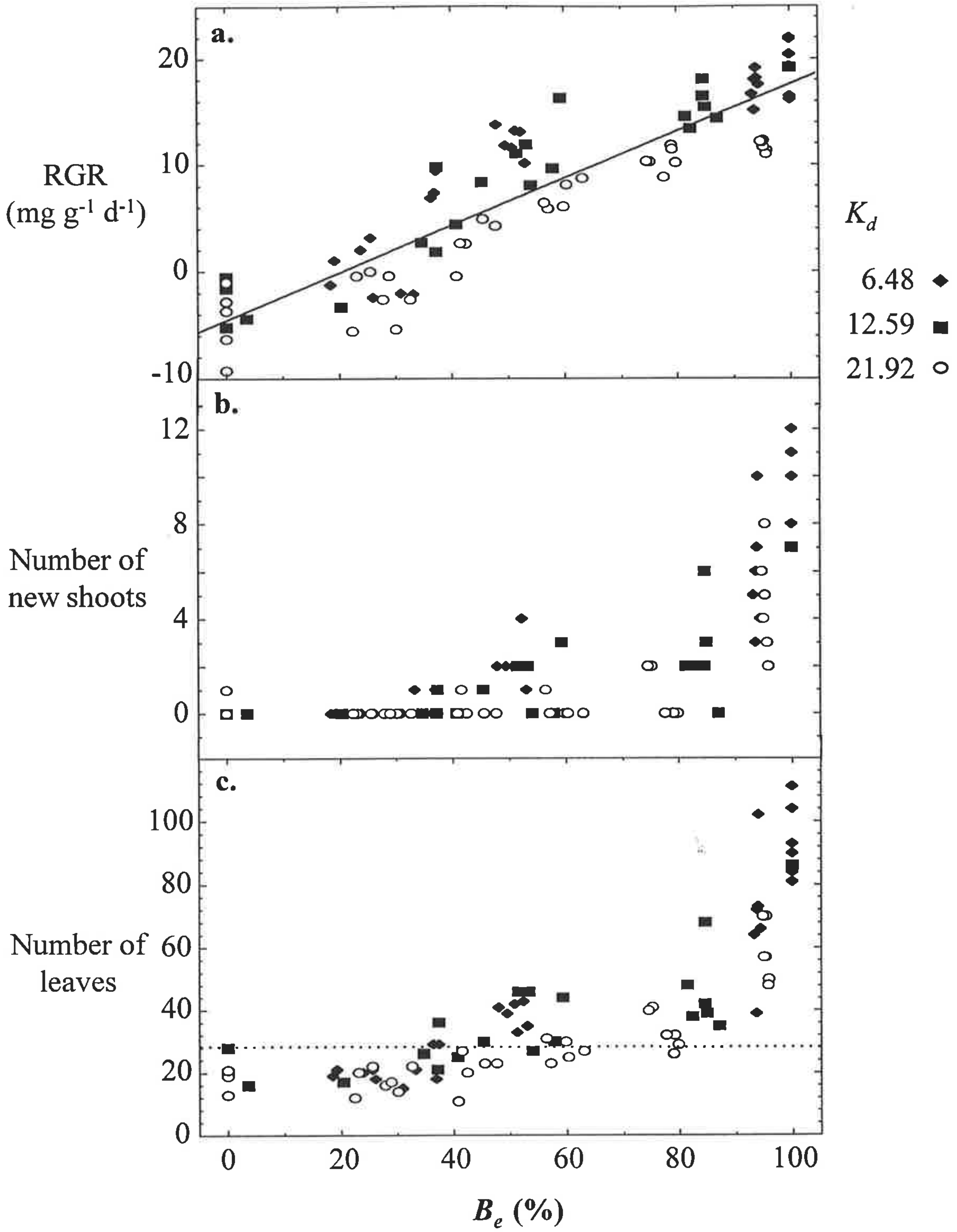
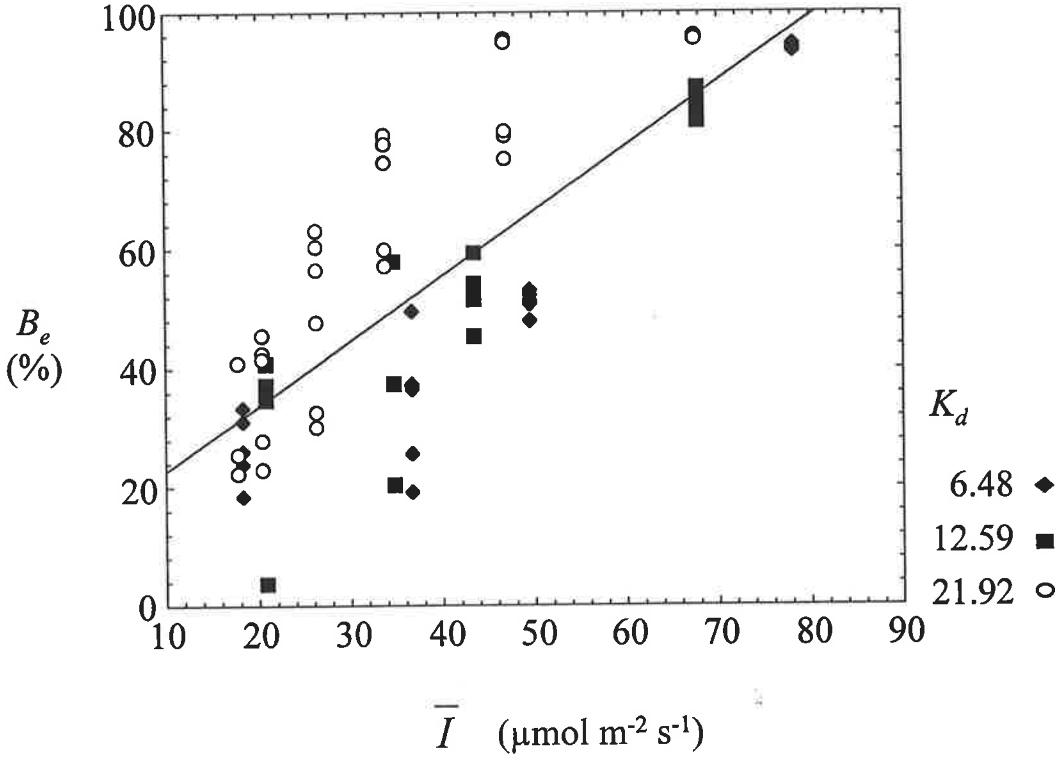

a.
b.
c.
RGR (mg g-1 d-1)
Number of new shoots
Number of leaves
K_d
6.48 ◆
12.59 ■
21.92 ○
20
10
0
-10
12
8
4
0
100
80
60
40
20
0
0
20
40
60
80
100
B_e (%)

Figure 7.17. Relationship between $\overline{I}$ and B_e for all K_d (r^2=0.661, P<0.0001).


100
80
60
40
20
0
B_e
(%)
10
20
30
40
50
60
70
80
90
$\overline{I}$ (µmol m^{-2} s^{-1})
K_d
6.48 ◆
12.59 ■
21.92 ○

Chapter 8

Photosynthesis-irradiance and respiration characteristics of *Vallisneria americana* in turbid water

8.1 Introduction

Vallisneria americana Michx. var. *americana* is a dominant submersed species in the turbid Lower Murray. It can grow in low-light conditions which exclude other species *e.g.* turbid wind-stirred wetlands and under overhanging riparian vegetation. In the pond experiment, plants survived 3 months in very low light (Chapter 7), suggesting a high degree of physiological shade tolerance. Shade-tolerance is characterised by low light compensation and saturation points (I_c and I_k respectively), and high photosynthetic efficiency, α (Table 8.1) (Kirk, 1983; van der Bijl *et al.*, 1989). *Vallisneria* has been shown to have low I_c and I_k and high α compared to a range of submersed macrophytes in the northeast USA (Meyer *et al.*, 1943; Titus and Adams, 1979; Madsen *et al.*, 1991; Harley and Findlay, 1994). In one of the earliest studies of the light dependence of photosynthesis in submersed macrophytes, Meyer *et al.* (1943) observed considerable carbon assimilation in *V. americana* (25% of maximum rates) at 10 m depth in Lake Erie, USA, where irradiances were only 0.5% of that at the surface. This chapter presents data for *Vallisneria* grown in highly turbid water (turbidity 209 NTU), and compares it to published data for *Vallisneria* and a range of freshwater and marine angiosperms from around the world. In particular it examines how photosynthesis, respiration and chlorophyll *a* (chl *a*) vary with leaf age and depth in plants grown in highly turbid water. These physiological characteristics are then interpreted to explain the growth and recruitment patterns in relation to light detailed in Chapter 7. Data are also used to model daily canopy assimilation and whole-plant carbon balance at low and high light in Chapter 9.

Young leaves extend up to 1.1 cm d^{-1} in *Vallisneria* before reaching the surface (Chapter 7). Compared to young leaves of apically-growing species, new leaves in *Vallisneria* are placed into a sub-optimal light environment. Upwards growth into more

Table 8.1. Symbols employed in the photosynthesis-irradiance (P-I) study.

Symbol	Definition	Units
P_{net}	Net photosynthesis	mg C g dw^{-1} h^{-1} or mg C chl *a* h^{-1} or mg C dm^{-2} h^{-1}
P_{max}	Maximum light-saturated P_{net}	mg C g dw^{-1} h^{-1} or mg C chl *a* h^{-1} or mg C dm^{-2} h^{-1}
R	Dark respiration	mg C g dw^{-1} h^{-1}
I_c	Irradiance at which gross photosynthesis equals (compensates) respiration	µmol m^{-2} s^{-1}
I_k	Onset of light-saturated photosynthesis (=P_{max}/α)	µmol m^{-2} s^{-1}
α	Photosynthetic efficiency; the linear slope of the light-limited section of the P-I curve	mg C g dw^{-1} h^{-1}(µmol m^{-2} s^{-1})$^{-1}$
$\bar{I}$	Average irradiance between the water surface and sediments in the absence of plants	µmol m^{-2} s^{-1}
RGR	Whole-plant relative growth rate; calculated as instantaneous growth per initial dry weight	mg g^{-1} d^{-1}
NAR	Net assimilation rate; the assimilatory efficiency per unit leaf area	g cm^{-2} d^{-1}

favourable irradiances must be largely supported by existing leaves. In particular, old leaves appear to support new leaf production as they are very green, suggesting high chlorophyll concentrations, but do not extend. The effects of leaf aging on respiration and photosynthesis-irradiance characteristics in submersed species has received little attention (but see Mazzella and Alberte, 1986), though evidence from terrestrial species indicates significant age-related patterns in metabolic activity (Dawson and Bliss, 1993; Ogren and Sundin, 1996). Accordingly rates of light-saturated net photosynthesis, I_c, I_k, α and dark respiration (Table 8.1) were determined as functions of relative leaf age in *Vallisneria*, from the hyperbolic tangent model of Jassby and Platt (1976).

Depth-effects on metabolic activity are important in determining growth (Titus and Adams, 1979; Goldsborough and Kemp, 1988; van der Bijl *et al.*, 1989; Maberly, 1993; Schwarz and Howard-Williams, 1993; Masini *et al.*, 1995). A plant which stratifies its biomass approximately exponentially with depth would be expected to maximise photosynthesis (Titus and Adams, 1979). Adams *et al.* (1974) measured carbon uptake in 10 cm lengths of

Myriophyllum spicatum stem over the water column. Fifty-seven percent of total carbon was fixed within 20 cm of the surface. Fixation declined with depth, and the contribution of each depth class (biomass x fixation rate) also declined as biomass declined. Photosynthesis was greatest close to the surface in *Potamogeton pectinatus* due to higher irradiances, higher chlorophyll and higher α (van der Bijl *et al.*, 1989). α fell and I_c increased with depth.

Growth in *Vallisneria* is positively correlated with the average irradiance between the water surface and sediments, $\bar{I}$ (Chapter 7). As turbidity levels and/or depth increase, shoot and leaf recruitment slows, and relative growth rate (RGR) decreases. As net assimilation rate (NAR), which largely determines RGR, is an estimate of net photosynthesis over the whole plant (Harper, 1977, p311), one may expect assimilation to decline with depth. Photosynthesis in shallow plants with a dense surface canopy was compared to that in deep plants with most of their leaf biomass near the sediments (and below the penetration of compensation-level irradiances). In this chapter, 'canopy' refers to all leaves rather than just those at the surface (e.g. Titus and Adams, 1979), which are collectively referred to as the 'surface canopy'. Patterns in chl *a* across depths and leaf age were investigated. The effects of depth to soil on root and stolon respiration were also examined.

8.2 Methods

Vallisneria was collected from the littoral zone of the Lower Murray and grown in turbid water in outdoor ponds for 7 months (turbidity, 209 NTU; downwelling extinction coefficient, 12.59 m^{-1}; see Methods, Chapter 7). Light attenuation was rapid: 10% of subsurface irradiance penetrated to 19 cm and 1% to 36 cm.

8.2.1 Dark respiration and net photosynthesis measurements

Dark respiration and net photosynthesis were measured as rates of oxygen uptake or production by tissue pieces with a Clarke-type oxygen electrode (at 12°C unless stated otherwise). The reaction medium was 10 mM MES (KOH), 1.0 mM $NaHCO_3$, pH 6.1-6.26. This bicarbonate concentration was chosen to simulate observed ranges in the Lower Murray (0.8-1.3 mM; median from 1978-86, Mackay *et al.*, 1988).

Dark respiration was measured initially. Tissues were then illuminated by a slide projector and irradiance levels varied with neutral density filters in the range 1-1000 µmol m^{-2} s^{-1} PAR. The sides of the oxygen chamber were painted black to reduce focussing of light onto the leaf pieces (Fig. 8.1). Irradiances in the centre of the chamber were estimated as that at the front of the chamber minus half the difference between that measured at the front and the back.

Leaf pieces were 1.6 cm wide and 0.6-2.2 cm long, depending on depth. Two or occasionally three pieces were used for measurements for narrow leaves from deep water (total dry weight 0.03-0.11 g). Attached clay and epiphytes were gently removed with distilled water. Pieces were held vertically (with cut edges vertical) in the oxygen chamber. Leaf pieces were stored in the laboratory in pond water at 10-16°C and irradiances of 20-80 µmol m^{-2} s^{-1} for 1-4 hours to overcome wound respiration (Richards, 1896). Respiration in roots and stolons was measured in the dark. For each, tissues were sampled from shoots of varying ages and pooled.

Root and stolon respiration was measured in tissues collected at 5 pm and 7 am. During measurements tissues were placed in a mesh bag above the stirring rod in the chamber (copper wire, 1 mm mesh).

Oxygen production rates were measured from approximately the second to the eighth minute for each light level, over which time rates were quite uniform and considered to represent *in situ* responses. Plants yielding morning samples were covered with black plastic the previous evening to prevent photosynthesis prior to collection. Respiration was measured for 12 mins for most samples but over 1-3 h in several to determine the effects of carbohydrate depletion overnight on respiration rate. Dry weight was determined after overnight drying at 80°C. Oxygen production was converted to carbon assimilation assuming a photosynthetic quotient of 1.2 and a respiratory quotient of 1.0 (Dennison, 1987; Madsen *et al.,* 1991).

8.2.2 Chlorophyll a determination

Chl *a* determination was conducted on small (c. 0.5 x 1 cm) leaf sections cut adjacent to those used for P-I measurements. Leaf material was stored in turbid pond water at 10-16°C and <20 µmol m^{-2} s^{-1} after cutting, then washed in distilled water and homogenised in 90%

ethanol. Tissues were homogenised with a fitted plastic pestle in a 10 mL centrifuge tube using acid-washed sand. Suspensions were stored overnight at 4°C in the dark, then centrifuged (2000 rpm for 10 minutes). Absorbances were measured at 665 and 750 nm ($A_{665-750}$) on an Hitachi U-2000 spectrophotometer using 90% ethanol with sand as a blank. Readings were taken twice to check for precision. Chl *a* concentration was determined as:

$$\text{Chl } a \ (\mu\text{g sample}^{-1}) = (1000/82) * A_{665-750} * v/l$$

where 82 is the specific spectral absorption coefficient for Chl *a* in 90% ethanol, sample volume *v* was 10 mL and the cell path length *l* was 1 cm (Standards Australia, 1991). Concentrations were expressed as per dry weight using relationships between area and dry weight for each of the pairs of adjacent tissues.

8.2.3 *Effects of leaf age and depth on metabolic activity*

Effects of relative leaf age on net photosynthesis

To examine the influence of leaf age on carbon assimilation and parameters of the P-I relationship, P-I measurements were made in sections of leaf number 1, 2, 3, 4, 5 and 8. Leaf 1 was 2 weeks old, and the top half of leaf 8 had senesced. All leaf pieces were taken from depth 6-8 cm. Depth to the sediment was 11 cm.

Effects of distance below the surface on net photosynthesis

Photosynthesis-irradiance relations were determined in a piece of leaf from depths 5, 15 and 50 cm in a 53 cm long leaf (depth to soil was also 53 cm). Net photosynthesis was normalised to dry weight, unit chl *a* and surface area. The initial slope of the P-I response, α, was calculated with least-squares linear regression for irradiances below 25 μmol m^{-2} s^{-1} in two leaf pieces from each of the three depths.

Effect of rooting depth on chlorophyll a, net photosynthesis and respiration

The effect of depth to soil was examined in leaves of plants growing at 24 cm ('shallow') and 82 cm ('deep'). Plants in the former had the majority of their photosynthetic tissue above the depth corresponding to the mean daily light compensation depth (19 cm, see Fig. 7.15, Chapter 7). Consequently they showed relatively high RGR over the experiment

Table 8.2. Calculated noon irradiances for determination of P_{net}. Irradiances were calculated at 9 depths between 0 and 82 cm depth from the Lambert-Beer relationship. These values were used to permit carbon assimilation to be modelled in Chapter 9. Experimental irradiances established with filters (to simulate calculated irradiances) are given. Irradiance levels were determined from the mean irradiance profile over the experiment (cf. Fig. 8.2)

Depth	Calculated *in situ* irradiance		Experimental irradiances
(cm)	(μmol m^{-2} s^{-1})	% subsurface irradiance	(μmol m^{-2} s^{-1})
1	397	88	528
3	308	68	326
6	211	47	237
11	113	25	120
20	36	8	47
20	10	2.2	9
30	3	0.006	3
40	1	0.002	1
75	0.1	0.0002	0.1

(15 mg g^{-1} d^{-1}) and leaf production (0.53 $week^{-1}$). Plants at 82 cm had most of their canopy below this depth, producing negative RGR (-2 mg g^{-1} d^{-1}) and minimal leaf recruitment (0.03 $week^{-1}$). Four to ten leaves were used for each depth except for the shallowest 4 depth ranges in the deep plants in which only 1 leaf occurred. Net photosynthesis was determined in leaf pieces at the irradiance calculated as the mean noon irradiance received at that depth (Table 8.2). This served two purposes: determination of midday depth-photosynthesis profiles, and provided estimated maximum *in situ* net photosynthesis values for modelling daily canopy assimilation or depth ranges (see Chapter 9). Leaves of varying ages were used to account for age-related P-I effects. A greater proportion of measurements were made in pieces taken close to the surface where irradiances decline rapidly.

8.3 Results

8.3.1 *Comparison of P-I and respiration in* Vallisneria *with other species*

The P-I characteristics of *Vallisneria* indicate a relatively high degree of physiological shade-tolerance compared to freshwater and marine angiosperms throughout the world (Table 8.3). This is indicated by low values of I_c and I_k and high α. Values of I_c are in the range 2-82 μmol m^{-2} s^{-1}, with a mean of c. 20-30 μmol m^{-2} s^{-1}. These mean values are similar to those published for known shade-adapted species (*e.g. Elodea canadensis*, I_c=12 μmol m^{-2} s^{-1}, *Potamogeton obtusifolius*, I_c=10-13 μmol m^{-2} s^{-1}, and *Amphibolus griffithii*, I_c=20 μmol m^{-2} s^{-1}), and below the value of 60 μmol m^{-2} s^{-1} suggested as the general maximum for submersed macrophytes by Bowes and Salvucci (1989). The low minimum I_c values for *Vallisneria* (2-3 μmol m^{-2} s^{-1}) coincide with the minimum reported I_c values for all submersed macrophytes (Bowes and Salvucci, 1989). The onset of photosaturation in *Vallisneria* is generally lower than for most freshwater species, and at similar irradiances to most marine angiosperms. Considerable variation in I_k occurs in *Vallisneria* grown in different conditions however, suggesting photosynthetic plasticity (cf. Bowes and Salvucci, 1989). I_k was much lower in *Vallisneria* plants from the Lower Murray than in plants grown at much lower turbidity in the North American studies (*e.g.* K_d of 1.6-2 m^{-1}, Harley and Findlay, 1994, and S. Findlay, pers. comm.). Values as low as 30-40 μmol m^{-2} s^{-1} were frequently found in Murray plants which is well below that reported elsewhere.

Mean photosynthetic efficiency is 0.042-0.053 mg C g dw^{-1} h^{-1}(μmol m^{-2} s^{-1})$^{-1}$ for *Vallisneria*, but values up to 0.1 mg C g dw^{-1} h^{-1}(μmol m^{-2} s^{-1})$^{-1}$ were found in this study. α is generally lower for freshwater species (0.013-0.031 mg C g dw^{-1} h^{-1}(μmol m^{-2} s^{-1})$^{-1}$), but similar maximum values occur in *Potamogeton* species which also inhabit low-light environments.

Published rates of maximum P_{net} in submersed macrophytes are 0.9-13.0 mg C g dw^{-1} h^{-1}, with those for *Vallisneria* in the mid to low range (0.3-4.7 mg C g dw^{-1} h^{-1}). Maximum P_{net} in this study is similar to that reported by Adams *et al.* (1974) and Titus and Adams (1979), but lower than the maximum reported by Harley and Findlay (1994). The higher $P_{\max}$ in the latter was probably due to higher temperatures; 20°C (S. Findlay, pers. comm.) compared to 12°C in this study.

Table 8.3. Photosynthetic characteristics of selected freshwater and marine angiosperms from published studies. Net maximum photosynthesis (P_{max}) and dark respiration (R) rates are expressed per mg C g dw^{-1} h^{-1}. Data are generally presented as either minimum, mean or maximum values. Some values are the given or calculated mean minimums ('mean min') or mean maximums ('mean max'). Where necessary data were expressed as carbon assimilation assuming a photosynthetic quotient of 1.2 and respiratory quotient of 1.0 (mol O/ mol C; Fourqurean and Zieman, 1991; Madsen *et al.*, 1991). α is the photosynthetic efficiency (mg C g dw^{-1} h^{-1} (μmol m^{-2} $\mathrm{s}^{-1})^{-1}$). Units of the light-compensation irradiance, I_c, and the onset of light-saturated photosynthesis, I_k, are μmol m^{-2} s^{-1}. * Determined from published graphs. See also Kirk (1983, p226), Madsen and Adams (1989), Menendez and Peñuelas (1993).

Species	P_{max}	R	α	I_c	I_k	Location	Source
FRESHWATER ANGIOSPERMS							
Vallisneria americana	mean 0.7	0.51	0.042	20	42	SE Australia	This study
	†min 0.3	0.19	0.005	3	18		
	max 2.7	0.98	0.100	37	95		
V. americana	mean 3.4	0.64	0.053	30	179	NE USA	Harley & Findlay (1993)
	min 2.5	0.34	0.025	2	100		
	max 4.7	1.09	0.068	82	279		
V. americana	min 1.2	-	*0.010	*10	140	N USA	Titus & Adams (1979)
	max 2.3						
V. americana	mean 1.4	0.4	-	10	-	NE USA	Madsen *et al.* (1991)
Egeria densa	mean min 1.0	1.70	-	-	-	SE USA	Barko & Smart (1981)
	mean max 2.0	2.25	-	-	-		
Elodea canadensis	mean 1.8	0.57	-	12	-	NE USA	Madsen *et al.* (1991)
E. potamogeton	6.7	-	-	-	583	Chile	Pizarro & Montecino (1992)
Hydrilla verticillata	mean min 0.7	1.05	-	-	-	SE USA	Barko & Smart (1981)
	mean max 1.1	1.30	-	-	-		

† In plants grown at irradiances just above I_c-levels.

Table 8.3 (continued)

Species	P_{max}	R	α	I_c	I_k	Location	Source
Myriophyllum spicatum	mean 2.9	0.64	0.013	84	341	NE USA	Harley & Findlay (1993)
	min 2.8	0.34	0.006	40	173		
	max 4.5	0.90	0.019	114	452		
M. spicatum	mean 2.3	0.64	-	37	-	NE USA	Madsen *et al.* (1991)
Potamogeton perfoliatus	mean 4.5	0.69	0.016	52	387	NE USA	Harley & Findlay (1993)
	min 2.5	0.53	0.006	29	250		
	max 5.7	1.01	0.019	73	487		
P. perfoliatus	mean min 4.7	-	0.030	25	-	NE USA	Goldsborough & Kemp (1989)
	mean max 11.5	-	0.073	57	-		
P. obtusifolius	mean min 9.0	0.33	0.031	10	123	UK	Maberly (1993)
	mean max 13.0	0.48	0.095	13	423		
P. pectinatus	min 0.2	0.19	0.006	10	-	Denmark	van der Bijl *et al.* (1989)
	max 2.5	2.25	0.120	180	-		
P. amplifolius	mean 1.4	0.42	-	12	-	NE USA	Madsen *et al.* (1991)
P. gramineus	mean 1.9	0.65	-	22	-	NE USA	Madsen *et al.* (1991)
P. praelongus	mean 1.4	0.54	-	12	-	NE USA	Madsen *et al.* (1991)
P. robbinsii	mean 0.9	0.33	-	20	-	NE USA	Madsen *et al.* (1991)
MARINE ANGIOSPERMS							
Amphibolus griffithii	-	0.19	-	20	70	SW Australia	Masini *et al.* (1995)
Cymodocea nodosa	2.6	0.89	0.014	61	-	Mediterranean	Enriquez *et al.* (1995)

Table 8.3 (continued)

Species	P_{max}	R	α	I_c	I_k	Location	Source
Haludole wrightii	min 1.4	0.58	0.005	37	189	SW USA	Dunton & Tomasko (1994)
	max 11.0	1.17	0.024	177	453		
Posidonia australis	-	0.12	-	25	90	SW Australia	Masini *et al.* (1995)
P. oceanica	2.2	0.36	0.014	21	-	Mediterranean	Enriquez *et al.* (1995)
P. sinuosa	-	0.15	-	24	*57	SW Australia	Masini *et al.* (1995)
Ruppia cirrhosa	min 1.8	0.16	-	17	186	Spain	Menedez & Peñuelas (1993)
	max 3.4	0.67	-	167	642		
R. drepanensis	0.6	-	0.002	86	333	Spain	Garcia *et al.* (1991)
R. maritima	5.0	0.54	0.019	23	-	Mediterranean	Enriquez *et al.* (1995)
Thalassia testudinum	*3.8	-	0.011	-	*410	E USA	Fourqurean & Zieman (1991)
Zostera marina	0.9	0.08	-	10	100	NE USA	Dennison & Alberte (1982)
Z. maritima	2.1	0.64	0.014	40	-	Mediterranean	Enriquez *et al.* (1995)
Z. noltii	3.8	1.02	0.014	56	-	Mediterranean	Enriquez *et al.* (1995)

Dark respiration rate, *R*, varies considerably between species and environments, ranging from 0.08 mg C g dw^{-1} h^{-1} in *Zostera marina* to 2.25 mg C g dw^{-1} h^{-1} in *Elodea canadensis.* Values for *Vallisneria* are again low-mid range (mean of 0.5 mg C g dw^{-1} h^{-1} in this study, up to 1.09 mg C g dw^{-1} h^{-1} reported by Harley and Findlay (1994).

8.3.2 Effects of relative leaf age on net photosynthesis in Vallisneria

Photosynthesis and respiration was highly dependent on relative leaf age (Fig. 8.3). The youngest and most rapidly extending leaf had the highest dark respiration and lowest P_{max}. P_{max} was highest in leaves 2 and 4 with older leaves less active (Fig. 8.4a). More young-mid aged leaves were at the surface than very young or old leaves. They also have a more efficient photosynthetic pathway, with low I_c and high α (Fig. 8.4d). High light availability and harvesting efficiency, coupled with a large surface area in this age class, suggest it is responsible for the bulk of carbon fixation. Older leaves (5 and 8) had low respiration rates (0.06-0.13 mg C g dw^{-1} h^{-1}) and so cost less to maintain, but also assimilated less (P_{max} 0.55-0.60 mg C g dw^{-1} h^{-1}). Net photosynthesis in older leaves occurred at very low irradiances compared to younger leaves and other submersed species (I_c=2.5 and 5 μmol m^{-2} s^{-1}, leaves 5 and 8 respectively, and Table 8.3). P_{max}:R increases to leaf 5, then declines in leaf 8 (Fig. 8.4.b) and explains the minimal extension in leaves of this age and older (see Chapter 7). Van der Bijl *et al.* (1989) suggest reduced photosynthetic capacity observed during the growing season in *Potamogeton pectinatus* is due to leaf age but did not test this. Values for I_k ranged between 18 and 31 μmol m^{-2} s^{-1}, being highest for leaf 2 and lowest for leaf 1. These values are very low compared to values reported for *Vallisneria* and other species (Table 8.3).

Taken together these results show that the older, non-extending leaves (which also have high chl *a* concentrations, see Fig. 8.7a) can fix carbon at very low irradiances, and may be important in supporting leaf initiation and extension in the youngest leaves. Newly recruited leaves had a high respiration rate, low P_{max} and high I_c, suggesting they relied on older leaves for energy.

8.3.3 Effect of depth in the canopy on P-I relations

Net photosynthesis decreased with increasing depth in the canopy (Fig. 8.5). P_{max} at 15 cm depth was c. 65% that at 5 cm (expressed per dry weight or chl *a*), or 43% when expressed per leaf area. No net photosynthesis occurred at 50 cm. Irradiances received at 5, 15 and 50 cm depths were 53, 15 and 0.2% of subsurface irradiances, respectively. Respiration was 25% greater at 5 cm than at 15 cm (-1.54 *v.* -1.24 mg C g dw^{-1} h^{-1}). Rates of P_{net} and R were much higher at 25°C than in leaves at 12°C. As in all plants, photosynthesis in *Vallisneria* is temperature sensitive over this temperature range, and is optimal at 32.6°C (Titus and Adams, 1979). P_{max} was c. 7 mg C g dw^{-1} h^{-1} at 25°C and 0.8-1.4 mg C g dw^{-1} h^{-1} at 12°C. As P-I responses were similar whether expressed per dry weight, chl *a* concentration or surface area, data are presented as per dry weight. This was necessary for comparisons between modelled plant carbon balances and RGR (Chapter 9).

There was no indication that *Vallisneria* alters its photosynthetic metabolism to increase assimilation under low light. The onset of saturation, I_k, increased from 67 μmol m^{-2} s^{-1} at 5 cm to 95 μmol m^{-2} s^{-1} at 15 cm. Reported values of I_k for North American *Vallisneria americana* plants range from 100-279 μmol m^{-2} s^{-1} (Table 8.3), much higher than in Murray plants. This is probably due to higher temperatures employed in these studies (c. 20°C, S. Findlay, pers. comm.). In addition genetic differences between North American and southeastern Australian plants are quite probable, and likely to considerably influence P-I relations. Ninety-one allozyme phenotypes were found in one *Vallisneria americana* bed in the Detroit River, USA, indicating high genetic diversity (Lokker *et al.,* 1994). Lovett-Doust and Laporte (1991) found considerable variation in *Vallisneria* sex ratios in the Great Lakes, USA, which they suggest is genetically based. In general, water clarity is lower in the Lower Murray than in these North American waterbodies, and may have selected for highly shade-tolerant phenotypes.

Photosynthetic efficiency, α, declined exponentially with depth. The corresponding log-linear relationship, $\alpha=0.17-0.04*\ln depth$ ($r^2=0.98$, $P<0.001$), predicts a maximum α of 0.17 mg C g dw^{-1} h^{-1}(μmol m^{-2} s^{-1})$^{-1}$ in very shallow water (Fig. 8.6). Though chl *a* data are not available for these tissues, a general reduction in pigment concentration with depth (see Fig. 8.7) suggests α may be approximately uniform across depth when normalised to chl *a*. α increased at low light in *Potamogeton perfoliatus* when normalised to dry weight, apparently due to increased levels of chl *a* rather than improvements in enzyme activity (Fig. 3a in Goldsborough and Kemp, 1988).

Van der Bijl *et al.* (1989) also observed higher photosynthetic efficiencies in tissues close to the surface than in basal leaves in *Potamogeton pectinatus*. α ranged from 0.019 to 0.119 mg C g dw^{-1} h^{-1}(μmol m^{-2} s^{-1})$^{-1}$ in apical pieces, and 0.003 to 0.031 mg C g dw^{-1} h^{-1} (μmol m^{-2} s^{-1})$^{-1}$ in basal pieces.

8.3.4 *Effect of rooting depth on chlorophyll a, net photosynthesis and respiration*

Chl *a* concentrations varied according to leaf age and depth in the canopy (Fig. 8.7). In leaves produced in shallow water (24 cm), the bases of young leaves had the lowest concentrations of all leaves (depth 20 cm in leaves 1 and 2; c. 2 mg chl *a* g dw^{-1}). The tips of these leaves, however, had close to peak levels (8-9 mg chl *a* g dw^{-1}) (Fig. 8.7a). In the mid-aged leaves (ages 3-7) peak concentrations occurred at 6-10 cm or 47-28% of subsurface irradiance (5-8 mg chl *a* g dw^{-1}). In the leaf at rooting depth 82 cm, chl *a* concentrations peaked 20 cm below the surface - at twice the concentration at 0 cm (10 and 5.3 mg chl *a* g dw^{-1} respectively, Fig. 8.7b). This is probably a consequence of photo-oxidation at higher irradiances in chlorophyll formed at very low intensities then carried to the surface and air (Smirnoff, 1993). At irradiances less than 8% of subsurface (deeper than 30 cm), chl *a* concentrations were markedly reduced (Fig. 8.7b).

As leaves matured chl *a* concentrations near the base increased (depth 20 cm, Fig. 8.7a). (Note that leaves 8 to 10 were clipped to 10 cm long prior to the experiment (see Methods, Chapter 7), and chl *a* data are only available for depth 20 cm). This suggests pigments are concentrated toward the bottom of leaves as the tips senesce, and may explain the lower irradiances at which photosynthesis balances respiration in older leaves (cf. I_c in Fig. 8.4b).

Net photosynthesis measured at simulated noon irradiances declined with depth (Fig. 8.8). Mean maximum rates were 1.2 mg C g dw^{-1} h^{-1} in shallow plants and 1.4 mg C g dw^{-1} h^{-1} in deep plants (Fig. 8.8). Assimilation rates over the top 10 cm of the water column were unaffected by rooting depth. The minor peak at 6 cm is due to higher chl *a* concentrations than at the surface for most leaves (Fig. 8.7a). The reduction in net photosynthesis with depth mirrors the attenuation of PAR. This is evident by comparing photosynthetic rates with the depth-irradiance curve (Fig. 8.8). A similar exponential decline in photosynthetic rate with depth was observed in *Myriophyllum spicatum* (Titus *et al.*, 1975).

Photosynthesis was 2-3 times higher at the surface than at 3 cm, indicating the importance of canopy formation in turbid water. The depth at which net photosynthesis is zero in leaves at 82 cm rooting depth corresponds to an average daily irradiance of 5 µmol m^{-2} s^{-1} (depth 30 cm, or 2.3% of subsurface irradiance), which is approximately the minimum light compensation point for leaves of all ages (Fig. 8.4d). Respiration was greater than photosynthesis below 30 cm, where the bulk of the plant's biomass is concentrated (see below). The effect of the high respiratory demand of the basal meristems on net photosynthesis can be seen in tissues at 20 cm depth in shallow plants. No net oxygen evolution occurred despite sufficient light (cf. net photosynthesis in tissues at 20 cm in deep plants) and chl *a* concentrations for net photosynthesis (2-5 mg g dw^{-1}, Fig 8.7a). Day *et al.* (1985) found dark respiration in the meristematic tissues in perennial rye grass (*Lolium perenne*) to be 60-230% higher than in mature tissues. This highlights the importance of accounting for the high respiration of meristems in calculating carbon budgets.

For each rooting depth, respiration was largely independent of depth (hence irradiance) in the canopy. The assumption of the independence of respiration from PAR is often made in calculating carbon budgets for macrophytes (van der Bijl *et al.* 1989, Fourqurean and Zieman 1991). Maximum rates occurred at the surface, where most carbon is fixed, and at the leaf bases. Respiration was 40-260% higher throughout the canopy in shallow plants than in deep plants. Mean rates in the former were 0.60 to 0.75 mg C g dw^{-1} h^{-1} and 0.20 to 0.50 mg C g dw^{-1} h^{-1} in the latter. Higher respiration in shallow plants was in spite of similar rates of net photosynthesis for both rooting depths, and underlies the higher leaf recruitment rates at 24 cm than at 82 cm (0.53 *v* 0.03 per week, Table 7.6 in Chapter 7).

8.3.5 Root and stolon respiration

Root respiration was an order of magnitude lower in the 7 am samples than in the 5 pm samples due to sugar depletion overnight (Table 8.4). Maximum rates of c. 2 mg C g dw^{-1} h^{-1} occurred in shallow plants in the late afternoon after 10 h of photosynthesis (Fig. 8.9). Rates were c. 25% lower at the same time in deep plants (Table 8.4). Respiration rate decreased over time in roots harvested at 5 pm, falling 35% in 80 mins (Fig. 8.9a). Following 12 h of darkness, carbohydrate stores in the roots were almost depleted, as indicated by the fairly constant (and much reduced) rates at 7 am.

Table 8.4. Rates of respiratory oxygen consumption in roots and stolons in *Vallisneria americana* plants grown in shallow (24 cm to sediments) and deep (82 cm) water. Tissues were collected at 5 pm and 7 am.

Depth		Respiration rate ($mg\ C\ g\ dw^{-1}\ h^{-1}$)	
		Roots	Stolons
Shallow	5 pm	1.92	0.48
	7 am	0.88	0.21
Deep	5 pm	1.40	0.13
	7 am	0.78	0.12

Stolon respiration was always considerably less than root respiration and remained relatively constant over 1-3 h. Stolon respiration in shallow plants fell 60% overnight (falling from 0.48 to 0.21 mg C g $dw^{-1}\ h^{-1}$). In deep plants, morning and evening rates were similar (c. 0.12 mg C g $dw^{-1}\ h^{-1}$), suggesting insufficient carbon fixation to support vegetative spread. Indeed no shoots were recruited at this depth over the experiment (Chapter 7).

8.4 Discussion

8.4.1 Relative physiological shade-tolerance of Vallisneria

Several studies have concluded that *Vallisneria* is physiologically shade-tolerant (Meyer *et al.*, 1943; Titus and Adams, 1979; Madsen *et al.*, 1991; Harley and Findlay, 1994). The results for Lower Murray plants are in agreement with these studies, but they had generally lower I_c and I_k, and similar to higher α. *V. americana* is widespread throughout eastern North America, southeastern Australia and also occurs in pan-Pacific countries (Lowden, 1982; Catling *et al.*, 1994; Jacobs and Frank, in press). It has colonised a wide range of lotic and lentic ecosystems, from clear oligotrophic lakes (Madsen *et al.*, 1991) to turbid floodplain rivers (Walker *et al.*, 1994; Kimber *et al.*, 1995a,b) to tidal freshwater estuaries (Carter *et al.*, 1996). Its success in recovering from periods of high turbidity (Carter *et al.*, 1996), drought (Kimber *et al.*, 1995b) and invasion by canopy-forming species (Titus and

Adams, 1979) seems in large part due to physiological shade-tolerance. Low light compensation and saturation points permit the attainment of P_{max} in low light and before most other submersed species. A high and varying α enables rapid response to altered light availability. Goldsborough and Kemp (1988) suggested the ability to vary α permitted *Potamogeton perfoliatus* to survive in the Hudson River, USA, which experiences periods of transient high turbidity. Similarly, a variable and potentially high α in *Vallisneria* would permit it to survive periods of high turbidity, and allow rapid recovery.

Titus and Adams record an increase in I_k from 140 to 800 µmol m^{-2} s^{-1} two days after being placed in high light. Very low I_k values (30-40 µmol m^{-2} s^{-1}) were recorded in Murray plants. Selection for highly shade-tolerant phenotypes appears to have enabled *Vallisneria* to attain saturation at such low irradiances, which only penetrate 0.6-1.5 m in Murray water, and much less when the Darling River contributes significant flow (Woodyer, 1979). Titus and Adams (1979) suggested *Vallisneria americana* was able to exist under dense surface canopies of the exotic *Myriophyllum spicatum* because it photosaturated at lower irradiances. Rates of net photosynthesis and dark respiration for *Vallisneria* are in the low-mid range for published values for submersed macrophytes (Table 8.3). In this study, metabolic activity was measured at 12°C, below its optimum (32.6°C, Titus and Adams. 1979), and hence rates of will be lower than maximum.

The exact biochemical process involved in changing light use efficiency (e.g. Frost-Christensen and Sand-Jensen, 1992) in plants grown under varying light conditions is not well understood. Beer *et al.* (1991) suggest changes in photosynthesis in submersed macrophytes are due to lower ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) activity rather than internal inorganic supply (which are high) or photorespiration (which is suppressed). Rubisco activity explained variations in photosynthesis over a broad range in PAR in *Ceratophyllum demersum* (Spencer and Wetzel, 1991). The higher level of shade-tolerance in Murray *Vallisneria* plants compared to that in plants grown in lower turbidities may be explained by higher Rubisco activity, and warrants investigation.

Large floods may persist for 3 months, and frequently longer, in the Lower Murray (Fig. 1.5). Deep flooding and high turbidities reduce light penetration to *Vallisneria* plants in the littoral zone to very low levels. The growth experiment indicated plants could survive 3 months at irradiances at or below I_c. Cessation of shoot production and production of long, thin and narrow leaves in existing shoots eventually allowed plants at 1 m depth to place photosynthetic tissue at the surface. These physiological and morphological adaptations to low light enable *Vallisneria* to survive in turbid water.

8.4.2 P-I relations and canopy carbon assimilation

The P-I response in *Vallisneria* leaves depends on leaf age, depth of the leaf in the canopy and depth to the sediment. Maximum net photosynthesis rates were obtained at the surface where average noon subsurface irradiances were 450-600 μmol m^{-2} s^{-1} at 12°C (1.4 - 1.5 mg C dw^{-1} h^{-1}, Fig. 8.8). Depth in the canopy reflects the tissues' photohistory (Pizarro and Montecino, 1992), chl *a* concentration and age. Newly recruited leaves have a high respiratory demand but an insufficiently developed photosynthetic metabolism to meet that demand. This is evident in a low P_{max}, high I_c and low P_{max}:R (Fig 8.6), and despite near-maximum chl *a* concentrations in the leaf tip (8.5 mg chl *a* g dw^{-1}). With age a greater proportion of the leaf reaches the surface and achieves photosaturation over the day. Consequently P_{max}:R increases and I_c declines (Fig. 8.6). The function of old, non-extending leaves appears to be to harvest photons at low flux densities to support leaf production (I_c=2-5 μmol m^{-2} s^{-1}). Chl *a* concentrations are high in the bases of senescent leaves (8-10 mg chl *a* g dw^{-1}). Their relatively high P_{max}:R indicates significantly greater sugar fixation than required for their own maintenance (minimal growth respiration, and presumably low maintenance respiration, cf. Thornley, 1970), allowing them to acts as sources of carbohydrates for other tissues *e.g.* for leaf initiation.

The dynamic nature of age-related photosynthesis in leaves of submersed macrophytes has not been widely addressed. P_{net}, I_c and α were found to be age and depth dependent in eelgrass *Zostera marina* (Mazzella and Alberte, 1986). Carbon assimilation has also been observed to vary with leaf age in a range of terrestrial species, including wild species (Dawson and Bliss, 1993; Ogren and Sundin, 1996), crops (Schaffer *et al.*, 1991; Wullschleger and Oosterhuis, 1992) and horticultural species (Lieth and Pasian, 1990). In general, maximum photosynthetic rate and photosynthetic efficiency are highest in young to mid-aged leaves, with a reduced capacity in older leaves related to lower stomatal conductance (Ogren and Sundin, 1996). In submersed *Vallisneria*, which has no stomata, the decline in photosynthetic capacity may be related to lower Rubisco activity (Bowes and Salvucci, 1989; Beer *et al.*, 1991; Madsen *et al.*, 1993).

Surface chl *a* concentrations decreased with age and may be a consequence of photo-oxidation (Macrae and Ferguson, 1985; Smirnoff, 1993; Greer, 1995). The tips of new leaves exhibited near-maximal chl *a* concentrations despite receiving less-than I_c-level irradiances (Fig. 8.7b). Leaf extension rates of up to 1.1 cm d^{-1} would rapidly expose the tip to high irradiances and possible desiccation at the surface, causing superoxide and singlet oxygen production, leading to lipid peroxidation (Smirnoff, 1993). Pigment concentration changes due to variation in light intensity are also ascribed to photoadaptation (Barko and Filbin, 1983; Robe and Griffiths, 1990; van der Bijl *et al.*, 1989). To what extent reductions in chl *a* concentrations at the surface in *Vallisneria* are a consequence of photo-oxidation or a strategy to maximise assimilation warrants investigation. Physical damage from waves and bleaching in air are likely to further reduce concentrations under natural conditions. Peak chl *a* levels instead occurred at depths 6-0 cm, or 47-28% of subsurface irradiance.

Carbon budgets for submersed macrophytes generally regard plants as being of homogeneous temporal and depth distribution (Dennison, 1987; Maberly, 1993; Fourqurean and Zieman, 1991; Zimmerman *et al.,* 1991), yet this is not likely to be the case. Data presented here indicate considerable variation in P_{max}, R , α and I_c due to leaf age in *Vallisneria. Potamogeton pectinatus* photosynthesis also decreased with leaf age, though this was confounded by depth in this apically-growing species (van der Bijl *et al.,* 1989*)*.

Photosynthesis declined rapidly with depth, whilst respiration was comparatively uniform (for each rooting depth). The implication is that growth will be low to negative in plants without a surface canopy in the turbid Murray. No indication of photoadaptation at lower depths was observed in *Vallisneria*, when normalised to dry weight. However, α appears highly correlated with chl *a* concentration, as found for *Potamogeton perfoliatus* by Goldsborough and Kemp (1988). Any capacity for photoadaptation may have been outweighed by rapid light extinction in the water column. Instead I_k increased and α decreased with depth. Shade-tolerance in *Vallisneria* is due rather to lower irradiances necessary for photosynthesis compared to most submersed macrophytes (Table 8.3, and Harley and Findlay, 1994). Minimum and mean reported I_c values are 2-3 μmol m^{-2} s^{-1} and 10-30 μmol m^{-2} s^{-1} in *Vallisneria*, and 10-40 μmol m^{-2} s^{-1} and 12-80 μmol m^{-2} s^{-1} for most freshwater and marine angiosperms. The dominance of *Vallisneria* in the submersed macrophyte community in the turbid Murray is due to its physiological shade-tolerance and plastic leaf morphology (Chapter 7). Its strong malleable leaves are able to remain close to the surface to maximise light interception whilst withstanding wave action.

8.4.3 Canopy formation in turbid water

Plants were grown at a turbidity of 209 NTU in which the euphotic depth was 36 cm and mean penetration of compensation-level irradiances was 19 cm (Fig. 7.15, Chapter 7). Plants at rooting depth 82 cm had 87% of their biomass below the mean I_c-depth and consequently a negative RGR (see Chapter 9). Whole-plant RGR and leaf recruitment were significantly higher in shallow plants (Chapter 7), in which c. 75% of canopy biomass was above the mean I_c-depth. The high correlation between RGR and the proportion of leaf biomass experiencing greater-than I_c-level irradiances in the pond experiment corroborates this. Shoot recruitment was negligible in plants at a low average irradiance, $\bar{I}$.

Diel changes in below-ground respiration suggest insufficient carbon was assimilated for vegetative spread in deep plants. Stolon respiration remained low and uniform over 24 h (0.12 mg C g dw^{-1} h^{-1}; Table 8.4), suggesting little sugar accumulation over the day. Interestingly root respiration doubled from early morning to late afternoon, suggesting that energy production continues at this depth, though insufficient for vegetative reproduction. This energy may only be sufficient for maintenance and nutrient acquisition.

Canopy formation is a common adaptation to life in turbid waters, and is documented in a range of species (*Potamogeton pectinatus,* van der Bijl *et al.,* 1989; *Myriophyllum spicatum,* Madsen *et al.*, 1991, and Titus and Adams, 1979; *Lagarosiphon major*, Schwarz and Howard-Williams, 1993). It also confers a competitive advantage over species which concentrate their biomass lower in the water column (Adams *et al.*, 1974, Chambers and Kalff, 1987; Huisman and Weissing, 1994). North American studies report *Vallisneria americana* does not develop a significant surface canopy (Titus and Adams, 1979; Madsen *et al.*, 1991). Whilst the absence of waves in the pond experiment may have allowed more leaves to lie at the surface than do so in the Lower Murray's littoral, observations of natural populations suggest canopy formation is common. Canopy formation may have developed in response to the high and variable turbidity regime in the Murray (Oliver, 1990). Genetic and morphological studies have found very high genetic diversity within even restricted geographical areas (Lokker *et al.*, 1994; Lovett Doust and Laporte, 1991).

8.4.4 Appropriateness of methodology

The measurement of P-I responses in leaf pieces is a highly intrusive procedure. Leaf segments are unable to export accumulated sugars, with equilibrial balances likely to be affected. Oxygen saturation in the reaction medium can occur with highly photosynthetic leaves, necessitating rapid measurements. However, sufficient time for species with significant lacunal gas storage, such as *Vallisneria*, to evolve O_2 at rates truly reflecting net photosynthetic rates is also required. Hence timing of measurements is critical.

Notwithstanding allowances for wound respiration O_2 production is likely to be curtailed as energy is expended on repairing damaged tissues. This may lead to an underestimation of photosynthetic rates. In addition sediment CO_2 is an important carbon source for some rooted macrophytes (Robe and Griffiths, 1990), and is removed by cutting. In sediment-CO_2 users, carbon limitation is therefore possible in leaf segments, though this may be offset by increasing uptake across the leaf surface. Also, the congener *Vallisneria spiralis* was found to store malate as a carbon source for use when exogenous CO_2 was limiting (Helder and van Harmelen, 1982; MacFarlane, 1985). Storage of carbohydrate as malate in *V. americana* may allow it to continue to metabolise when cut. Taken together these suggest P-I measurements in leaf segments in *V. americana* may be appropriate.

Fig. 8.1. Oxygen chamber (front view).

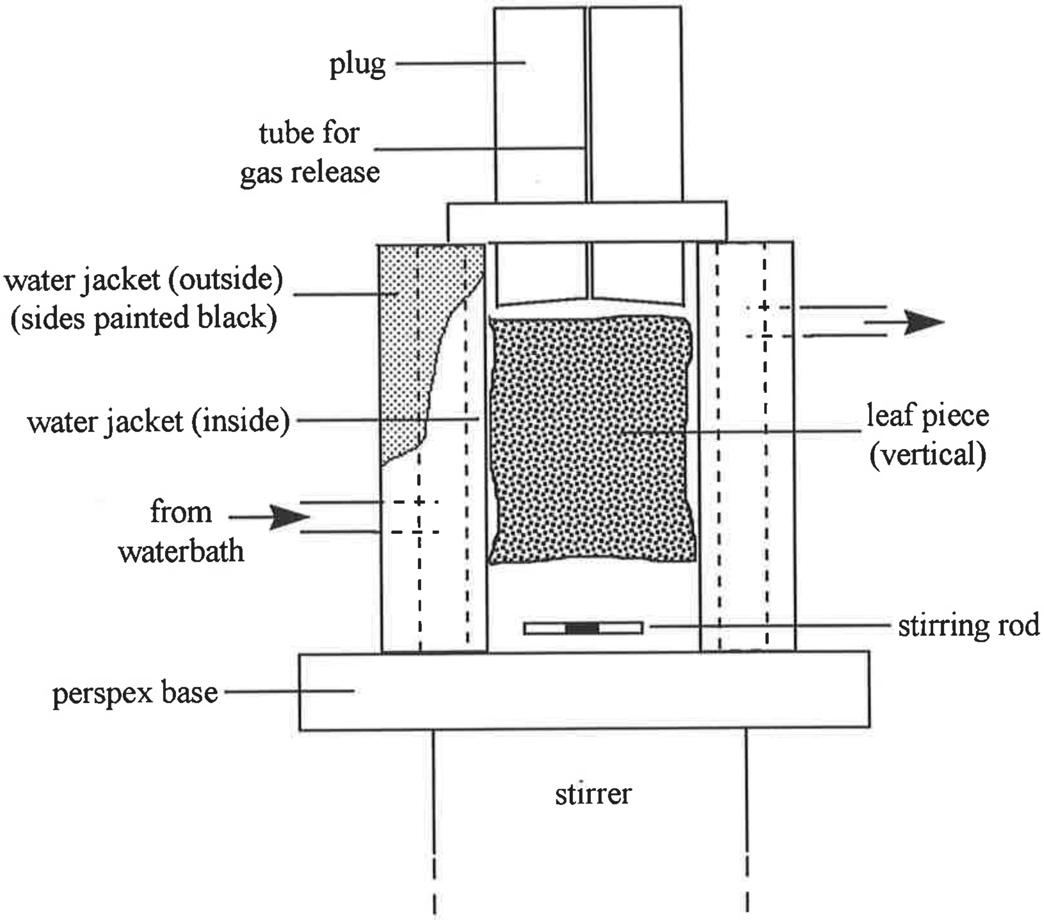

plug
tube for gas release
water jacket (outside) (sides painted black)
water jacket (inside)
from waterbath
perspex base
leaf piece (vertical)
stirring rod
stirrer

Fig. 8.2. Mean hourly incoming solar irradiance profile over the of experiment (line). Recorded hourly irradiances (circles) are the averages of 60 instantaneous measurements. Surface reflectance was 29%.

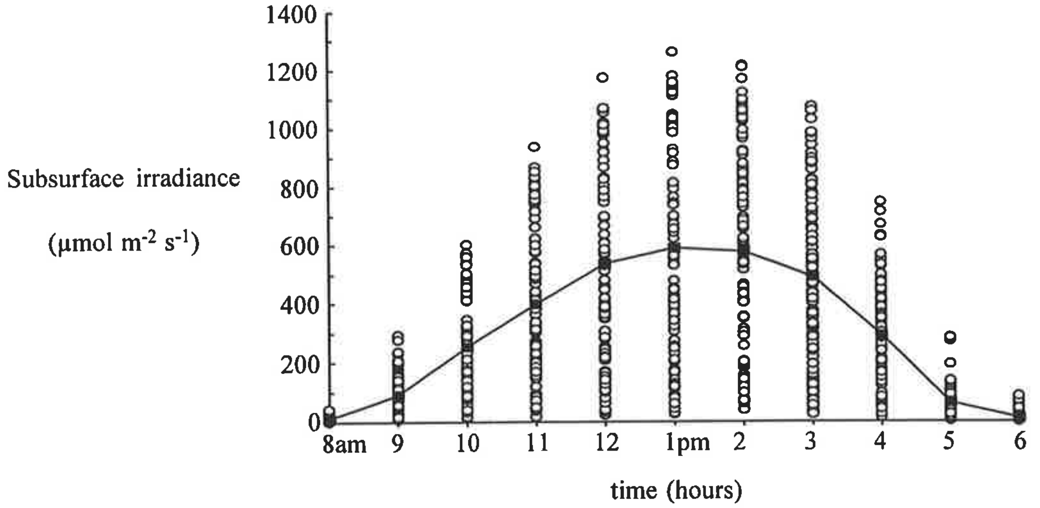

Subsurface irradiance
(µmol m-2 s-1)
1400
1200
1000
800
600
400
200
0
8am
9
10
11
12
1pm
2
3
4
5
6
time (hours)

Fig. 8.3. Photosynthesis-irradiance response as a function of relative leaf age. Depth to sediment is 11 cm, and leaf pieces from depth 6-8 cm.

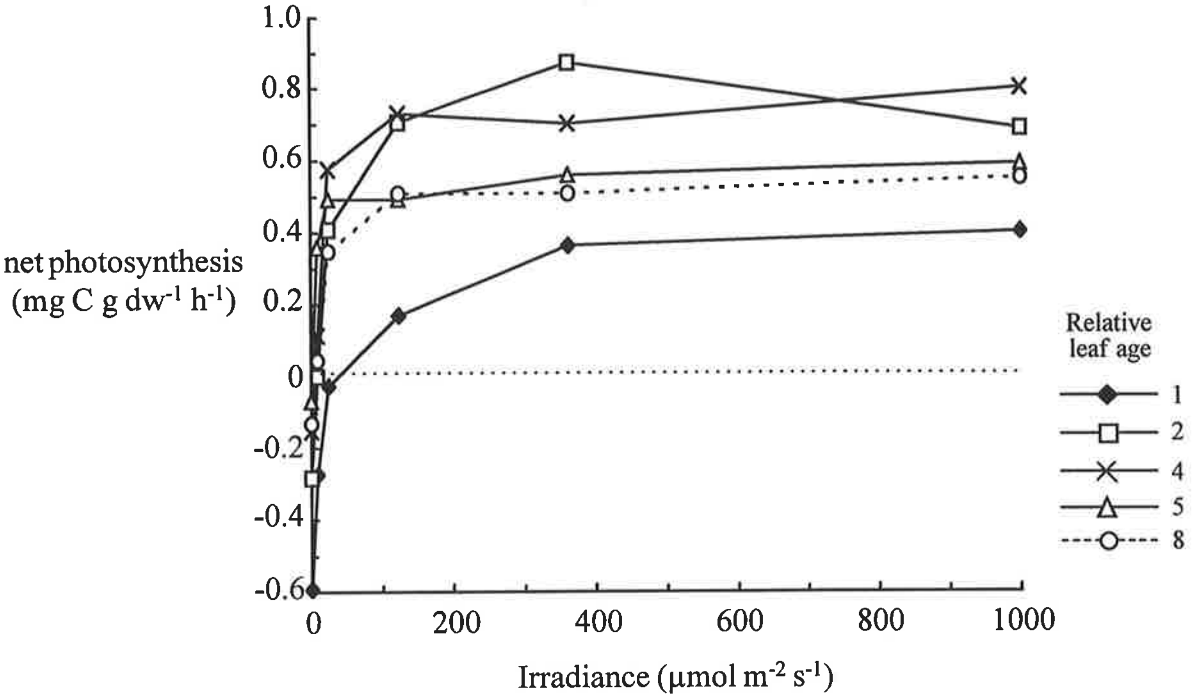

1.0
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
net photosynthesis (mg C g dw^{-1} h^{-1})
0
200
400
600
800
1000
Irradiance (µmol m^{-2} s^{-1})
Relative leaf age
1
2
4
5
8

Fig. 8.4. Effect of leaf maturation on P-I parameters. a. Maximum net carbon assimilation and dark respiration. b. Ratio of maximum net photosynthesis to dark respiration. c. Onset of light-saturation. d. Compensation irradiance I_c and photosynthetic efficiency α. Reliable data for photosynthesis in leaf 3 are not available (suggested values shown by dashed lines).

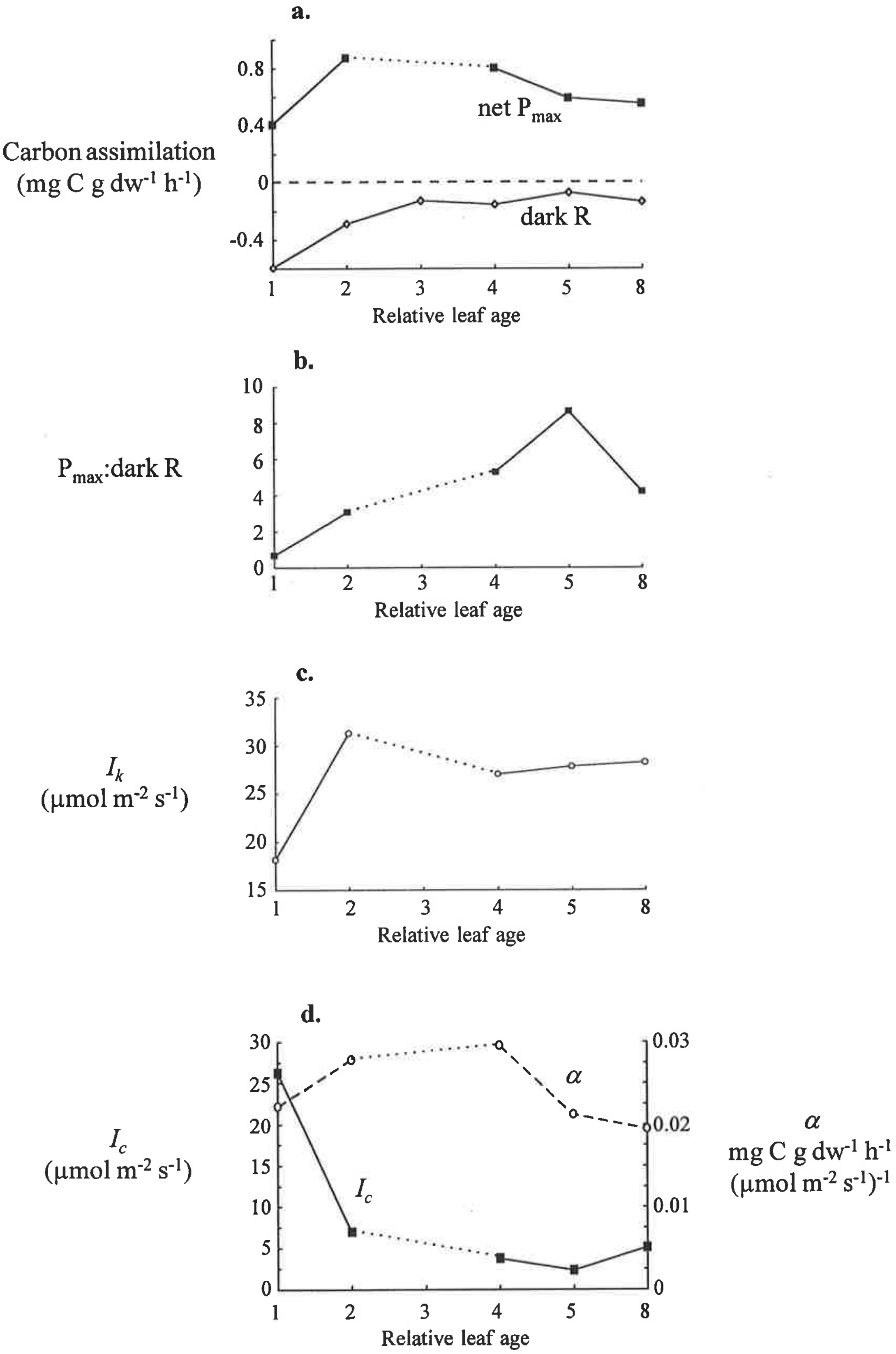
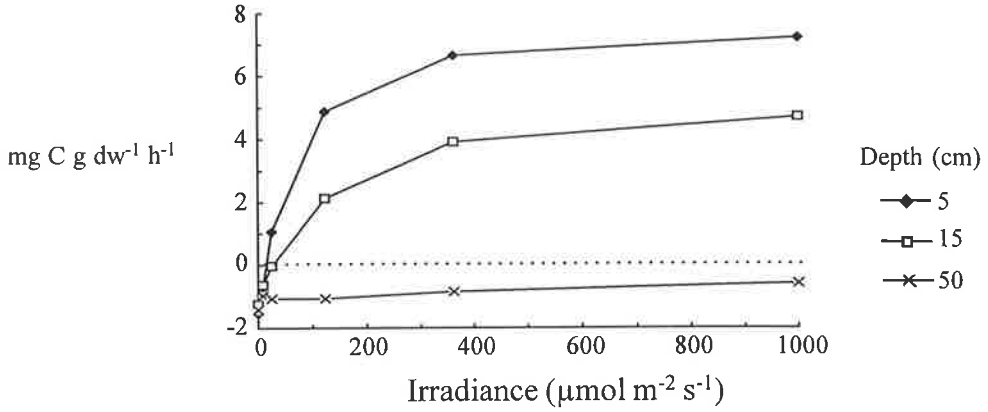
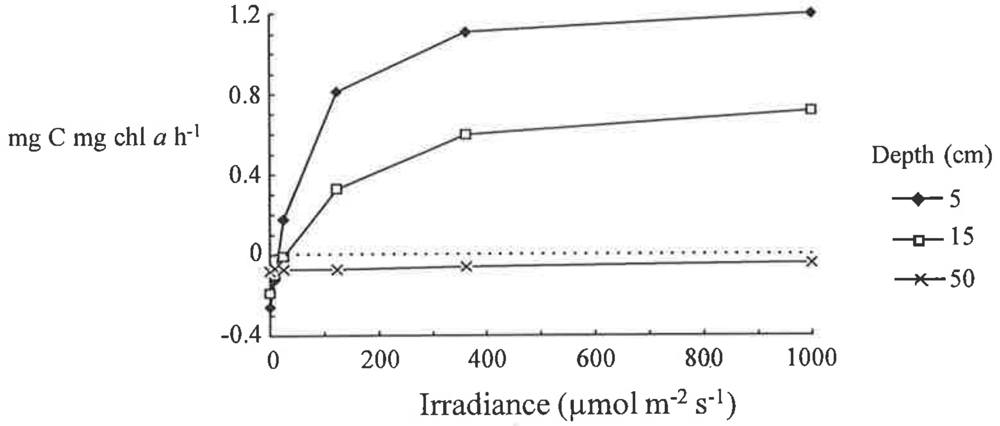

a.
Carbon assimilation (mg C g dw-1 h-1)
0.8
0.4
0
-0.4
net Pmax
dark R
1
2
3
4
5
8
Relative leaf age
b.
Pmax:dark R
10
8
6
4
2
0
1
2
3
4
5
8
Relative leaf age
c.
Ik (µmol m-2 s-1)
35
30
25
20
15
1
2
3
4
5
8
Relative leaf age
d.
Ic (µmol m-2 s-1)
30
25
20
15
10
5
0
α
Ic
0.03
0.02
0.01
0
α mg C g dw-1 h-1 (µmol m-2 s-1)-1
1
2
3
4
5
8
Relative leaf age

Fig. 8.5. Net photosynthesis-irradiance response in *Vallisneria* leaf pieces from 5, 15 and 50 cm below the surface, expressed per a. dry weight, b. chl *a* concentration per dry weight and c. leaf area. Each datum represents one measurement. Depth to soil is 53 cm. Rate of downwelling extinction is 12.59 m^{-1}, and water temperature is 25°C.

a. dry weight



b. chl *a* concentration



c. leaf area

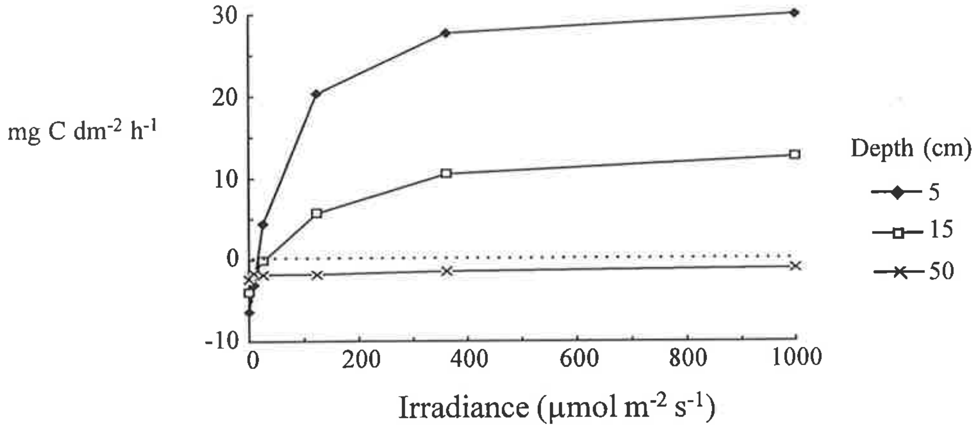


Fig. 8.6. Photosynthetic efficiency α as a function of ln depth. Measurements were made at 25^{o}C.

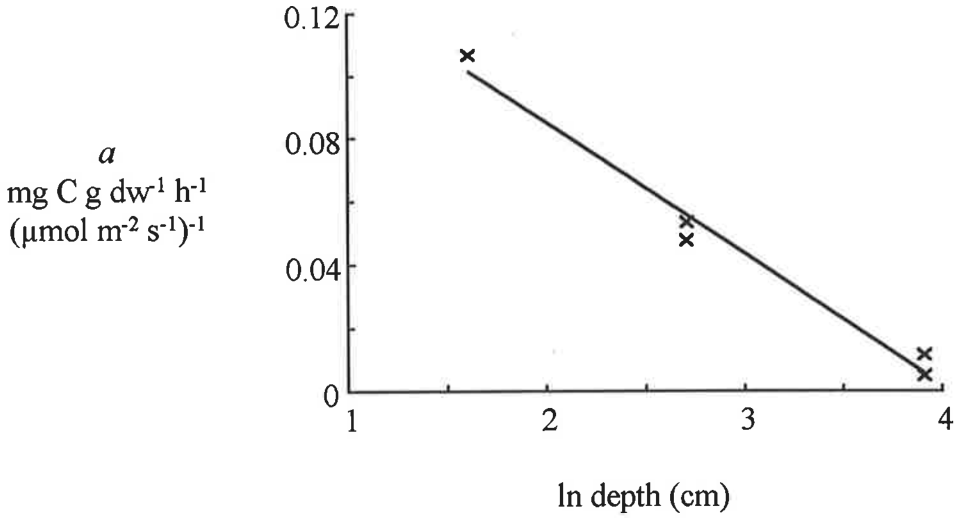
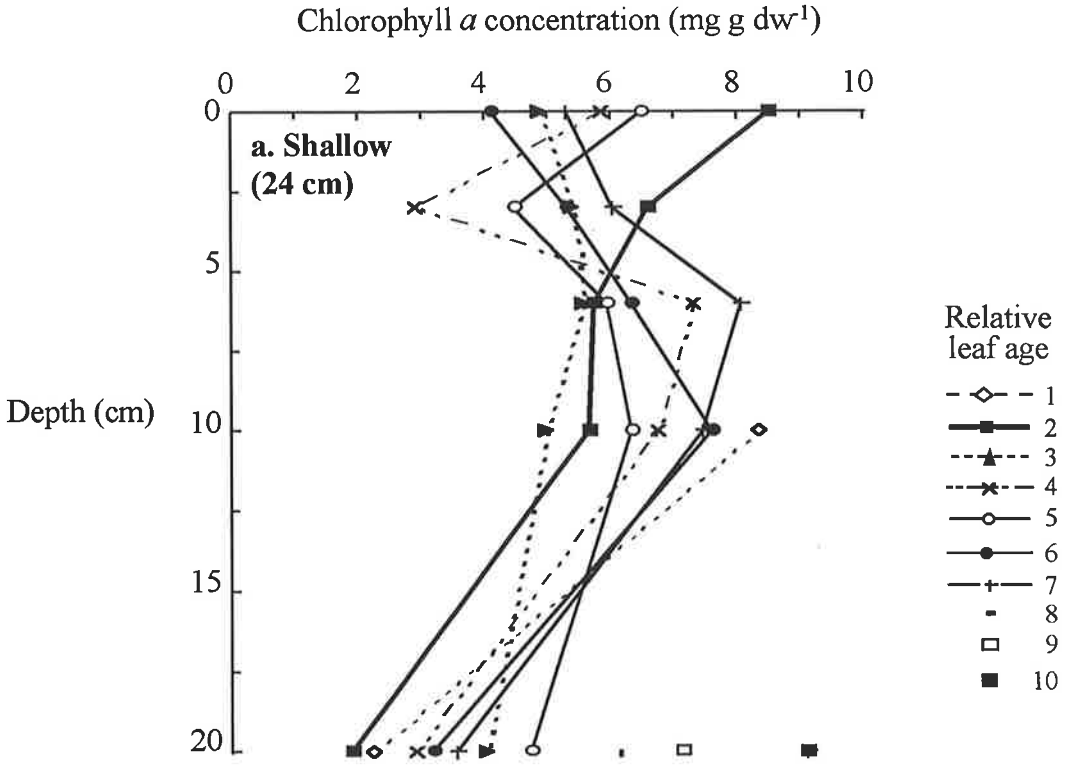

a
mg C g dw-1 h-1
(µmol m-2 s-1)-1
0.12
0.08
0.04
0
1
2
3
4
ln depth (cm)

Fig. 8.7. Chlorophyll *a* concentration in leaves of varying ages in plants at two rooting depths a. 24 and b. 82 cm. Note different scales. The leaf at 82 cm was leaf 2.


Chlorophyll *a* concentration (mg g dw^{1})
0
2
4
6
8
10
a. Shallow (24 cm)
Depth (cm)
0
5
10
15
20
Relative leaf age
1
2
3
4
5
6
7
8
9
10

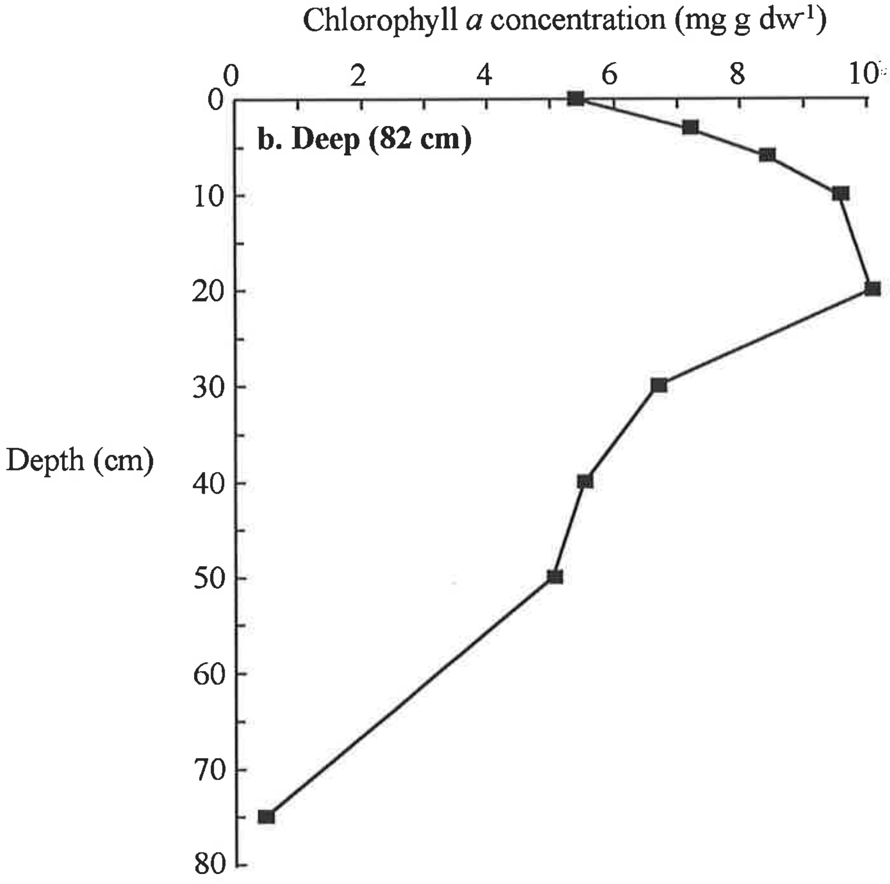

Chlorophyll *a* concentration (mg g dw^{1})
0
2
4
6
8
10
b. Deep (82 cm)
Depth (cm)
0
10
20
30
40
50
60
70
80

Fig. 8.8. Mean net photosynthesis and dark respiration at various depths in the canopy in plants at rooting depths 24 and 82 cm. Net photosynthesis is compared with percent subsurface irradiance.

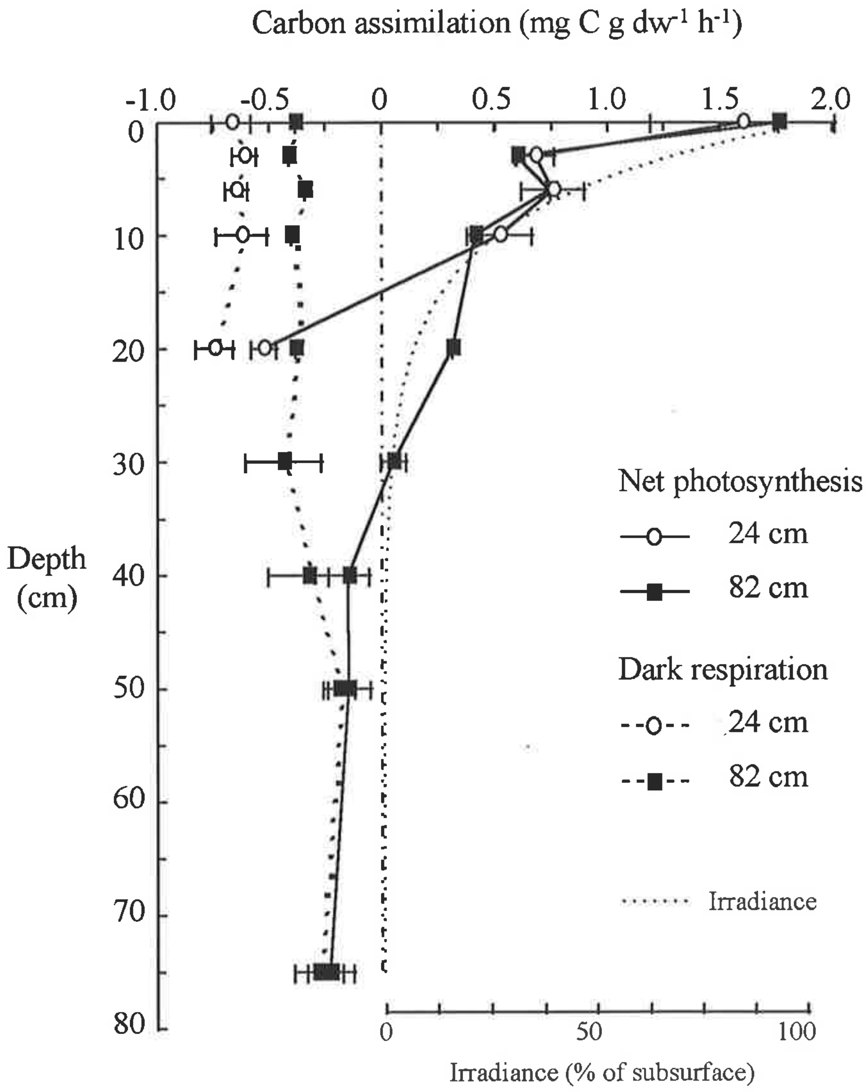
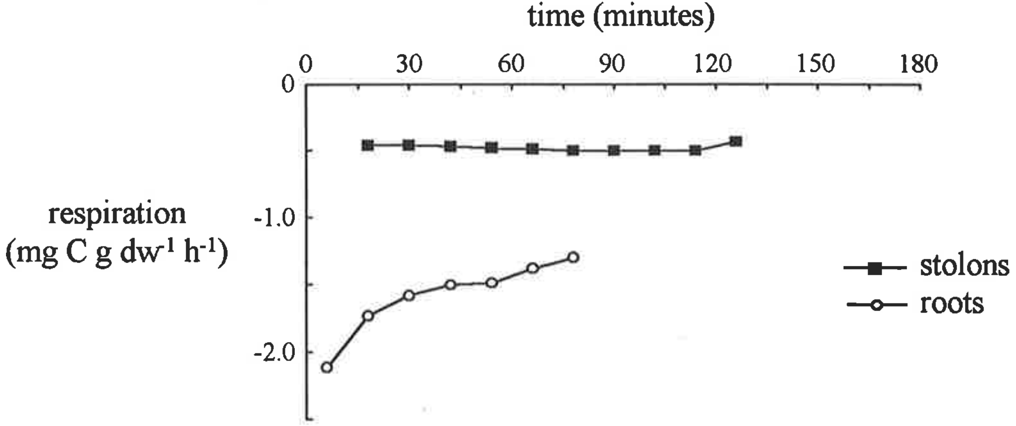
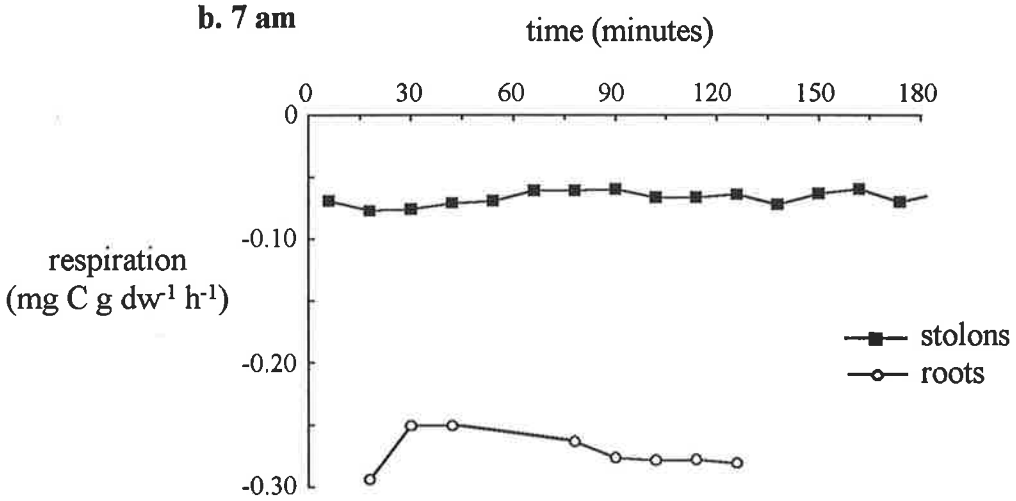

Carbon assimilation (mg C g dw^{-1} h^{-1})
-1.0
-0.5
0
0.5
1.0
1.5
2.0
Depth (cm)
0
10
20
30
40
50
60
70
80
Net photosynthesis
24 cm
82 cm
Dark respiration
24 cm
82 cm
Irradiance
0
50
100
Irradiance (% of subsurface)

Fig. 8.9. Root and stolon respiration in late a. afternoon and b. early morning. Data points are the mean rate over 12 mins. Note different scales on the y-axes.

a. 5 pm


time (minutes)
0
30
60
90
120
150
180
0
-1.0
-2.0
respiration
(mg C g dw^{-1} h^{-1})
stolons
roots

b. 7 am


time (minutes)
0
30
60
90
120
150
180
0
-0.10
-0.20
-0.30
respiration
(mg C g dw^{-1} h^{-1})
stolons
roots

Chapter 9

Canopy assimilation model and daily carbon balance in *Vallisneria americana* in turbid water

9.1 Introduction

The effects of turbidity on photosynthesis and growth in submersed macrophytes has been widely examined (cf. Chapters 7 and 8, and references cited therein). The degree to which carbon fixation is reduced in water of poor clarity is dependent upon the depth distribution of leaves relative to the vertical light gradient. Photosynthetic activity is greatest within the upper strata of the canopy, with negligible fixation occurring below 1 m or less. For example, Adams *et al.* (1974) found that eighty-three percent of assimilation by *Myriophyllum spicatum* plants growing in water 2.4 m deep in Lake Wingra, USA, occurred within 0.5 m of the surface (see also van der Bijl *et al.*, 1989; Schwarz and Howard-Willimas, 1993). Plants which are unable to place a sufficient proportion of their canopy at the surface are likely to have a low or negative carbon balance, and consequently growth and recruitment. Dennison (1987) found a strong correlation between modelled carbon assimilation and leaf production in eelgrass *Zostera marina* and concluded that the model could be used to predict growth given a known mean annual irradiance profile for the water column. However, other studies have suggested models based on mean irradiance profiles or mean rates of downwelling extinction overestimate the colonisation depth or productivity of submersed macrophytes, as even short periods of reduced light penetration (which are masked by averaging) cause large declines in growth (Wetzel and Neckles, 1986; Zimmerman *et al.*, 1991, 1994; Carter *et al.*, 1996). These declines are disproportionately large due to the non-linear P-I response; a reduction in 50 µmol m^{-2} s^{-1} over the light-limited part of the P-I curve reduces photosynthesis much more so than an extra 50 µmol m^{-2} s^{-1} increases photosynthesis at photosaturating irradiances.

In this chapter, the relationship between oxygen evolution in the short-term and growth and recruitment over the medium-term in *Vallisneria americana* is investigated. I hypothesised that plants with high modelled canopy carbon assimilation would exhibit high RGR, NAR, and shoot and leaf recruitment. Conversely, negative RGR and low recruitment is predicted to be due to a low or negative carbon balance. To test this hypothesis, daily canopy carbon assimilation in plants in high and low-light environments was modelled, and compared to their performance in the pond experiment (Chapter 7).

Photosynthesis was examined by oxygen evolution in leaf pieces in the laboratory (cf. Chapter 8). Daily assimilation was modelled using the Jassby and Platt (1976) hyperbolic tangent function and mean hourly irradiances. Daily sum canopy assimilation was calculated by integrating across depth ranges over the day. The effect on daily assimilation estimates of varying *v.* mean irradiances was examined using recorded hourly irradiances for each day of the study and mean hourly irradiances averaged over the experiment. Varying irradiances were hypothesised to reduce assimilation due to the non-linearity of the P-I relationship.

Carbon assimilation in plants with a dense surface canopy was compared to that in plants with most of their leaf biomass near the sediments (and below the penetration of compensation-level irradiances). Night-time leaf, and 24 h root and stolon respiration were also measured. A simple whole-plant daily carbon balance was then constructed, incorporating canopy assimilation, nightly leaf, root and stolon respiration

The principal aim of the investigation of photosynthesis and respiration in *Vallisneria* was to determine the influence of depth in the canopy and leaf age on carbon assimilation (cf. Chapter 8). These data were also used to model canopy assimilation. Consequently fewer data were available for modelling the whole-plant carbon balance than daytime canopy assimilation in these plants, and the approach to modelling whole-plant carbon balance, rather than actual model predictions, are emphasized.

9.2 Methods

9.2.1 Daily canopy carbon assimilation

Carbon assimilation in plants at depths 24 cm and 82 cm in water with a downwelling extinction coefficient of K_d 12.59 m^{-1} was modelled using data from Chapter 8 (cf. Fig. 8.8). For each daylight hour (7 am-7 pm), assimilation (mg C) was calculated as the product of the rate of net photosynthesis and the dry weight in 5 (shallow) or 9 (deep) depth ranges. The rate of net photosynthesis P_{net} per depth range for each hour was calculated from the hyperbolic tangent model of Jassby and Platt (1976) (see also van der Bijl *et al.*, 1989; Zimmerman *et al.*, 1994) using a mean hourly irradiance (I) profile over the day (cf. Fig. 8.2):

$$P_{net} = P_{max(gross)} * \tanh(\alpha I / P_{max(gross)})_{(12\text{ h})} + R \qquad (1)$$

where $P_{max(gross)}$ is the maximum net photosynthetic rate plus the absolute value of dark respiration R (hence numerically equivalent to photoassimilation, cf. Titus and Adams, 1979). Values of α were estimated from the linear relationship with ln depth (Fig. 8.6). The linear relationship between α and ln depth was determined at 25°C, and measurements of $P_{max(gross)}$ at 12°C (Fig. 8.8). However, as α is regarded as being generally temperature-insenstive (van der Bijl *et al.*, 1989), this relationship was considered satisfactory for the purposes of this model. Numbers of leaf pieces were 4-10 per depth, except for the shallowest four depth ranges in deep plants where only one leaf occurred.

P_{net} was measured at irradiances simulating the calculated *in situ* solar noon irradiance $I_{in\ situ}$ at the midpoint of each depth range (Table 8.2). This rate was considered the maximum achieved photosynthetic rate at that depth. Rates were then measured at a photon flux density of 1175 µmol m^{-2} s^{-1} to determine if higher P_{max} rates were possible. If so, this indicated that light-saturation was not reached at $I_{in\ situ}$, and P_{net} at 1175 µmol m^{-2} s^{-1} was used for P_{max}. This was generally true for photosynthetic tissues in very low light. Attenuation by the canopy was not incorporated in the model. No indication of photoinhibition was observed at photon flux densities of 1175 µmol m^{-2} s^{-1}.

Mean hourly incoming solar irradiance was recorded on a Li-Cor quantum sensor (see Section 7.3.3 and Fig. 8.2) and the photosynthetically active radiation received at the midpoint of the depth ranges calculated from the Lambert-Beer relationship assuming 29% surface reflectance (see Section 7.4.1).

9.2.2 *Estimation of the vertical distribution of canopy biomass*

The depth distribution of leaf biomass relative to the light gradient was determined by estimating the leaf length in depth ranges from the water surface to the sediments. An expression relating leaf length to dry weight was then used to determine the vertical distribution of leaves. Destructive harvests of leaves within the depth ranges was not a feasible alternative as all plants were required for the determination of growth and reproduction at the end of the experiment.

A novel method of determining the distribution of leaf length across depth ranges was established using the following procedure. The following expression relates the leaf length to any point below the surface L as a function of water depth:

Leaf length $L = 3.10-1.46*(\text{depth below surface})+1.03*(\text{depth to sediments})$ (units cm)

($r^2=0.998$, $P<0.0001$). For example, the length of a leaf falling within the depth range 4-8 cm below the surface is calculated as $L_{4\ cm} - L_{8\ cm}$. It was determined by measuring the leaf length from the sediment to the point at which the leaf was 1, 3, 6, 8 and 12 cm below the water surface. Data were collected from 16 leaves which were positioned at depths from 11 to 90 cm. Leaf lengths were 15-90 cm. As *Vallisneria* leaves become less flexible with age, and hence influence the curve that they describe below the surface, leaves of varying ages were used.

Regardless of the length of a leaf lying along the surface, it remained within 10° of vertical below 12 cm under the surface, and was considered vertical below that depth. If the leaf length was >10% longer than the water depth, length did not influence the curvature below the surface. Measurements were made in an aquarium for depths 11-40 cm, and an outdoor pond for depths 40-90 cm. Individual leaves were held on the bottom with lead weights. The relationship was determined using least-squares multiple linear regression (SYSTAT, 1990).

The corresponding leaf biomass falling within each depth range was then calculated using the following relationship between leaf length and dry weight:

Dry weight (g) = 0.0025*leaf length (cm) ($r^2=0.944$, $P<0.001$)

For each depth, the relationship was established with 15-25 leaves of varying ages, lengths and widths.

9.2.3 Whole plant daily carbon balance

A basic daily carbon balance model was constructed by subtracting night-time leaf respiration and 24 h root and stolon respiration from modelled canopy assimilation. This allowed an investigation of the relative importance of each of the components (daytime assimilation, night leaf respiration and below-ground respiration) in determining growth.

Night leaf respiration (7 pm-7 am) for each depth was estimated as 40% of the dark respiration rate in leaves harvested during the day. This adjustment reflects reduced respiration through the night as sugar stores are depleted. Dawn respiration in root and stolon tissues in this experiment were typically 30-70% of late afternoon rates, and similar reductions in rate in leaves and roots through the night are reported for terrestrial species (Williams and Farrar, 1990; Mitchell *et al.*, 1991).

Twenty-four hour root and stolon respiration were calculated from rates presented in Table 8.4. Root respiration was more dynamic than stolon respiration and was assumed constant and high from 10 am-8 pm, and constant and low from 12 am-7 am (at the rates measured at 5 pm and 7 am, respectively). Rates were assumed to change linearly with time at other times. The 24 h mean rate of stolon respiration was calculated as the mean of 7 am and 5 pm rates.

Twenty-four hour carbon balances were expressed as change in dry weight, assuming structural carbon is 45% of tissue dry weight (Madsen and Sand-Jensen, 1991; Maberly, 1993). This allowed for the comparison of predicted RGR from short-term oxygen production measurements with observed RGR from the pond experiment (Chapter 7).

9.3 Results

9.3.1 Daily canopy carbon assimilation

Modelled daily assimilation for each depth range illustrates the rapid reduction in maximum rate with depth (Fig. 9.1). Assimilation in the surface canopy (depth 0-2 cm) in both shallow and deep plants was two to three times that at depth 2-4 cm. In shallow plants, only photosynthetic tissues within 15 cm of the surface are predicted to have positive net photosynthesis (Fig. 9.1a). Net photosynthesis is predicted to be positive in the uppermost 25 cm in deep plants (Fig. 9.1b). No net photosynthesis in the 15-25 cm depth range in shallow plants is due to the high respiratory demand of basal meristems. Photosynthesis is predicted to be saturated by 9 or 10 am in the upper 15 cm of the canopy in both shallow and deep plants.

Daily canopy assimilation was high and positive in shallow plants but negative in deep plants (Table 9.1). Assimilation summed over all depth ranges over 12 h is predicted to be 21.208 mg C in shallow plants and -2.219 mg C in deep plants. In the former, 1.550 g or 42.0% of the canopy biomass was within 2 cm of the surface and assimilated 23.4 mg C in 12 h. These surface canopy tissues received 78-100% of subsurface irradiances over most of the day. In contrast, daily assimilation in the surface canopy of deep plants was only 0.121 mg C in deep plants, due to much lower canopy biomass at the surface (0.007 g or 1.0%). In deep plants, 87% of the canopy was within 27 cm of the sediments. The daily carbon balance model predicts 2.184 mg C is lost per day in the 55-82 cm depth range. These data illustrate the importance of forming a surface canopy for maintaining a positive carbon balance in turbid waters. Deep inundation exacerbates the effects of rapid light extinction by reducing the proportion of the canopy receiving irradiances sufficient for net photosynthesis. This underlies the relationship between the proportion of the canopy receiving greater-than compensation level irradiances and RGR, and shoot and leaf recruitment determined in the pond experiment (cf. Fig. 7.16).

Modelled daily canopy assimilation data are in general agreement with observed growth data from the pond experiment (Table 9.2). Shallow plants, which had positive daily carbon balances, had positive relative growth rates and net assimilation rates (15 mg g^{-1} d^{-1} and 61 mg g^{-1} d^{-1}), and low and constant from 12 am-7 am (0.28 mg g^{-1} d^{-1}, cf. Fig. 8.9). Rates were assumed to decline by 0.4 mg C g dw^{-1} h^{-1} every hour from 8 pm-12 am, and increase by 10^{-6} g cm^{-2} d^{-1} respectively), and shoot and leaf recruitment. The negative canopy carbon balance in deep plants correlates well with the observed negative relative growth rate and net assimilation rate (-2 mg g^{-1} d^{-1} and -16 x 10^{-6} g cm^{-2} d^{-1}), zero shoot recruitment and negligible leaf production.

9.3.2 *Night-time leaf and 24 h root and stolon respiration*

Sum night-time leaf respiration (7 am-7 pm) is predicted to be 12.578 mg C in shallow plants and 0.949 mg C in deep plants (Table 9.3). Both values represent substantial

Table 9.1. Modelled daily canopy carbon assimilation for shallow and deep *Vallisneria* plants. Leaf net photosynthesis P_{net} and dark respiration R are determined for five or nine depth ranges. Carbon assimilation was calculated from Eq (1) relating $P_{max(gross)}$, irradiance and R to P_{net} (Fig. 9.1) and the relationship between α and ln depth (see Fig. 8.6). Daily P_{net} is calculated using the mean daily irradiance profile (cf. Fig. 8.2).

				Net photosynthesis P_{net}		
				P_{net} (mg C g dw^{-1} h^{-1}) at irradiances		
Depth (cm)	†Irradiance $I_{in\ situ}$ (µmol m^{-2}s^{-1})	Leaf dry weight (dw) (g)	% dw	$I_{in\ situ}$ (µmol m^{-2}s^{-1})	1175 (µmol m^{-2}s^{-1})	Daily $^{a}P_{net}$ (12 h) (mg C)
a. Shallow plants (rooting depth=24 cm)						
0-2	528	1.550	42.0	1.602	*1.687	23.400
2-4	326	0.177	4.8	0.679	*0.776	1.065
4-8	237	0.368	10.0	*0.757	0.737	1.776
8-15	120	0.643	17.4	*0.521	0.520	1.123
15-25	47	0.950	25.8	-0.525	*-0.347	-6.159
Total		**3.688**				**21.208**
b. Deep plants (rooting depth=82 cm)						
0-2	528	0.007	1.0	*1.763	1.301	0.121
2-4	326	0.002	0.3	*0.600	0.310	0.007
4-8	237	0.003	0.5	0.746	*0.456	0.017
8-15	120	0.008	1.2	*0.412	0.400	0.017
15-25	47	0.015	2.2	*0.313	0.192	-0.003
25-35	9	0.015	2.2	0.049	§*1.280	-0.064
35-45	3	0.015	2.2	-0.149	*0.316	-0.060
45-55	1	0.023	3.4	-0.149	*0.180	-0.056
55-82	0.1	0.591	87.0	-0.229	*0.089	-2.184
Total		**0.679**				**-2.219**

† Simulated noon irradiance at the midpoint of the depth range (see Table 8.2).

* Rates of net photosynthesis used for determining daily photosynthesis (higher of the two).

[a] See Eq (1)

§ High rate in the tip of a young leaf with high chl *a* concentration.

Table 9.2. Comparison of modelled canopy assimilation with growth and recruitment in shallow and deep *Vallisneria*. NAR is the net assimilation rate and RGR the relative growth rate (cf. Chapter 7). Night leaf respiration and root and stolon respiration are not included in modelled canopy assimilation. Canopy assimilation data are from Table 9.1.

Treatment	% leaf dry weight within 2 cm of surface	Daily canopy assimilation	Growth and recruitment parametres			
			RGR	NAR	Shoot recruitment	Leaf recruitment
		(mg C)	(mg g^{-1} d^{-1})	(10^{-6} g cm^{-2} d^{-1})	(over 102 d)	($week^{-1}$)
Shallow (24 cm)	42	21.208	15 ± 1	61 ± 4	mean=2.5 range=0-6	0.53
Deep (82 cm)	1	-2.219	-2 ± 1	-16 ± 6	0	0.03

proportions of daytime assimilation: 60% and 43% for shallow and deep plants, respectively.

Modelled 24 h root respiration was 10 times that of stolon respiration in shallow plants, and 15 times in deep plants (Table 9.3). The large diel variation in root respiration is shown for shallow plants in Fig. 9.2. Rates were assumed constant and high from 10 am-8 pm (2.0 mg g^{-1} d^{-1}), and low and constant from 12 am-7 am (0.28 mg g^{-1} d^{-1}, cf. Fig. 8.9). Rates were assumed to decline by 0.4 mg C g dw^{-1} h^{-1} every hour from 8 pm-12 am, and increase by 0.5 mg C g dw^{-1} h^{-1} every hour from 7 am -11 am. The magnitude of the change in rates was determined from Fig. 8.9 in which root respiration declined by 0.4 mg C g dw^{-1} h^{-1} every hour. The rate at which respiration increased from 7-11 am was assumed to be higher (0.5 mg C g dw^{-1} h^{-1} every hour).

9.3.3 Effects of varying v. mean irradiance on modelled canopy assimilation

Modelled canopy assimilation data presented in Fig. 9.1 and Tables 9.1 and 9.3 are based on the mean hourly irradiance profile over the 3 month experiment. However, considerable variation in subsurface irradiance occurred over the period due to transient cloud cover and seasonal variation in solar radiation (Fig. 8.2). For example, mean hourly irradiances were in the range 30-1250 μmol m^{-2} s^{-1} from 1-2 pm, whilst the mean daytime irradiance, averaged over the experiment, was 589 μmol m^{-2} s^{-1}. Given the non-linear relationship between photosynthesis and irradiance (cf. Eq (1), and Zimmerman *et al.*, 1994), predictions of mean daily canopy assimilation may be expected to be different using varying hourly irradiances (*varying irradiances*) (with assimilation summed over 102 days), and the mean irradiance for each hour, averaged over the experiment (*mean irradiances*). When this comparison is made, the difference between the two values for mean daily assimilation was found to depend on the depth distribution of canopy biomass. In shallow plants modelled carbon assimilation was 9% lower using *varying irradiances* compared to *mean irradiances*. The reduction results from the interaction of the non-linear P-I response and the high proportion of the canopy at the surface (42% of plant dry weight, cf. Table 9.2). Net photosynthesis was saturated at irradiances greater than c. 50 μmol m^{-2} s^{-1} (Table 8.3). Thus, irradiances greater than I_k, which occurred at the surface from 9 am-5 pm (Fig. 9.1), do not appreciably increase photosynthesis in

Table 9.3. Whole-plant carbon budget for *Vallisneria* plants in shallow and deep water. Sum daytime canopy assimilation across all depth ranges is presented as a single value (see Table 9.1 for calculation). Night-time leaf respiration was assumed to be 40% of daytime dark respiration.

a. Shallow plants (rooting depth=24 cm)

		Respiration *R*	
Depth (cm)	Leaf dry weight (g)	*R* rate (mg C g dw^{-1} h^{-1})	Respiration (*R* rate x dw x time[a]) (mg C)
Leaf			
0-2	1.550	-0.268	-4.985
2-4	0.177	-0.245	-0.520
4-8	0.368	-0.260	-1.148
8-15	0.643	-0.250	-1.929
15-25	0.950	-0.299	-3.410
Leaf	**3.688**		**-11.992**
Root	[b]0.430	[c]-	**-12.578**
Stolon	0.170	-0.309	**-1.261**
Total plant	**4.288**		

Modelled net photosynthesis =21.208 mg C (cf. Table 9.1)

Daily carbon balance $= P_{net(12\text{ h})} + R_{leaf(12\text{ h})} + R_{root(24\text{ h})} + R_{stolon(24)}$

$= (21.208 - 11.992 - 12.578 - 1.261)$ mg C d^{-1}

$= -4.623$ mg C per 4.288 g dw d^{-1}

$= -1.078$ mg C g dw^{-1} d^{-1}

∴ Predicted whole-plant relative growth rate = -2.4 mg dw g dw^{-1} d^{-1} (assuming structural carbon is 45% of dry weight (Madsen and Sand-Jensen, 1991; Maberly, 1993))

Observed whole-plant relative growth rate = 15 mg dw g dw^{-1} d^{-1}

---

[a] Dark respiration is calculated over 12 h for leaves and 24 h for roots and stolons.

[b] Leaf dry weights are estimates, below-ground dry weights are observed datum.

[c] 24 h root respiration was modelled on an hourly basis (see Fig. 9.2).

Table 9.3. (continued).

b. Deep plants (rooting depth=82 cm)

Depth (cm)	dry weight (g)	Respiration R	
		R rate mg C g dw $^{-1}$ h^{-1}	R (R rate x dw x time) mg C
Leaf			
0-2	0.007	-0.153	-0.013
2-4	0.002	-0.164	-0.004
4-8	0.003	-0.137	-0.005
8-15	0.008	-0.160	-0.015
15-25	0.015	-0.153	-0.028
25-35	0.015	-0.175	-0.032
35-45	0.015	-0.130	-0.023
45-55	0.023	-0.076	-0.021
55-82	0.591	-0.114	-0.808
Leaf	**0.679**		**-0.949**
Root	0.120	-	**-3.240**
Stolon	0.090	**-0.103**	**-0.222**
Total plant	**0.889**		

Modelled net photosynthesis =-2.219 mg C

Daily carbon balance = $P_{net(12\ h)} + R_{leaf(12\ h)} + R_{root(24\ h)} + R_{stolon(24)}$

= (-2.219 - 0.949 - 3.240 - 0.222) mg C

= -6.630 mg C per 0.889 g dw^{-1} d^{-1}

= -7.458 mg C g dw^{-1} d^{-1}

∴ Predicted whole-plant relative growth rate = -16.6 mg dw g dw^{-1} d^{-1}

Observed whole-plant relative growth rate = -3 mg dw g dw^{-1} d^{-1}

approximately half of the canopy. However, throughout the water column irradiances less than I_k, which were experienced frequently on cloudy days, considerably reduced photosynthesis due to the light limitation of photosynthesis. The reduction in assimilation in the surface canopy, when varying irradiances were $<I_k$, was larger than the increase in carbon fixation due to higher penetration in lower canopy strata at irradiances >589 μmol m^{-2} s^{-1}. For this reason a variable light environment is likely to favour plants with a high proportion of the canopy somewhat below the surface where less of the canopy is saturated at 'mean' irradiances.

The increase in modelled assimilation in plants at 82 cm under varying irradiances was negligible compared to mean irradiances however (1%) (data not shown), as 87% of the biomass was within 27 cm of the sediments (55-82 cm, Table 9.1). Even at the highest recorded subsurface irradiance of 1250 μmol m^{-2} s^{-1}, the irradiance at 55 cm is only 1.2 μmol m^{-2} s^{-1}; below the compensation irradiance for *Vallisneria*

9.3.4 Whole plant carbon balance

The simple whole plant balance suggests a negative daily value for both shallow and deep plants (Table 9.3). Comparisons of modelled and observed whole-plant RGRs from the pond experiment (Chapter 7) indicate that the model grossly underestimated biomass production in both shallow (modelled; -2.4 mg g^{-1} d^{-1} and observed; 15 mg g^{-1} d^{-1}) and deep plants (modelled; -16.6 mg g^{-1} d^{-1} and observed; -3 mg g^{-1} d^{-1}). Overestimation of night-time leaf respiration and underestimation of assimilation by the leaves on the surface are the most probable reasons for the underpredictions.. The carbon balance is based on mean irradiances for each hour over the experiment. When calculated as the sum daily assimilation using varying irradiances over the experiment, the whole plant carbon balance was closer to the observed RGR but still negative (-0.5 mg g^{-1} d^{-1}).

9.4 Discussion

9.4.1 Approaches to modelling carbon assimilation in submersed macrophytes

The canopy carbon assimilation balance and whole plant carbon budget presented in this chapter are of intermediate complexity compared to published models relating the influence of photon flux density on photosynthesis or growth in submersed macrophytes.

These range from empirical relationships relating the maximum colonisable depth to Secchi depth or K_d (Spence, 1982; Chambers and Kalff, 1985; Schwarz *et al.*, 1996; Middelboe and Markager, 1997), through simple models predicting the depth limits of seagrasses from the minimum necessary daily duration of compensating or saturating irradiances (in hours; H_{comp} and H_{sat} respectively; Dennison and Alberte, 1982; Dennison, 1987; Zimmerman *et al.*, 1994), to more computationally complex simulation models driven by a range of biotic and abiotic inputs and density-dependent feedback mechanisms (Titus *et al.*, 1975; Wetzel and Neckles, 1986; Scheffer *et al.*, 1993). The calculation of daily carbon balances by multiplying H_{sat} by the photosaturation rate, as used in modelling seagrass production (cf. Dennison, 1987), is unlikely to prove useful in the study of submersed macophytes of turbid rivers. This is principally due to growth depending upon the depth distribution of biomass relative to the light gradient, rather than simply the time that saturating irradiances occur at the leaf tips.

The model employed in this study was designed to allow a comparison of carbon assimilation in the canopy of *Vallisneria* plants grown at different depths in turbid water. In particular, this allowed an investigation of the depth distribution of photosynthetic activity over the water column, thus complementing the examination of plant performance as a function of the average water-column irradiance, $\bar{I}$ (cf. Chapter 7). Daily carbon assimilation in the canopy was modelled using the following inputs: the depth distribution of leaf biomass, the irradiance received at those depths over the day, a relationship between photosynthetic efficiency α and depth, the maximum rate of net photosynthesis P_{net} for each depth, and the dark respiration rate R for each depth. By including data on night leaf and 24 h root and stolon respiration, a simple daily carbon balance was also determined.

Measurements of oxygen production were used rather than a ^{14}C technique to allow dark respiration to be determined. As the determination of the depth distribution of photosynthetic activity was the prime aim of the study, measurement of the production of oxygen in leaf segments from a range of depths in the canopy was required, rather than in intact shoots *e.g.* Dunton and Tomasko (1994) and Fourqurean and Zieman (1994). Whilst proceedurally less intrusive, the whole-shoot method can not be used to investigate the variation in net photosynthesis through the canopy. This is particularly so in turbid water where the irradiance received at the leaf tip can be several orders of magnitude higher than that received at the base (Table 8.2).

9.4.2 Carbon assimilation in the canopy of Vallisneria

Modelled canopy assimilation indicates that *Vallisneria* plants which do not develop a significant surface canopy in turbid water are unable to maintain a positive carbon balance. Assimilation was high in plants grown at depth 24 cm, but negative at 82 cm (21.208 *v.* -2.219 mg C per day, respectively, Table 9.1). This was due to the establishment of a surface canopy in the former, in which an estimated 42% of leaf biomass was within the depth range 0-2 cm (Table 9.2). In comparison, only 1% was at the surface in deep plants, but 87% below the depth of I_c-level irradiances.

These data are in broad agreement with the performance of *Vallisneria* at these depths. Plants at 24 cm had higher RGR and NAR, and leaf and shoot recruitment (Table 9.2). Plants at 82 cm had negative RGR and NAR, and minimal recruitment. This confirms that the RGR-$\bar{I}$ and NAR-$\bar{I}$ responses (Figs 7.5 and 7.6) are long-term manifestations of the sum P-I responses of individual leaves of all ages at all depths over diel and seasonal irradiance regimes.

Dennison (1987) and Dennison and Alberte (1982) determined correlations between canopy carbon assimilation and leaf production in the seagrass *Zostera marina*. In the latter study, the daily carbon balance was calculated as H_{sat} x photosynthetic rate. As a significant proportion of the canopy in *Vallisneria* in the Murray is at sub-saturating irradiances, the procedure of Dennison (1987) is likely to significantly underestimate assimilation. The modelling approach using the P-I response of Jassby and Platt (1976) used in this chapter is likely to prove more accurate in turbid conditions.

Investigations of the depth distribution of photosynthetic activity in submersed macrophytes have generally used similar-sized depth increments when stratifying the canopy. Titus *et al.* (1975) and Titus and Adams (1979) used 30 cm depth classes in studies of *Myriophyllum spicatum* and *Vallisneria americana*, whilst Adams *et al.* (1974) used 10 cm classes in a complementary study of *M. spicatum*. Similar-sized depth increments may be approriate in waterbodies where light penetration is high, as in these northern temperate lakes in Wisconsin, but are likely to mask the rapid changes in photosynthesis which occur with depth in turbid water (Fig. 8.8). Depth increments which reflect the approximately exponential decay in irradiance with depth, as used in this chapter, are likely to produce more accurate estimates of canopy assimilation.

7.4.3 Effects of reducing the variability of irradiance data on carbon budgets

In shallow plants modelled canopy assimilation based on the mean daily irradiance profile was 9% higher than when based on the highly variable recorded irradiances. The implication is that modelled maximum colonisable depths of submersed macrophytes in very variable aquatic environments are overestimated for canopy forming species when based on mean light profiles (Wetzel and Neckles, 1986; Zimmerman *et al.*, 1994). Plants with a large proportion of their biomass receiving less-than saturating intensities are suggested to benefit from a variable light field, particularly if physiologically disposed to maximise light capture from short-term light flecks (Kueppers and Schneider, 1993; Kursar and Coley, 1993). In deep plants, this increase was negligible (1%) as 87% of the canopy biomass was below the depth of penetration of greater-than I_c-levels of irradiance at even the highest subsurface intensities. The observed colonisation depth of eelgrass *Zostera marina* was considerably less than that predicted from mean daily irradiances and P-I profiles in San Francisco Bay (Zimmerman *et al.,* 1991). The authors conclude periods of low light penetration due to transient high turbidity events reduced growth substantially. Also, in modelling the effects of irradiance on *Zostera marina*, Wetzel and Neckles (1986) found productivity was very sensitive to even minor variation in irradiance, with the potential to cause plant mortality. Failure to include such variability by instead using average irradiance values may overestimate submersed macrophytes photosynthesis and growth.

If carbon budgets are to be of use in the research and management of submersed macrophytes, measurements of light penetration of sufficient temporal and spatial density must accompany the development of simulation models. At present, water resource agencies responsible for managing submerged vegetation in the Lower Murray have no systematic and regular sampling prodcedure for collecting underwater irradiance data. Zimmerman *et al.* (1994) argue that continuous monitoring of irradiance may be necessary (and certainly feasible given current data logging technology) for the accurate prediction of seagrass growth in Monterey Bay, California. Daily or hourly logging of irradiance in the

Murray would allow the implementation of growth models for the adaptive management of flows for aquatic vegetation; either using the approach detailed in Chapter 7 or the daily carbon balance presented in this chapter.

9.4.4 Whole plant carbon balance

The whole-plant carbon balance underestimated RGR in both shallow and deep plants. Methodological artefacts and assumptions based on relatively few datum, as well as inherent difficulties in estimating long-term growth from short-term carbon balances, are suggested as the reasons for this discrepancy.

Night leaf respiration was assumed to be 40% of dark respiration in leaves harvested during the day. After cutting, leaf pieces were pre-treated to irradiances 20-80 μmol m^{-2} s^{-1} for 1-4 h prior to measuring dark respiration to allow for wound respiration. Increased Rubisco activity and accumulation of sugars over this period may have produced dark respiration rates greater than *in situ* levels. By virtue of the large contribution of leaves to total plant biomass (77-91%, Table 7.5), even minor discrepancies in night leaf respiration estimates are bound to significantly affect the carbon balance. Measurements of the change in respiration between dusk and dawn are necessary to increase the models' accuracy.

Whilst roots constitute only 6-16% of plant biomass (Table 7.5), their high respiration rate (up to 2.1 mg C g dw^{-1} h^{-1}, which is equivalent to the maximum rate of net photosynthesis) means accurate measurements of rates over 24 h are required. Diel variations in rates were large: from 2.1 mg C g dw^{-1} h^{-1} at 5 pm to 0.3 mg C g dw^{-1} h^{-1} at 7 am. Rates were found to vary with the age of the attached shoot and the proportion of young *v.* old roots (data not shown). Rapid changes in root respiration associated with changing irradiances have been examined primarily in crops *e.g.* Williams and Farrar (1990) observed a 60% reduction in barley *Hordeum distichum* root respiration within 6 h of complete shading of the leaves.

The age distribution of leaves in shallow plants varied and was not always similar to that in plants used for P-I measurements. Frequently the proportion of young to mid-aged leaves was higher. As these had higher P_{max}:R than mean values underpinning the carbon balance (though not used directly), the predicted RGR would have been lower than recorded rates.

The budget did not incorporate losses of carbon from exudation nor biological processes such as senescence, self-shading or sexual reproduction (Titus *et al.*, 1975; Scheffer *et al.*, 1993). At present such data is largely unavailable for *Vallisneria*, and it may be argued that a more profitable approach to modelling may be that detailed in Chapter 7. Indeed, Scheffer *et al.* (1993) conclude their discussion on modelling submersed vegetation with the remark "...that proper predictive modelling of submerged plant dynamics should be impracticable in general". It should be noted that their rather pessimistic conclusion referred to the difficulty in attempting to model a generalised response of P_{max} to factors such as inorganic carbon and nutrients. If only one species were to be modelled, however, the determination of the effects of such factors on P_{max} would be more feasible.

The RGR-$\bar{I}$ response determined for *Vallisneria* (Chapter 7) presents a viable alternative to modelling growth in submersed macrophytes using carbon balances. Both rely on inputs of irradiance, depth and downwelling extinction, and can predict maximal growth rates and minimum light requirmements. However, the RGR-$\bar{I}$ response also incorporates the effects of biological processes such as senecence and sexual reproduction, and, at least under the experimental conditions employed in the *Vallisneria* study, gave good predictive power whilst making no assumptions regarding the depth distribution of canopy biomass.

9.4.5 Improvements to the carbon balance model

The model presented in this chapter presents a simple but effective framework for investigating the depth distribution of photosynthesis and respiration in submersed macrophytes, and simulating plant growth. The following improvements to input data would increase the model's accuracy in simulating the daily carbon balance in *Vallisneria*:

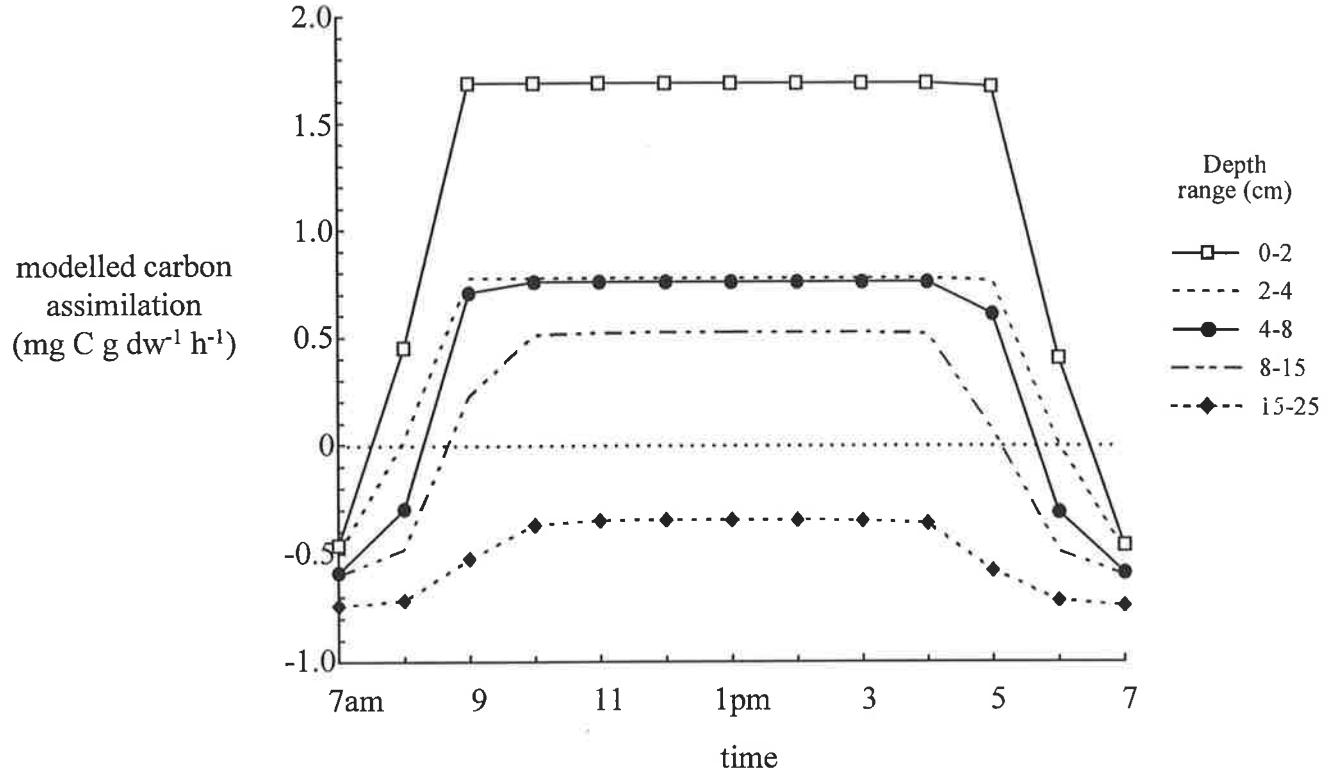
- Measurements of respiration in leaves during the night. Considerable variation in the estimated loss of carbon during the night can be introduced by minor changes in the respiration rate as leaves represent a high proportion of total biomass (77-91%, Table 7.5)

- Determination of a relationship between photosynthetic efficiency α and depth which accounts for changes in α with leaf age (Figs 8.4 and 8.6). To be of greatest accuracy, such a relationship may need to incorporate a measure of the frequency of leaves of varying ages.

- P-I characteristics of leaf tissue in the surface canopy change with the residence time at the surface. For example, values of $P_{max(gross)}$ along the part of the leaf at the surface of up to three times that where the leaf first reached the surface were found. As the proportion of total leaf biomass in the surface canopy can be high, such variation needs to be included.
- The influence of leaf orientation and inclination on P-I characteristics require investigation (Fourqurean and Zieman, 1991; Stockle, 1992).
- Measurements of photosynthetic and respiratory quotients (mol 0_2 evolved/ mol C fixed) for the study species.
- More accurate estimations of $P_{max(gross)}$ are required than are possible using only two irradiances per tissue.

Figure 9.1. Modelled canopy carbon assimilation at various depths in the canopy in a. shallow and b. deep plants. Assimilation over the day is calculated using the hyperbolic tangent model of Jassby and Platt (1976) (Eq (1)). The model is based on the recorded mean daily irradiance profile averaged over the experiment. Integrated daily assimilation for each depth is shown in Table 9.1.

a. Shallow (24 cm)



b. Deep (82 cm)

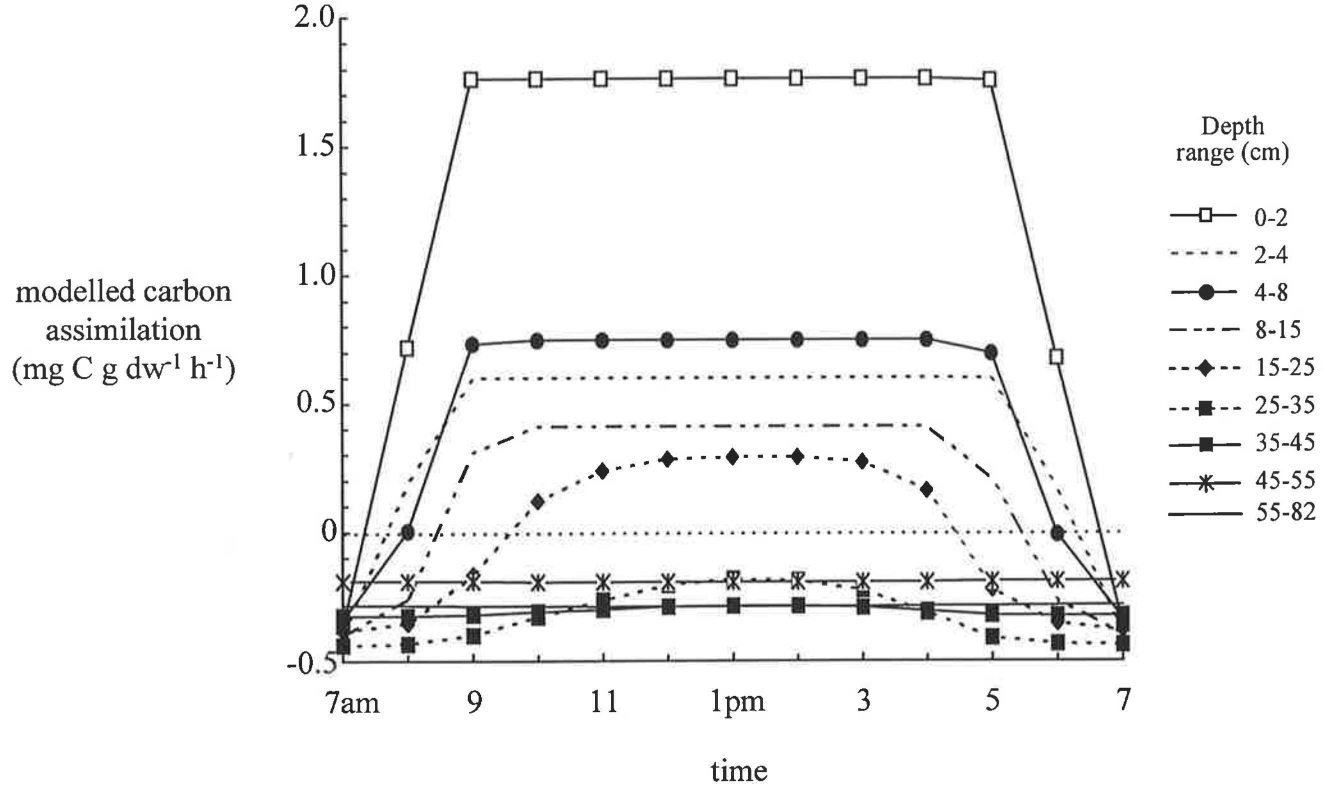
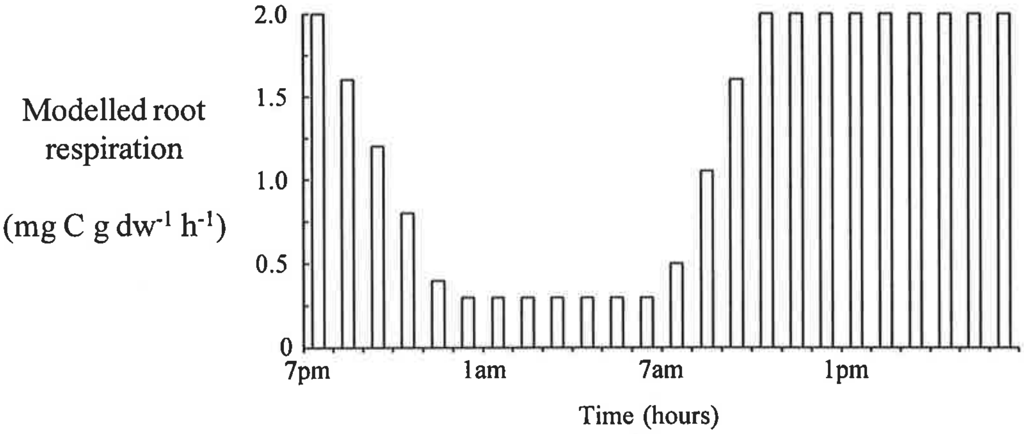


Figure 9.2. Modelled 24 h root respiration based on data in Fig. 8.9 (see text).


Modelled root respiration
(mg C g dw^{-1} h^{-1})
2.0
1.5
1.0
0.5
0
7pm
1am
7am
1pm
Time (hours)

Chapter 10

A field study of the effects of water level variability on growth in *Vallisneria americana*

10.1 Introduction

Submersed vegetation was shown to occur primarily in the lower reaches of weir pools of the Lower Murray in Chapters 2 and 3. These reaches present a hydrologically stable environment for desiccation-intolerant species as *Vallisneria*, *Potamogeton* spp and some *Myriophyllum* spp during low-flow periods (Fig. 10.1). Such species require water for support and have negligible structural tissues. Water loss is rapid when plants are exposed due a reduced cuticle and thin leaves (Sculthorpe, 1967). With increasing distance upstream of each weir, the influence of weir operations over water levels decreases, and the littoral experiences larger, more frequent and more rapid changes in water level (Walker *et al.*, 1994; Chapter 2). Submersed species were found to occur infrequently in the mid and upper reaches of weir pools, where desiccation-resistant species such as *Phragmites australis*, *Bolboschoenus medianus* and several rhizomatous grasses were dominant.

Whilst a fall in water level may expose plants and cause desiccation, inundation with turbid water reduces the penetration of irradiances necessary for net photosynthesis (Kimber *et al.*, 1995a). Reductions in photosynthesis and growth with depth have been reported for *Vallisneria* in Chapter 7 and by Titus and Adams (1979), and generally for submersed species by Spence (1982) and Chambers and Kalff (1985). Thus submersed species must tolerate both exposure and low-light conditions in the Lower Murray, particularly in the upper reaches of weir pools where the elevation range corresponding to suitable growth conditions is highly constrained.

This chapter contrasts the survival, shoot and leaf recruitment, and biomass production in potted *Vallisneria americana* plants in stable and variable water-level regimes in the Lower

Murray. A field experiment was designed to test the hypothesis that performance is lowest in the variable regime. However, the results and discussion are presented only in brief as recruitment and biomass were confounded at the variable water-level site by wash from boats, overgrowth by filamentous algae and other factors, making interpretation of the data difficult. Nevertheless, the methods and experimental design employed are reported in detail to facilitate future studies.

A general discussion of the effects of flow regulation by weirs operated by SA Water is presented in Chapters 2 and 3. In this thesis, the term *water regime* is used as a broad descriptor of the different yet related aspects of hydrology, namely depth, change in water level, length and frequency of flooding and rates of change. Whilst this allows a more holistic approach to studying plant responses to flooding than water depth alone, an experimental approach was considered most informative if, so far as possible, only one or two aspects of the water regime were manipulated. In this experiment, the two aspects of water regime of most interest were changes in water level variability and depth. Hence water regime was manipulated by growing plants at different elevations relative to weir pool level (0.1, 0.5 and 1.0 m below pool level, Table 10.1) on the upstream and downstream side of Lock 1 (stable and variable water-levels, respectively). The impacts of these manipulations of water regime were considered to be most accurately interpreted by investigating plant responses to elevation and relative changes in water level. I tested the hypothesis that growth was greatest in the stable regime due to the absence of exposure. In addition, plants grown 0.5 m below pool level in this regime were hypothesised to exhibit the highest recruitment and biomass production across all treatments due to more favourable depth and light availability (cf. Fig. 3.6).

10.2 Materials and Methods

The experiment was conducted during a period of low flows in which the river remained below bankfull capacity (Figs 10.1 a and b). Repeated exposure in plants 0.1 m below pool level in the Murray's littoral produces short leaves and slows growth. Growth is most vigorous in the depth range 0.3-0.6 m, but declines below this as recruitment declines under low light (Chapter 7).

Water level variability upstream of the lock was considerably lower than that downstream of the lock over the study period, and seldom fell below pool level (Fig. 10.1b). For simplicity, these experimental treatments will be referred to as the *stable* and *variable* water-level treatments. These terms refer to contrasting points on a continuum of variation in river level during normal low-flow conditions, rather than absolutes.

Experimental sites were located in areas sheltered from wash as far as possible to control for wash from boats damaging plants. However, as shown below, this was not achieved for the variable treatment.

A site 10 km upstream of Lock 1 was chosen for the *stable* treatment, and a site 2 km downstream of Lock 1 as the *variable* treatment (Fig. 10.2). For the former, a small creek connecting a large backwater with the main channel at Sinclair Flat was used. The creek is 0.8-2 m deep and 4-10 m wide. Bankslope is between 40 and 75°. A log-jam and dense vegetation at the entrance prevented strong currents and waves entering the creek.

The variability in water levels caused by weir operations declines rapidly with distance downstream of weirs (Walker *et al.*, 1994; Blanch and Walker, in press). This necessitated a site for the variable treatment to be located within c. 5-10 km of the Lock. However, no sheltered creeks occurred in this reach as the water levels maintained by the barrages at the Murray Mouth are below the elevation at which creeks enter the channel during low flows (cf. Fig. 1.4). As a compromise, a site was chosen 2 km downstream of Lock 1 on the inner bend of the main channel. This afforded plants protection from the strong current and turbulence, and plants were located within a restricted-speed zone for boats (adjacent to 'Riverbanks Estate') in an attempt to reduce wash. River levels recorded by SA Water on the upstream and downstream of Lock 1 were assumed to be those experienced at the stable and variable treatments (*i.e.* a negligible change in water-level elevation between the weir and the sites).

Three replicate localities were used per site. In the variable treatment these were spaced every 50 m, but only every 10 m in the stable treatment due to a lack of suitable environs. The primary factor in the experiment was elevation relative to pool level, with water-level variability a nested factor. This was necessary as the effect of variability is dependent on depth (shallow plants will be affected more than deep plants by changes in level). Thus, the

Table 10.1. Elevations of pot surfaces relative to weir pool level for stable (upstream of Lock 1) and variable (downstream of Lock 1) water-level treatments. Plants at -0.1 m elevation relative to pool level are shallowest (sediment surface 10 cm below pool level).

Elevation relative to pool level[a] (m)	Elevation of pot surfaces (m AHD)	
	Stable treatment (upstream of Lock 1)	Variable treatment (downstream of Lock 1)
-0.1	3.10	0.65
-0.5	2.70	0.25
-1.0	2.20	-0.25

[a] The elevation of the design pool level on the upstream side of Lock 1 is 3.20 m AHD (Australian Height Datum, equivalent to mean elevation above sea level). Downstream of Lock 1, the pool level of 0.75 m AHD is maintained by the barrages at the Murray Mouth (171 km downstream) (see Fig. 1.1).

experimental design was 3 elevations x 2 levels of water-level variability x 3 replicate locations per variability level. Eight replicate plants were used per elevation x variability treatments.

Vallisneria shoots were harvested from a natural population growing in sandy-loam sediments in the littoral zone of the main channel adjacent to Sinclair Flat (depth 0.2-0.6 m, Fig. 10.2). Shoots consisting of leaves, stolons and roots were planted in 10 L pot bags (diameter 33 cm, depth 18 cm) filled with commercially-available sandy-loam. Leaf height was 0.2-0.7 m and shoot fresh weight 10-140 g. Roots and stolons were of similar length for all shoots. All shoots were female. Nutrients were supplied as in the pond expteriment. Plants were established for one month in shallow water (20-50 cm) in the backwater at Sinclair Flat. Water temperature was 11-14°C, noon surface irradiance 100-1500 μmol m^{-2} s^{-1} and turbidity 25-80 NTU.

Plants were allocated randomly to treatments. Half were transported in a covered trailer (distance 11 km) to the site downstream of Lock 1, and half were placed in the adjacent creek for the stable treatment. Plants were kept moist with hessian whilst in transit. To position the pot surface 0.1, 0.5 or 1.0 m below pool level pots were placed on a wire platform supported by steel posts. Bankslope was generally too great to place pots directly on the sediments. Platforms were constructed of steel wire (0.5 mm thick, mesh 50 mm x 50 mm; platform size 0.65 m x 1.80 m) with raised sides to secure pots in position. Each platform held eight pots. A trial experiment was completely grazed by birds. Thereafter waterbirds were discouraged by wire cages (25 mm galvanised wire mesh, 50 cm high, 65 cm wide and 1.80 m long) during both the establishment phase and experiment. Cages prevented entry from the top and all sides, but were open at the bottom. They were positioned so that the top was initially 5-10 cm above the water surface by being attached to the steel posts which supported the platforms. For plants at elevation 1.0 m, approximately a 0.5 m gap occurred between the bottom of the sides of the cage and the pots.

The experiment commenced on 6 June 1994. On this day the river level was 10 cm above pool level upstream of Lock 1, and 15 cm above downstream. Hence platforms were positioned respectively 10 and 15 cm lower relative to river level. The experiment lasted 7 months. Numbers of shoots and numbers of leaves per shoot were recorded every 14-28 days. Rapid light attenuation through the water column prevented censusing visually for the two deeper platforms. At low shoot density (over winter), numbers of shoots and leaves could be determined by touch. As shoot density increased it became necessary to remove pots from the platforms and place in the shallows for censusing. The rate of downwelling extinction, K_d, was determined on censusing occasions for each location.

Plants were harvested in summer (7 January 1995) by agitating in water with a 1 mm sieve at the site. These were then transported to the lab in sealed plastic bags. Tissues were then separated into leaves+peduncles+shoot bases, roots and stolons by flotation, then oven dried at 80°C to constant weight (72 h).

10.3 Results

10.3.1 Changes in water level in stable and variable treatments over the experiment

Over the seven month experiment, variation in water level was considerably greater downstream of Lock 1 than upstream (Fig. 10.1b). For example, the difference between minimum and maximum recorded level was 4 times greater in the former (-0.25 to 0.31 m downstream, and -0.02 to 0.11 m upstream). Fluctuations were more variable below than above the weir over both weekly and monthly time scales. From early June to mid July Pool 1 was maintained mostly above pool level, then fell to 10-25 cm below pool level from early August to late October. A rise in level occurred in November, followed by a return to 5-25 cm below pool level over the last 5 weeks of the study. Daily water level fluctuations downstream of the lock were more erratic when below pool level than when above, with frequent rises and falls of 20 cm over 3-5 days. Fluctuations above the weir were less erratic than below the weir. The rate of light extinction was in the range 2.2-5.1 m^{-1}, but generally 2.5-3.5 m^{-1}.

10.3.2 Survival

No plants survived in the shallowest depth (-0.1 m relative to pool level, Table 10.2) downstream of Lock 1. Plants were partly exposed for several days in mid-June, then almost continuously from mid-July. Infrequent wetting over spring maintained growth in a few shoots. In these, the basal meristem was afforded some protection from desiccation by the bases of the senesced leaves which, when chlorotic or brown, curled around the meristem. Essentially continuous exposure in late spring and summer killed all plants in this treatment. Shoot mortality occurred in 14-78 days after nearly-continuous exposure. Considerable difficulty was encountered in determining whether a plant was alive or dead. A basal meristem was often green and presumably capable of regrowth despite the majority of leaves being brown and few roots remaining. If no green tissues were visible with gentle parting of the brown leaf bases, the shoot was considered dead. Death probably occurred more quickly in the pots than in natural populations once the river level fell below the pot base.

Seven of the 24 plants at -0.1 m elevation in the stable treatment survived. Mortality occurred in plants supported by two of the three platforms from mid-spring as river levels temporarily fell below pool level. In these two platforms the pot surfaces were 1-4 cm shallower than in the third (in which all plants survived). This suggests the platforms were too shallow by several centimetres (see below).

At elevations -0.5 m and -1.0 m below pool level in both stable and variable treatments, the numbers of replicate plants remaining at harvest were less than 24 (Table 10.2). For plants in the variable treatment at -0.5 m, wash from boats killed most plants by damaging leaves, from exposure to air causing photo-oxidation (e.g. Smirnoff, 1993) and desiccation, then completely dislodging shoots. In many cases the sediments and pot bags were washed away. Waves were frequently to 30 cm high, and boat traffic increased from spring. The speed restriction zone in which the treatment was sited afforded no real protection from boat wash, as waves travelled with little diminution in force from mid-channel, where speed was unrestricted.

The suspended sediment load downstream of the weir appeared to be much higher than that upstream due to turbulence and erosion. Many plants at -1.0 m downstream of Lock 1 were covered by sediments. The platform base was 5-20 cm above the submerged river bed for the three replicate platforms. Sediment deposition over the 7 month experiment was in this range however, and even higher as many pots (18 cm high) were completely buried.

For -1.0 m elevations in both stable and variable treatments, growth was low in plants with short leaves. Irradiance penetrating to the pot surface was <11%, and occasionally <0.4% (when K_d was 5 m^{-1}). Plants growing at very low irradiances were more prone to damage by feeding fish, particularly carp *Cyprinus carpio*, and the burrowing crayfish *Cherax destructor*. Some plants in the -1.0 m elevation treatments were grazed by waterbirds. Difficulties encountered whilst censusing shoot and leaf production in 1 m deep turbid water also caused some damage to plants. Some were occasionally damaged when being removed and replaced from the platform for counting. Long leaves frequently became entangled and tore easily. Clonal spread between pots became common toward the end of the experiment. In addition, some pots in both stable and variable treatments were vandalised.

Dense mats of filamentous green algae, predominantly *Spirogyra* spp and *Cladophora* spp, formed on plants, cages, pots and platforms at the variable treatment from spring. Algal growth was minimal at the more remote stable treatment site at Sinclair Flat. This is ascribed to inputs of nutrients from Blanchetown, and particularly septic tanks on the floodplain adjacent to the variable treatment site. Algal mats were removed on censusing occasions, but reformed rapidly.

10.3.3. Biomass production and percent allocation

Analysis of variance was not conducted due to the absence of data for the -0.1 m elevation below Lock 1, unequal sample sizes (Table 10.2) and the high variance in data (standard deviations were c. 25-50% of the means). The variation in plant performance was sometimes marked between replicate platforms per site. This was partly due to small differences in platform elevation (particularly in the shallowest treatments) and the height of potting sediment in individual pot bags. Other factors which influenced plant responses at the level of replicate location were: shading by large overhanging riparian trees (one redgum, *Eucalyptus camaldulensis*, shaded a platform at Sinclair Flat, causing lower growth for all plants), boat wash was higher at two locations downstream of the weir than in the third, and half the plants at one downstream location were vandalised. Hence it was necessary to pool data for each elevation x water level variability treatment.

Mean total plant biomass at harvest was greatest in plants grown 0.5 m below pool level when water levels were relatively stable (Table 10.2). Total biomass was similar in plants grown 1.0 m below pool level in both stable and variable treatments (26.58 and 26.34 g, respectively). This indicates that established *Vallisneria* plants can tolerate submersion to 1 m in the Lower Murray, despite occurring infrequently below 0.6 m below pool level (Fig. 3.6). Many of these plants grew leaves to the surface, thereby greatly increasing canopy carbon assimilation (Chapters 7 and 9). Lower biomass production at -0.5 m elevation in plants below Lock 1 is attributed to frequent exposure of the leaves due to the combined effects of weir operations, wash from boats, and smothering by algal mats. Biomass in plants 10 cm below pool level upstream of Lock 1 was low as the majority of leaves experienced some degree of senescence, and shoot recruitment was low.

Maximum mean relative growth rates (RGR), calculated as ln (final dry weight)/Δt, were 15.3-15.8 mg g^{-1} d^{-1} in plants at -1.0 m and -0.5 m upstream of Lock 1. These rates do not include initial dry weights in the calculations and so may be overestimates. The change in dry weight over the experiment could not be calculated as both buried pot identification tags were removed by wave action in many pots (particularly downstream of the weir), making matching of final and initial biomass data impossible. Nevertheless these RGR values are similar to those calculated as the change in dry weight over time in the pond

Table 10.2. Effect of elevation relative to pool level and water level variability on biomass in *Vallisneria*. Elevation of the pots is relative to the design pool level on the upstream side of Lock 1 for stable treatments, and the design level for the Barrages at the Murray Mouth for variable treatments. Plants at -0.1 m are shallowest. Leaves include female peduncles and shoot bases. The number of plants remaining at harvest is shown. Data are mean and se. The initial number per treatment was 24 (three locations x eight replicates)

		Dry weights (g)					Percent		
Elevation relative to pool level (m)	Number of plants	Total	Leaves	Roots	Stolons	Above: below	Leaves	Roots	Stolons
Stable levels									
-0.1	7	1.60 ± 0.17	0.72 ± 0.12	0.53 ± 0.06	0.35 ± 0.04	0.83 ± 0.13	45.1	33.0	21.9
-0.5	22	29.93 ± 1.78	26.54 ± 1.65	2.03 ± 0.14	1.36 ± 0.11	8.32 ± 0.60	88.6	6.8	4.6
-1.0	17	26.70 ± 2.95	23.76 ± 2.67	2.02 ± 0.23	0.92 ± 0.15	8.78 ± 0.17	89.0	7.6	3.4
Variable levels									
-0.1	0	-	-	-	-	-	-	-	-
-0.5	7	18.44 ± 2.73	16.44 ± 2.52	1.23 ± 0.0.18	0.77 ± 0.11	8.44 ± 0.87	89.2	6.7	4.2
-1.0	10	26.34 ± 4.21	23.21 ± 3.82	2.17 ± 0.31	0.96 ± 0.17	7.72 ± 0.82	88.1	8.2	3.7

Table 10.3. Final numbers of shoots and leaves per plant, and maximum leaf length per plant, for selected treatments. Data are presented for plants 0.5 and 1.0 m below pool level in stable (above Lock 1) and variable (below Lock 1) treatments (mean and se). See Table 10.2 for numbers of replicates per treatment.

Elevation relative to pool level (m)	Number of shoots	Number of leaves	Mean maximum leaf length per plant (cm)
Stable levels			
-0.5	22.1 ± 1.6	176.6 ± 11.3	56.0 ± 2.6
-1.0	12.5 ± 1.1	100.3 ± 8.5	72.2 ± 3.4
Variable levels			
-0.5	11.7 ± 2.7	100.5 ± 22.9	26.6 ± 2.9
-1.0	10.3 ± 1.6	78.1 ± 14.8	42.3 ± 4.7

experiment (maximum RGR of c. 25 mg g^{-1} d^{-1} over winter-spring at the same nutrient loading, Chapter 7).

The above to below-ground biomass ratio was 7.7–8.8 in all -0.5 m and -1.0 m elevation treatments (Table 10.2). Mean percent allocation to leaves was remarkably constant across these treatments (88-89%). The small dense shoot bases incorporating the basal meristem (which are non-photosynthetic) were included with leaf tissues when weighing, and may have elevated these percent allocation values. Percent allocation to roots was 0.5-2 times higher than to stolons (6.7-8.2% and 3.5-4.6% respectively).

The contribution of leaves to total biomass was low in plants growing in shallow water (-0.1 m elevation, stable treatment). Despite most of the photosynthetic canopy senescing due to exposure, the root and stolon networks remained comparatively intact. This anchored the basal meristems, and allowed for regrowth when plants were reflooded. This was observed in shallow plants downstream of the weir when exposed then inundated in early July (Fig. 10.1b).

10.3.4 Shoot and leaf recruitment and maximum leaf length

Shoot recruitment over the experiment was highest for plants 0.5 m below pool level in the stable water-level treatment (Table 10.3). This corresponds to the observed optimum depth range for *Vallisneria* of 0.3-0.6 m in the Lower Murray (Chapter 3). Nearly twice as many shoots were produced at -0.5 m than at -1.0 m upstream of the weir (22.1 and 12.5 respectively). Recruitment in the latter was similar to that at both elevations shown for the variable treatment in Table 10.3. These data indicate that vegetative reproduction is curtailed by both low light and exposure. Data for shoot and leaf recruitment and leaf length are not available for plants at -0.1 m elevation. Rapid vegetative spread commenced in mid-spring (Fig. 10.3a). The effect of exposure on recruitment is indicated by the much lower rate of shoot production from mid-October onwards in the plants below than above the weir. This coincided with repeated exposure as the river level fell to 5-25 cm below pool level, boat traffic increased and algal mats developed as temperatures increased.

Leaf recruitment was also highest in plants submersed 0.5 m in the stable regime (Table 10.3). The more rapid rate of increase in number of leaves than shoots indicates a response to exposure and wave action is to allocate resources to leaf production in existing shoots more so than by the production of new shoots.

Maximum leaf length per plant was greatest in plants 1.0 m below pool level (Table 10.3). Maximum length was lower below the weir than above the weir. Though quite resilient to wave motion, leaves are damaged by prolonged exposure to high-energy waves such as those from power boats.

The considerable variance associated with means data for shoot and leaf recruitment and leaf length obviates firm conclusions. Much variation appears to have been due to initial biomass and shoot age. Future studies of *Vallisneria* should account for phenological age and biomass in experimental plants.

10.4 Discussion

10.4.1 Optimum elevation range for recruitment and biomass production

The water regime producing the highest biomass production and shoot and leaf recruitment in the experiment (-0.5 m elevation, stable water-level treatment) coincides with the observed optimum water regime for *Vallisneria* in the Lower Murray (Fig. 3.6). Field surveys and observations have determined distribution and abundance are greatest at depths 0.3-0.6 m when water levels are relatively stable (Chapters 2 and 3). Plants rooted 0.5 m below pool level upstream of Lock 1 were not exposed, and irradiances penetrating to the sediment surface were relatively high (5-27% of subsurface irradiances). This was equivalent to a minimum irradiance of 25 μmol m^{-2} s^{-1} (K_d of 5 m^{-1}, depth 0.6 m, solar noon subsurface irradiance I_o in winter of 500 μmol m^{-2} s^{-1}) and up to 400 μmol m^{-2} s^{-1} (K_d=2.2 m^{-1}, I_o=1500 μmol m^{-2} s^{-1} in summer). Laboratory studies show the mean light compensation point for net photosynthesis is 24 μmol m^{-2} s^{-1} and photosaturation commences at irradiances as low as 40 μmol m^{-2} s^{-1} (Chapter 8). As much of the canopy was within 20 cm of the water surface, a high proportion of photosynthetic area was probably photosaturated over much of the day. The minimum depth over the experiment was 47 cm and changes in level were much slower than that for downstream sites (Fig. 10.1b). Hence plants experienced more favourable light conditions and were not exposed to the atmosphere.

Plants in both shallower and deeper water had lower rates of recruitment and generally lower biomass. Repeated and prolonged exposure to air killed all plants in the -0.1 m elevation treatment downstream of the weir, and two-thirds of those upstream of the weir. (Table 10.2). Shoot recruitment in -1.0 m elevation treatments was approximately half that in plants in the optimum water regime but mean total biomass was only slightly lower (Table 10.3). Under low light, *Vallisneria* allocates resources to growing long leaves in existing shoots rather than to new shoots (see Chapter 7). Light penetration to the sediment surface in these treatments was low (0.4-11% of subsurface flux). This plasticity, and the species' physiological shade tolerance, allow it to survive prolonged flooding with turbid water.

Vallisneria and other submersed species such as *Potamogeton crispus*, *P. tricarinatus* and *Myriophyllum verrucosum* were observed very infrequently in the first 20 km downstream of Locks 4, 6, 7 and 10 during surveys in 1994-95 (unpub. data). These plants were mature but probably had low recruitment. The elevation range in which recruitment can occur is narrower than that for the persistence of established plants. Seedlings have little below-ground structure for anchorage and storing carbohydrates, and young leaves must meet their own respiratory demands from carbon assimilation at very low irradiances. In

Chapter 8 the youngest *Vallisneria* leaves were shown to be inefficient assimilators, with a high light compensation point and low photosynthetic efficiency. In addition, seedlings are probably highly intolerant of exposure. Thus, conditions suitable for seedling establishment probably occur very infrequently in reaches with highly variable waterlevels.

The physiological stresses of exposure to air and light limitation exert respectively upwards and downwards restrictions on growth, with an optimum range for growth of <0.8 m for *Vallisneria* (and probably other submersed species). The effect of increased water level variability with increasing distance upstream of a weir is to reduce this colonisable elevation range.

10.4.2 Confounding effects of boat wash and dense algal growth

The experimental design was confounded by the effects of boat wash and dense growth of filamentous green algae in the variable treatment. Grazing by birds, though deterred by the cages, was not completely prevented, and some plants at both sites were also vandalised. Nevertheless, mortality in the shallowest treatment at the downstream site is likely to have occurred from falling river levels, though perhaps less rapidly than in the presence of these factors.

Once the river level fell below the pot base, desiccation probably occurred more rapidly than in plants rooted in the Murray's littoral. Pots 45 cm high were employed to overcome this problem in the field study of *Bolboschoenus* (Chapter 6). The use of larger pots in the *Vallisneria* study was not feasible however. Due to the much larger changes in water level in this study, pots up to 1.5 m high would have been required. Future studies could avoid problems of soil moisture limitation by growing plants in natural sediments.

The effects of wave action, whether wind-generated or from power boats, have been widely studied (*e.g.* Keddy, 1983a,b; Nansson *et al.*, 1994). In this study, wash from power boats caused significant damage to *Vallisneria* shoots. Studies by Coops and van der Velde (1996) and Coops *et al.* (1991, 1996) found wave action reduced stem density and uprooted rhizomes in *Scirpus lacustris*, a structurally-depauperate submersed macrophyte, but not in *Phragmites australis,* which has stronger stems. Exposure to strong wave action reduced the biomass of submersed macrophyte populations in a study of Swedish lakes (Strand and Weisner, 1996). Bank erosion in the Gordon River, Tasmania, was found high when waves from boats were <30 cm high (Nansson *et al.*, 1994). Reducing boat speeds and traffic reduced wave heights and disturbance to littoral sediments. Clevering (1995) suggests wave action limits seedling establishment in submersed *Scirpus* spp in Dutch wetlands. In *Vallisneria*, leaves senesce more rapidly from the repeated exposure to air and physical disturbance. Roots also tear quickly, resulting in shoots being dislodged. Though not designed to test the effects of wash from boats on submersed macrophytes in the Lower Murray, this study suggests such impacts may significantly reduce growth in such species. This may occur particularly in areas of fluctuating water levels where plants are vulnerable to damage from strong waves by repeated exposure to air.

Sites were chosen as close to the upstream and downstream side of Lock 1 to reduce the effect of change in water-level elevation with distance on the water regime experienced by plants. This proved satisfactory for -0.5 m and -1.0 m elevations, but not for the shallowest treatment at the upstream site. Plants in the three replicate platforms at the shallowest depth in the stable treatment were at elevations differing by <5 cm. This was sufficient to significantly influence survival and growth however. Complete mortality in plants in the two shallowest platforms compared to 100% survival in the lowest platform highlights the importance of small changes in river level on plant performance. In studies designed to use the river levels recorded at gauging stations for determining experimental treatments, sites as close as possible to the station should be chosen.

10.5 Conclusion

This field study examined recruitment and growth in *Vallisneria americana* at three depths in stable and variable water-level regimes. Some evidence exists for supporting the hypothesis that performance is greatest in the stable treatment at depth 0.5 m, but the confounding effects of boat wash and algal growth, amongst others, in the variable treatment prevent firm conclusions. The study was also hampered by the absence of suitable and accessible sheltered sites downstream of Lock 1. However, the experimental design and methods employed provide a useful means of investigating these two important facets of water regime on the growth of submersed macrophytes.

Figure 10.1. Comparison of water levels upstream (thin line) and downstream of Lock 1. Levels fluctuate to a much greater extent downstream of the lock over yearly, monthly and weekly time scales. a. Over a seven year period of high and low flows. The amplitude of flooding downstream is up to twice that upstream (occurring approximately annually over this period). b. During low flows over the study, weekly and monthly changes in level are also more pronounced downstream. Rates of rise and fall are also more rapid. Dashed lines indicate weir pool level.

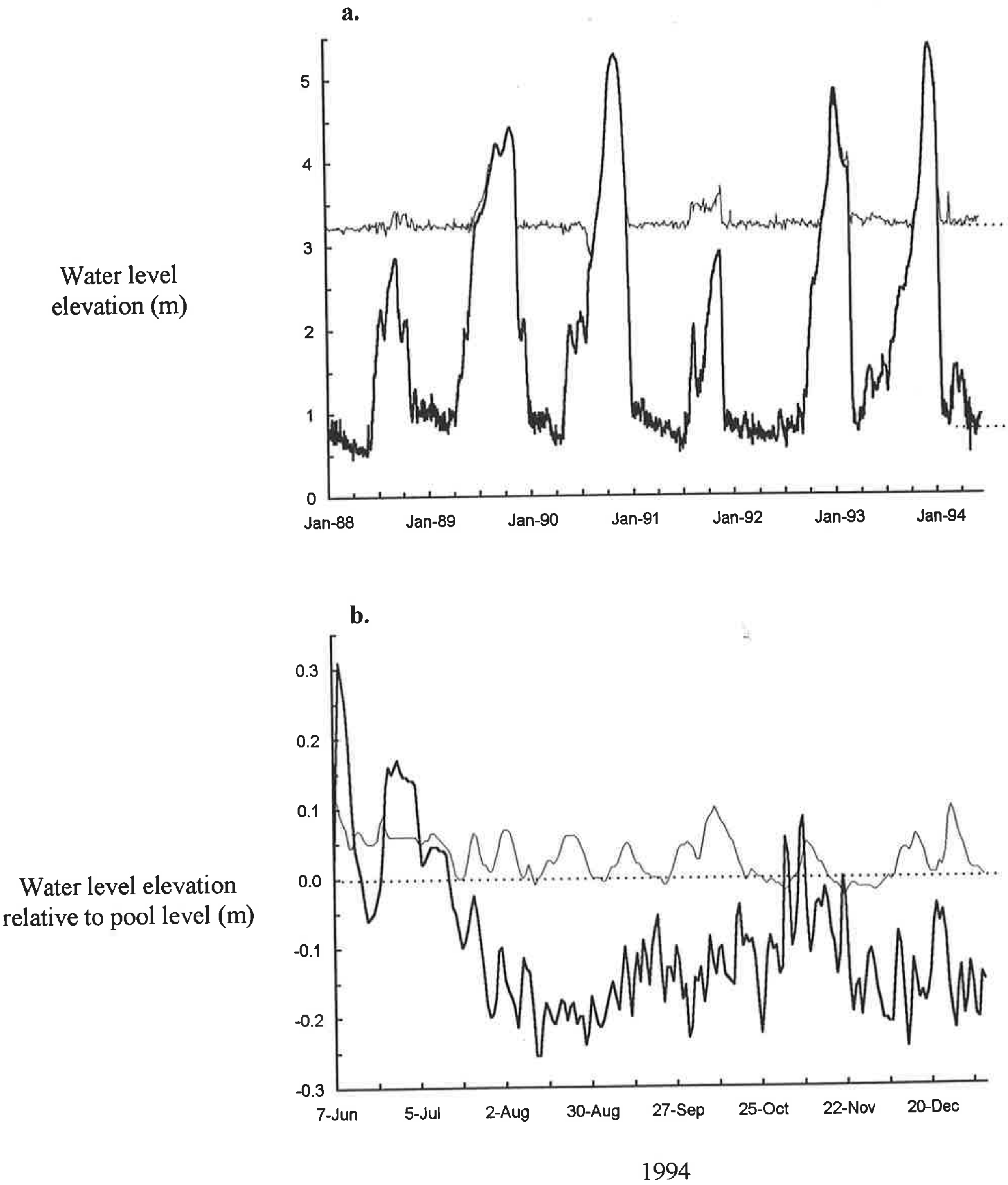

a.
Water level elevation (m)
5
4
3
2
1
0
Jan-88
Jan-89
Jan-90
Jan-91
Jan-92
Jan-93
Jan-94
b.
Water level elevation relative to pool level (m)
0.3
0.2
0.1
0.0
-0.1
-0.2
-0.3
7-Jun
5-Jul
2-Aug
30-Aug
27-Sep
25-Oct
22-Nov
20-Dec
1994

Figure 10.2. Location of stable (upstream of Lock 1) and variable (downstream) treatments. The direction of flow is shown by the arrow.

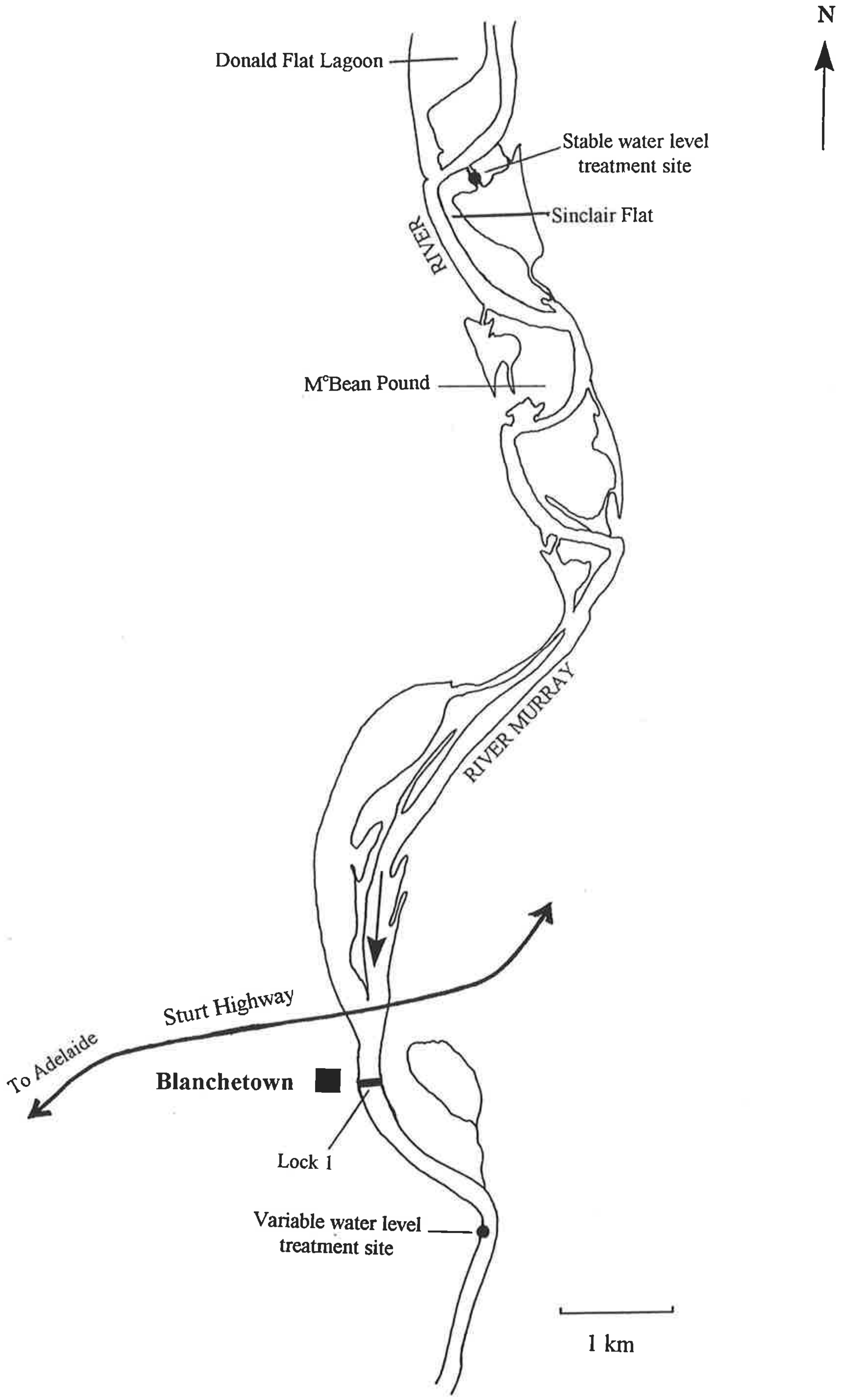
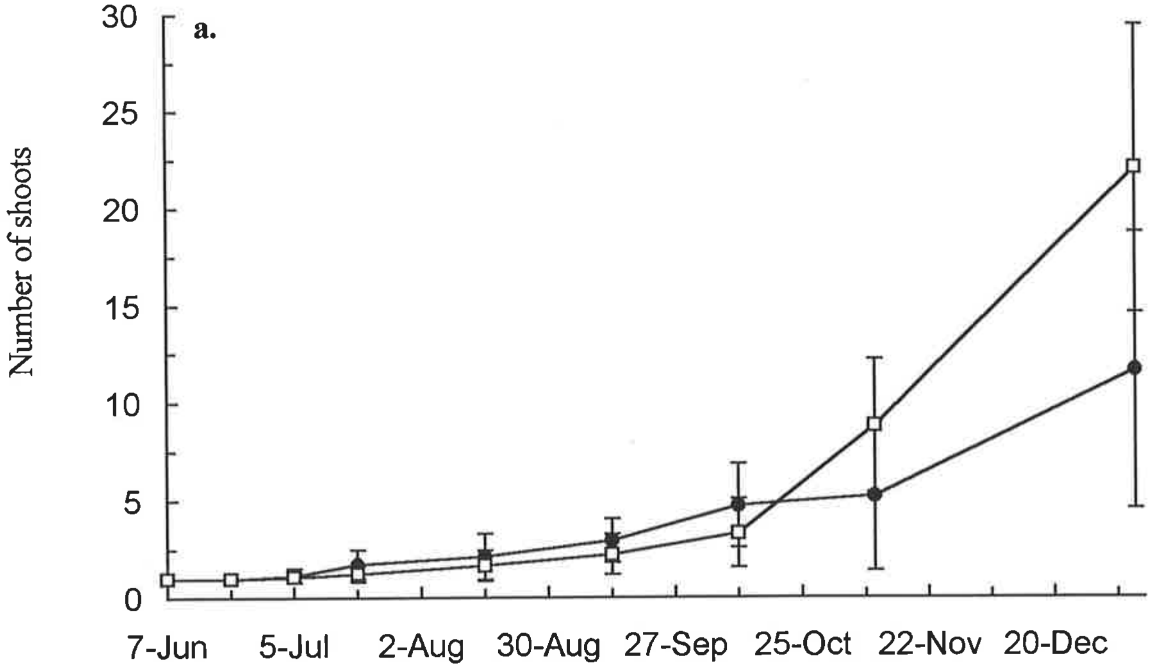
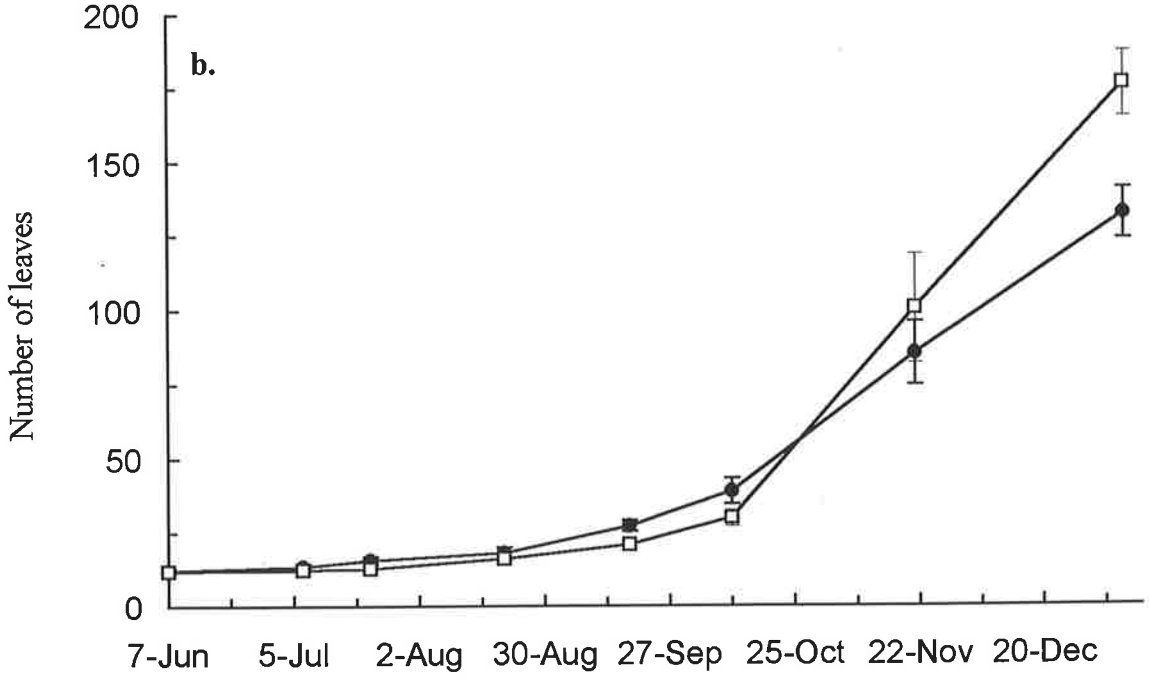

N
Donald Flat Lagoon
Stable water level treatment site
Sinclair Flat
RIVER
M^cBean Pound
RIVER MURRAY
Sturt Highway
To Adelaide
Blanchetown
Lock 1
Variable water level treatment site
1 km

Fig. 10.3. Numbers of a. shoots and b. leaves produced in -0.5 m elevation treatments over the 7 month study. (□)Stable treatment, (●) variable treatment. Data are mean and standard deviations.


a.
Number of shoots
0
5
10
15
20
25
30
7-Jun
5-Jul
2-Aug
30-Aug
27-Sep
25-Oct
22-Nov
20-Dec


b.
Number of leaves
0
50
100
150
200
7-Jun
5-Jul
2-Aug
30-Aug
27-Sep
25-Oct
22-Nov
20-Dec

Chapter 11

Summary and Recommendations

11.1 Influence of water regime on macrophytes of the Lower Murray

This thesis investigated the influence of water regime on macrophytes of the Lower River Murray at the level of the community, population and tissue. Its aims were to examine the influence of water regime on growth, vegetative recruitment, resource allocation and photosynthesis in selected species, and the adaptations permitting them to tolerate sub-optimal regimes. Field surveys examined how the distribution and abundance of macrophytes along water regime gradients reflected life-history strategies and physiological tolerances to flooding and exposure. Pond, field and laboratory experiments were then employed to address specific questions regarding how emergent and submersed macrophytes react to reduced levels of resource supply caused by changes in water level. Specifically, I investigated to what extent a reduction in resource availability (access to atmospheric gases, soil moisture, light) stimulates biomass allocation to the tissue responsible for the acquisition of the limiting resource. These questions were addressed using the emergent sedge *Bolboschoenus medianus* and the submersed herb *Vallisneria americana*. The following questions were addressed. How does resource limitation in *Bolboschoenus* affect vegetative recruitment, flower production and the sequestering of biomass below-ground for future growth? Does it 'react' to flooding by elevating its canopy to maintain a positive carbon balance, or conserve its resources below-ground and resume growth once water levels fall? In *Vallisneria*, how do changes in depth or water clarity influence biomass production, canopy morphology and clonal growth? How is photosynthetic and respiratory activity influenced by light history and leaf age? The following is a synthesis of these investigations.

The following models were presented to summarise the influence of water regime on aquatic and littoral plants:

- Similarities between perennial littoral plants using minimum spanning tree analysis (and interpreted using ordination, clustering and bond-strength analysis), and their distribution across water regimes (Figs 3.4 and 3.6);

- Growth and resource allocation in *Bolboschoenus medianus* across a depth gradient (Fig. 5.16);

- Relative growth rate as functions of $\overline{I}$ and depth in *Vallisneria americana* (Figs 7.5 and 7.9b, Table 7.8), and

- Daily canopy carbon assimilation and plant carbon balance in *Vallisneria* (Tables 9.1 and 9.3).

Ordination scores for the relative abundance of perennial species along Pool 5 were highly correlated with distance downstream of Lock 6 (Chapter 2). Clustering of sites based upon water regime indices suggested 7 broad water regime groups along longitudinal and vertical axes (Chapter 3), which illustrate the influence of weirs on hydraulic conditions of the Lower Murray. Species ordination scores were highly correlated with the frequency of flooding to 0-20 cm and exposure to ≥ 100 cm, and weakly with the frequency of flooding to 20-60 cm and ≥ 200 cm. Correlations between vegetation and the frequency of flooding to any depth were not significant, indicating flow manipulation should target specific species groups, determined by growth form and flooding requirements, rather than aim only to inundate a floodplain. Species groups suggested by clustering, and similarities determined by ordination and network analyses, provide a basis for selecting species for vegetation management programs. Species similarities are perhaps best illustrated by the minimum spanning tree diagram, which serves as a useful summary. Characterisation of flooding patterns using water regime indices provided an objective, quantitative approach to determining species' optimum water regimes and tolerance ranges.

The majority of species surveyed exhibited broad tolerances to water regime, with only four of the 26 perennials restricted to hydrologically stable weir pools. Approximately three times the number of obligate aquatics and species requiring high soil moisture are found across a broad elevation range of the littoral of the Lower Murray. This reflects selection for morphological and physiological adaptations and resource allocation strategies permitting tolerance to flooding and exposure.

Growth, vegetative recruitment, resource allocation and photosynthesis in *Bolboschoenus* and *Vallisneria* were influenced by water regime. In both species canopy structure was flexible in response to flooding, which is interpreted as a strategy to redress lower access to CO_2 and O_2 and light, respectively.

In *Bolboschoenus*, LAR increased to 60 cm depth, providing that 10% of leaf area was emergent, but otherwise declined rapidly (Chapter 5). LAR was maintained in the range 2.5-2.75 m^2 kg^{-1} *via* culm extension, vertical orientation of submersed leaves, and higher leaf recruitment when submersed. Culm elongation was supported by carbohydrates stored in tubers, and at the expense of allocation to roots and rhizomes. Leaves extended and became thinner in *Vallisneria* at low light, measured as an increase in LAR (Chapter 7). At values of $\bar{I} < 26$ μmol m^{-2} s^{-1}, the minimum light requirement for growth, LAR declined rapidly as shoot and leaf recruitment were negligible. NAR declined with increasing depth in *Bolboschoenus*, and with increasing depth/decreasing irradiance in *Vallisneria*.

Biomass declined linearly with emergent leaf area in *Bolboschoenus*. Culm recruitment and RGR were maximum at depths 0 and -20 cm in stable water levels. Recruitment was positively correlated with the duration of flooding to within ±20 cm of the sediment surface during natural flooding (Chapter 6). Leaf recruitment decreased and senescence increased with depth in culms produced before flooding (Chapter 5). In culms initiated when flooded, rates of recruitment were similar across the depth range, or marginally higher at -40 cm. In the field study, growth was dependent upon elevation above pool level (hence depth) and flooding pattern (*i.e.* hydrograph). Flowering only occurred in plants flooded to 0-40 cm for 4-6 weeks, then exposed slowly (2 cm day^{-1} for 4 weeks). In general, exposure reduced stomatal conductance and culm recruitment. Growth declined when exposed rapidly (10-12 cm day^{-1} for 7-13 days) but not slowly.

In the turbidity range 90-504 NTU, RGR in *Vallisneria* declined with increasing turbidity and depth (Chapter 7). However, plants survived 3 months without sufficient light for photosynthesis. The light environment was described using the average irradiance over the water column, $\bar{I}$. The RGR-$\bar{I}$ response followed a P-I curve, with values of RGR_{max}, $\bar{I}_c$, and $\bar{I}_k$ of 19.1 mg g^{-1} d^{-1}, and 26 and 58 μmol m^{-2} s^{-1}, respectively. RGR declined sigmoidally as functions of depth and downwelling extinction. Maximum leaf length increased linearly with depth. The biological validity of $\bar{I}$ is its relationship with B_e, the photosynthetically-effective (receiving irradiances>I_c) proportion of canopy biomass, B.

Tolerance of prolonged low-light in *Vallisneria* is due to physiological shade-tolerance: low values of I_c and I_k respectively; 3-37 and 18-95 μmol m^{-2} s^{-1} (Chapter 8). Photosynthetic efficiency, α, is in the mid-high range for submersed macrophytes (0.005-0.100 mg C g dw^{-1} h^{-1}(μmol m^{-2} s^{-1})$^{-1}$), and permits rapid responses to fluctuating light regimes. P-I parameters were dependent upon leaf age, depth in the canopy and depth to the sediment. P_{max} occurred at the surface in turbid water (K_d of 12.59 m^{-1}) in young-mid aged leaves (1.4 mg C g dw^{-1} h^{-1}). Very young and old leaves had lower P_{max}. Chlorophyll *a* concentrations peaked at depths 6-10 cm in most leaves (5-8 mg chl *a* g dw^{-1}), but were mostly uniform along older leaves.

The RGR-$\bar{I}$ response over 3 months reflected daily carbon balances. Plants at 24 cm placed 42% of their canopy biomass within 2 cm of the surface, and had positive modelled daytime canopy carbon assimilation in highly turbid water (K_d of 12.59 m^{-1}) (21.208 mg C per plant; Chapter 9). In plants at 82 cm, 87% of the canopy received insufficient irradiances for photosynthesis, and plants had a negative balance (-2.184 mg C). Observed RGR for these plants were 15 and -2 mg g^{-1} d^{-1}, respectively. As carbon assimilation declines rapidly with depth in turbid water, plants must place leaves at or just below the surface in the Lower Murray to maintain a positive carbon balance. Hence deep submersion and/or a reduction in light penetration reduce RGR by restricting carbon assimilation. Conversely, exposure to air causes senescence of leaf tissue and reduces shoot production (Chapter 10). The distribution of *Vallisneria* in the Lower Murray (Chapters 2 and 3) is thus largely explained by the twin factors of light-limitation and intolerance of exposure. In variable water regimes, the colonisable depth range is reduced and conditions amenable to recruitment less frequent.

The River Murray Hydraulic Model is of sufficient accuracy for use in ecological research and flow management, provided improved inputs are used (Chapter 4). Accuracy can be improved by reviewing the stage/discharge relationship at Lock 10, bathymetric data and bypass flows around weirs. However, complex file structures and data input/output formats limit its utility.

11.2 Implications for flow management

1. Water levels should be allowed to vary as much as technically feasible when within the channel. The maintenance of stable weir pools for prolonged periods in a semi-arid floodplain river is highly unnatural. Variations in stage of 30-50 cm should be instituted on a regular basis, with characteristics of the hydrograph determined as much as possible from pre-regulation data. During low flows, daily changes in water level should be generally <5 cm. Repeated exposure and flooding over a short period (weeks, months) should be avoided.

2. More frequent inundation of the floodplain is essential. To maximise vegetation diversity, the lower floodplain should be inundated every 2-4 years. Where possible, weir and storage operations should be used to increase the frequency and duration of inundation. This may only be feasible for low-lying floodplains. Cooperation between the water resource agencies and ecologists needs to be fostered to maximise the benefits of such efforts.

3. Flow management practices which reduce the duration of flooding and/or increase the rate of flood recession restrict the time-frame for growth and reproduction of littoral and floodplain vegetation. Rapid exposure causing low soil moisture restricts the allocation of resources to below-ground storage organs in emergent plants, thereby reducing reproductive potential for future growth.

11.3 Recommendations for future studies

11.3.1 Influence of water regime on growth and resource allocation in aquatic macrophytes

The duration and timing of flooding and exposure are important in structuring vegetation of floodplain rivers, but have not been widely studied (Mitchell and Rogers, 1985; Bornette and Amoros, 1991, 1996; Kirkman and Sharitz, 1993; Klimesova, 1994; Kimber *et al.*, 1995a,b; Blanch *et al.*, 1996). What duration of flooding/soil moisture is necessary to successfully recruit plants from the propagule bank, and what is their resilience to subsequent sub-optimal conditions? This is pertinent for determining the influences of reduced flooding frequency on floodplain species, and of elevated turbidity on submersed plants. Is there evidence for selection of plant phenotypes with differing tolerances to flooding and exposure? Are modifications to the natural flow regime in the Lower Murray reducing the resilience of vegetation to variability? How do the apparent water regime requirements of perennials suggested from surveys (cf. Table 3.5) compare with those determined from experiments? Laboratory and pond experiments provide controlled conditions for such experiments, but should be complemented by field studies for validation.

Can growth-irradiance responses in all submersed species be effectively described by RGR-$\bar{I}$ curves? How does the position of meristems throughout the plant influence such relationships? What are the $\bar{I}$ thresholds for growth and vegetative recruitment of common species? The *Vallisneria* field experiment suggests wash from power boats reduces growth in submersed species considerably at depths of <0.5 m. Do species with basal meristems withstand physical damage better than those with meristems at the surface?

11.3.2 Morphological and physiological adaptations to a variable water regime and low light

Whilst many species have a narrow optimum depth range in stable water levels (*e.g.* Chapters 5 and 10), adaptations permitting survival under a broad range of inundation and exposure conditions enable them to persist through much of the littoral (Chapter 3). For example, in stable water levels culm recruitment was highest at depths 0 and -20 cm in *Bolboschoenus medianus*, but plants occurred in 6 of the 7 water regime groups in Pool 5. Is morphological plasticity (biomass allocated to leaves/stems when flooded, and to roots when exposed) common amongst littoral plants? How rapidly can resource allocation strategies be ‘switched’ from above to below-ground in a variable hydrologic environment? Morphological adaptations include tubers and corms for storing carbohydrates and supporting stem growth (Grace, 1993; Blom *et al.*, 1990; Crawford and Braendle, 1996), rhizomes and stolons, regrowth from plant fragments (Brock, 1991), rapid seed production and tall stems (Cizkova-Koncalova *et al.*, 1992). Studies of these and other adaptations are likely to be profitable in interpreting vegetation dynamics across spatial and temporal scales. How long can seeds and vegetative propagules survive without wetting? How rapidly does germination success decline over this period?

Physiological adaptations to submersion in emergents include the stimulation of stem growth by ethylene (Armstrong *et al.*, 1994), convective flow of air to roots (Brix *et al.*, 1992), photosynthesis in the submersed portion of emergent leaves (Armstrong *et al.*, 1994), and clonal integration plant across depth/exposure gradients (Callaghan *et al.*, 1992; Evans and Whitney, 1992). How common are these adaptations, and to what extent do they determine vegetation patterns and processes? In floodplain plants, to what depth do roots penetrate at low soil moisture? Field studies may be complemented by laboratory investigations of drought-tolerance by regulating soil moisture potential with polyethylene glycol (Roberts, 1986; Rossi *et al.*, 1993; Wood *et al.*, 1993). Floodplain grasses have been little studied in the Lower Murray, despite their prevalence and importance in carbon cycling (Bunn *et al.*, 1997), and may prove particularly amenable to such studies, *e.g. Paspalidium jubiflorum, Sporobolus mitchellii, Paspalum distichum,* and cane grass (*Eragrostis australasica*).

Amongst submersed species, parameters indicating the degree of shade-tolerance, such as I_c, I_k, and α (Chapter 8), are likely to be correlated with species distributions. Is there a genetic basis for greater shade-tolerance in Lower Murray *Vallisneria* plants than in plants from North America? Is shade acclimatization common amongst Lower Murray macrophytes?

11.3.3 Monitoring the long-term effects of flooding on floodplain vegetation

The long term effects of flooding patterns on floodplain communities should be monitored to complement short-term population studies. Of particular importance are the influences of flood frequency, duration and recession rate on recruitment from the propagule-bank, clonal spread, flowering and propagule dispersal.

The methodology employed in Chapter 6 could be extended to examine natural populations and communities of emergent and submersed plants within the littoral zone (Nilsson, 1996). A more natural flooding regime could be engineered in several pools, with levels stable in control pools (Gore and Shields, 1995; Stanford *et al.*, 1996). Experiments must be conducted over larger spatial scales than used in Chapter 6 (Bayley, 1995). Such a regime needs to incorporate greater variability in water levels, with slower rates of recession than presently occur. For example, levels could be allowed to vary within a 0.5 m range over a 24 month period, using weir manipulations and releases from Lake Victoria where possible (Ohlmeyer, 1991). Differences between vegetation processes at the community level in flooded and stable pools may only be observed over the long-term if frequent natural flooding occurs in control pools (cf. Chapter 6).

Regular recording of downwelling light extinction would permit the modelling of growth in *Vallisneria* and other submersed species (Wetzel and Neckles, 1986; Dennsion, 1987; Zimmerman *et al.*, 1994). The RGR-$\bar{I}$ model provides a simple method for predicting changes in plant performance given values of K_d, depth and incoming irradiance (Chapter 7; Fig. 7.5). The influence of Lake Victoria operations on turbidity regimes and plant growth below Lock 7 could be simulated: *e.g.* a short period of high turbidity (mainly Darling water) followed by a long period of low turbidity (Murray water), *versus* continuous low-medium turbidities (Table 7.8).

Reduced flooding frequency has probably reduced plant diversity on the floodplain, whilst maintenance of permanent weir pools has increased the biomass of vegetation within the channel and adjacent wetlands. Diversity, composition and extent of floodplain communities have been altered by flow regulation. Whilst considerable anecdotal and historical information exists concerning these changes, to be of greatest use it requires verification and collation into a single document. Documentation of such changes, by making use of surveys (*e.g.* O'malley, 1990; Roberts and Ludwig, 1989, 1990), herbarium collections, knowledge of local Aborigines, personal accounts of explorers and naturalists (*e.g.* Sturt, 1833; Mitchell, 1839; Harris, 1963), and recollections of locals, would provide a useful resource and assist efforts to reverse the degradation of the Lower Murray. Such documents have been produced for the Hawkesbury-Nepean and Lachlan Rivers (Rosen, 1995; Roberts and Sainty, 1996, respectively).

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Appendix 1.

Higher plants of aquatic, littoral and low-floodplain environments of the Lower River Murray, Australia. Specimens were collected between Blanchetown and Wentworth from 1993-96, and identified by staff at the Herbarium of South Australia, Adelaide. Species recorded along the Lower Murray during other studies are also included and indicated as follows: [1], O'Malley (1990); [2], specimens held at the Herbarium of South Australia, and [3], Harris (1963). Nomenclature follows Black (1980), except where revised by Jessop (1993) (denoted by [§]). *Phyla canescens* follows Munir (1993) and *Vallisneria americana* var. *americana* follows Jacobs and Frank (in press).

FERNS

ADIANTACEAE
  Adiantum capillus-veneris L.
THELIPTERIDACEAE
  Christella dentata (Forsskal.)Brownsey & Jermy
MARSILEACEAE
  Marsilea drummondii A. Braun
  M. costulifera [§]
  M. hirsuta R. Br.
AZOLLACEAE
  Azolla filiculoides Lam.
  A. pinnata R.Br.

DICOTYLEDONS

SALICACEAE
  Salix babylonica L.
  S. x rubens Schrank
POLYGONACEAE
  Muehlenbeckia florulenta [§]
  M. horrida Gross
  Persicaria lapathifolium [§]
  P. prostrata [§]
  Polygonum aviculare L.
  Rumex bidens R. Br.
  R. brownii Campdera.
NYCTAGINACEAE
  Boerhavia dominii Meikle & Hewson[1]
AIZOACEAE
  Glinus lotoides L.
  Carpobrotus ?modestus S.T. Blake
PORTULACACEAE
  Portulaca oleracea L.
CARYOPHYLLACEAE
  Gypsophila australis (Schldl.)A. Gray
  Spergularia diandra (Guss.) Boiss.[1]
CHENOPODIACEAE
  Atriplex prostrata Boucher ex DC.
  A. suberecta I. Verd.
  Chenopodium glaucum L.
  C. nitrariaceum (F. Muell.) F. Muell. Ex Benth.

C. pumillio R. Br.
Dysphania glomulifera (Nees)Paul G. Wilson
Halosarcia indica (Willd.)Paul G. Wilson
H. pergranulata (J. Black)Paul G. Wilson
Pachycornia triandra (F. Muell.) J.Black
Salsola kali L.[1]
Threlkeldia diffusa R. Br.
AMARANTHACEAE
Alternanthera denticulata R. Br.
A. nodiflora R. Br.
RANUNCULACEAE
Ranunculus pentandrus J. Black
R. pumilio R.Br. ex D.C.
CERATOPHYLLACEAE
Ceratophyllum demersum L.
CRUCIFERACEAE
Lepidium africanum (Burman f.)DC.
Rorippa palustris (L.)Besser
R. nasturtium-aquaticum (L.)Hayek
Sisymbrium erysmoides Desf.
S. irio L.
S. officinale (L.)Scop.
S. orientale L.
CRASSULACEAE
Crassula helmsii (Kirk)Cockayne
LEGUMINOSAE
Acacia stenophylla Cunn. Ex Benth.
Glycrrhiza acanthocarpa (Lindley)J. Black
Vicia monantha Retz.
TROPAEOLACEAE
Tropaeolum majus L.
EUPHORBIACEAE
Euphorbia drummondii Boiss.
ELATINACEAE
Elatine gratioloides Cunn.
LYTHRACEAE
Ammania multiflora Roxb.
Lythrum salicaria L.
MYRTACEAE
Eucalyptus camaldulensis Dehnh.
E. largiflorens F. Muell.
HALORAGACEAE
Haloragis aspera Lindley
Myriophyllum caput-medusae Orch.
M. papillosum Orch.
M. simulans Orch.
M. verrucosum Lindley
ONAGRACEAE
Ludwigia peploides ssp. montevidensis (Sprengel) Raven
UMBELLIFERAE
Lilaeopsis polyantha (Gand.)H. Eichler
MENYANTHACEAE
Nymphoides crenata (F. Muell.)Kuntze[1]
CONVOLVULACEAE
Cressa erecta L.
BORAGINACEAE
Echium plantagineum L.[1]
Heliotropium supinum L.
VERBENACEAE

Phyla canescens
Verbena supinum L.
CALLITRICHACEAE
Callitriche sonderi Hegelm.
LABIATAE
Marrubium vulgare L.
Teucrium racemosum R. Br.
SOLANACEAE
Nicotiana glauca Graham
Solanum nigrum L.
SCROPHULARIACEAE
Glossostigma elatinoides (Benth.)Benth. ex Hook. f.
Limosella australis R. Br.
Mimulus repens R. Br.
Stemodia florulenta [§]
MYOPORACEAE
Eremophila divaricata (F. Muell.)F. Muell.
PLANTAGINACEAE
Plantago coronopus L.
CAMPANULACEAE
Pratia concolour (R. Br.)Druce
GOODENIACEAE
Goodenia glauca F. Muell.
Scaevola spinescens R.Br.[1]
Selliera radicans Cav.
ASTERACEAE
Aster subulatus Michaux
Brachycome basaltica var. gracilis Benth.
B. ciliaris (Labill.)Less var. ciliaris
Calotis cuneifolia R. Br.
C. scapigera Hook.
Centipeda cunninghamii (DC.)A. Braun & Asch.
C. minima (DC.)Domin
Conyza bonariensis (L.)Cronq.
Cotula australis (Sieber ex Sprenguel)Hook. f.
C. coronopifolia L.
Dittrichia graveolens (L.)Greuter
Eclipta platyglossa F. Muell.
Epaltes australis Less.
E. cunninghamii (Hook.)Benth.
Gnaphalium polycaulon Pers.
Lactuca saligna L.
L. serriola L.
Pseudognaphalium luteo-album (L.)Hilliard & B.L. Burtt
Senecio cunninghamii DC. ssp. cunninghamii
S. glossanthus (Sonder)Belcher
Vittadinia cuneata DC.
Xanthium californicum E. Greene
X. occidentale Bertol.
X. spinosum L.

MONOCOTYLEDONS

ALISMATACEAE
Alisma lanceolatum With.[2]
Damasonium minus (R.Br.) Buchen.[1]
Sagittaria graminea Michaux.[2]
HYDROCHARITACEAE
Hydrilla verticillata (L.f.)Royle.[3]

Ottelia ovalifolia (R.Br.)Rich.[3]
Vallisneria americana Michx. var. americana[¥]
JUNCAGINACEAE
Triglochin procera var. dubium (R. Br.)Benth.
T. striatum Ruiz Lopez & Pavon
POTAMOGETONACEAE
Potamogeton crispus L.
P. ochreatus Raoul[2]
P. pectinatus L.[2]
P. tepperi A. Bennett
P. tricarinatus F. Muell. & A. Bennett
Ruppia megacarpa R. Mason[2]
R. polycarpa R. Mason[2]
ZANNICHELIACEAE
Zannichelia palustris L.[1]
LIILIACEAE
Bulbine bulbosa (r. Br.)Haw.
B. semibarbata (R.Br.)Haw.
AMARYLLIDACEAE
Calostema luteum Sims
Crinum flaccidum Herbert
PONTEDERIACEAE
Eichornia crassipes (C. Martius)Solms in A & C DC[2]
JUNCACEAE
Juncus acutus L.
J aridicola L. Johnson
J. articulatus L.
J. bufonius L.[2]
J. holoschoenus R. Br.[2]
J. kraussii Hochst.
J. pauciflorus R. Br.[2]
J. subsecundus Wakef.[2]
J. usitatus L. Johnson
POACEAE
Agrostis avenacea J. Gmelin
Bromus catharticus M. Vahl.
B. rubens L.
Chloris truncata R. Br.
Cynodon dactylon (L.)Pers.
Distichlis distichophylla (Labill.)Fassett
Echinochloa crus-galli (L.)Beauv.
Enteropogon acicularis (Lindley)Lazarides
Eragrostis australasica (Steudel.)C.E. Hubb.
E. dielsii Pilger var. dielsii
E. elongata (Willd.)Jacq. f.
E. lacunaria F. Muell. ex Benth.
E. tenellula (Kunth)Steudel
Eulalia fulva (R. Br.)Kuntze
Hemarthria uncinata R. Br. var. uncinata
Homophilus prolutus [§]
Lolium perrene L.
Paspalum distichum L.
P. vaginatum Sw.
Paspalidium jubiflorum (Trin.)Hughes
Phragmites australis (Cav.)Trin. ex Steudel
Poa fordeana F. Muell.
Polypogon monspeliensis (L.)Desf.
Pseudoraphis spinescens (R. Br.)Vick.
Sporobolis mitchellii (Trin.)C.E. Hubb. ex S.T. Blake

S. virginicus (L.)Kunth
Triraphis mollis R. Br.
TYPHACEAE
Typha domingensis (Pers.)Steudel
T. orientalis C. Presl
LEMNANCEAE
Lemna disperma Hegelm.
Spirodella punctata (G. Meyer)C. Thompson[2]
CYPERACEAE
B. arthrophylla (Nees)Boeckeler
Baumea articulata (R. Br.)S.T. Blake
Bolboschoenus caldwellii (V. Cook)Sojak
B. medianus (V. Cook)Sojak
Carex appressa R. Br.
Cyperus bulbosus Vahl
C. difformis L.
C. exaltatus Retz.
C. gunnii Hook. f.
C. gymnocaulos Steudel
C. hamulosus M. Bieb.[2]
C. pygmaeus Rottb.
C. rigidellus (Benth.)J. Black
C. vaginatus R. Br.
C. victoriensis C.B. Clarke
Eleocharis acuta var. pallens Benth.
E. pallens (Benth.)S.T. Blake[2]
E. pusilla R. Br.
E. sphacelata R. Br.
Fimbristylis velata R. Br.
Isolepis austaliensis (Maiden & Betche)
I. fluitans (L.)R. Br.[2]
I. platycarpa (S.T. Blake)Sojak[1]
I. producta (C.B. Clarke)K.L. Wilson[1]
I. marginata (Thunb.)A. Dietr.[2]
Schoenoplectus litoralis (Schrader)Palla
S. pungens (Vahl)Palla
S. validus (Vahl)A. Love & D. Love

Appendix 2.

The following papers are bound in support of the thesis.

- Blanch, S. and Walker, K.: Life history strategies and water regime gradients in the Lower River Murray, South Australia. *Internationalen Vereinigung fur Theoretische und Angewandte Limnologiae*, in press.
- Blanch, S.J., Walker, K.F. and Ganf, G.G. 1994: *An evaluation of the River Murray Hydraulic Model and its value in environmental flow management.* Proceedings of a seminar on 'Environmental Flows' convened by the Australian Water and Wastewater Association, Canberra, 25-26 August, 1994.

Blanch, S.J. & walker, K.F. (1997) Littoral plant life history strategies and water regime gradients in the River Murray, South Australia.
Internationalen Vereinigung fur Theoretische und Angewandte Limnologiae.

Blanch, S.J., Walker, K.F. & Ganf, G.G. (1994) An evaluation of the River Murray hydraulic model, and its value in environmental flow management.
Presented at: Environmental Flows Seminar, Canberra Australia, 25-26th August