Ecological benefits of 'Environmental Flows' in the Eastern Mt. Lofty Ranges

by

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SUB CRUCE LUMEN

river
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management board

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Declaration

This thesis contains no material which has been accepted for the ward of any other degree or diploma in any university or other tertiary institution and to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text. I consent to the thesis being made available for photocopying and loan if accepted for the award of the degree.

………………………………

Brian Martin Deegan

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Summary

This thesis examined the impact of anthropogenic alterations in four riverine catchments of the Eastern Mt. Lofty Ranges, South Australia, to identify if creek restoration via environmental flows is a viable management option and if so, to determine;

1) Whether an aquatic / riparian viable seed bank was present and if so what was its composition
2) The ecological condition of selected riverine reaches. This in combination with the seed bank study would identify those creeks that would most benefit from the imposition of environmental flows
3) The response of key species to the water regimes likely to result from the imposition of environmental flows
4) The influence of nutrient enrichment under a fluctuating water level and to use this information to formulate best practice policy for environmental flows
5) Whether aquatic plants promoted by environmental flows were a significant fraction of the diet for higher trophic levels represented by Trichopterans and Amphipods.

The seed banks were of comparable density (ranging from 4,000 to 110,000 seeds m^{-2}) and species richness (ranging from 13 to 20 aquatic / riparian species) to the seed banks of other Australian rivers and wetlands, but this varied significantly among riverine sections and across catchments. Out of a total of 81 species recorded, 51 were classified as terrestrial (63% of all species recorded). What is of greater concern was the number of exotic (both aquatic and terrestrial) species recorded: 43% of the species recorded in the Angas, 47% of the species in the Finniss, 39% of the species in Tookayerta creek and 43% of the species recorded in Currency creek were exotic, which are significantly higher in comparison to other Australian studies. There were 24 to 28 aquatic / riparian species recorded in the extant vegetation of each catchment that were not recorded in their seed banks. Likewise, a number of species (3 to 7) were recorded in each catchments seed bank that were not recorded in the extant vegetation of those catchments. A species of particular interest is *Crassula sieberana*, which is on the State endangered plant species list.

Indices for assessing the ecological condition, health or integrity of a river or riparian habitat were employed to investigate the relationship between the river/riparian habitat and

the land and water management practices associated with those habitats. Of the four catchments surveyed, each catchment identified a unique set of site parameters (subindex indicators) that were strongly correlated with its ecological condition. Indicator species analyses revealed pasture grasses to be a significant indicator of reaches in very poor condition (p = 0.0010) along the Finniss and *Baumea juncea* of those reaches in good condition (p = 0.0230). Along the Angas, *Cotula coronopifolia* was an indicator of those reaches in average condition (p = 0.0240) and along Currency creek, *Cladium procerum* was an indicator of those reaches in good condition (p = 0.0190). However, when all 115 surveyed reaches were analysed together, those reaches of average to excellent ecological condition were all strongly correlated (R^2 = 0.50) with the subindex indicators: bank stability, % riparian cover, grazing, fenced, aquatic wood, and width of the riparian vegetation. This would indicate that these subindex indicators are the main site parameters determining the ecological condition of a riverine reach and hence its restoration potential. Those catchments or sub-catchments containing a high proportion of reaches classified to be in poor to very poor condition had significantly reduced seed banks.

The influence of water level fluctuations (±15 cm, ±30 cm and ±45 cm) on the growth of four species of emergent macrophytes (*Cyperus vaginatus, Phragmites australis, Typha domingensis* and *Triglochin procerum*) were species dependent. These species naturally inhabits different zones across the elevation gradient. *C. vaginatus*, which has a high elevation preference, was strongly inhibited by increasing water depth and fluctuations in water levels. In contrast, species with an intermediate elevation preference, such as *Phragmites australis* and *Typha domingensis*, were more tolerant to both depth and water level fluctuations. However, the biomass and relative growth rate (RGR) of *T. domingensis* and *P. australis* were depressed when grown under the combination of deep elevation and a highly fluctuating water level (±45 cm). Between the static and ±45 cm amplitude treatments, growth of *T. domingensis* was inhibited by 52%. The growth of *P. australis* appeared to be enhanced by fluctuating water levels and only showed a severe drop-off in growth in the deep elevation, ±45 cm amplitude treatment. In *C. vaginatus* the RGR was dependent of the average emergent surface area (and the implied rate of carbon acquisition) ($p<0.0001$; $r^2=0.7196$; $F=87.276$; $n=36$; RGR (mg g^{-1} day^{-1}) = -5.096 + 4.313 × ln (Average emergent surface area (cm^2)), but this was not the case in *P. australis* and *T. domingensis* ($p>0.05$) even when the photosynthetic canopy was partially inundated by rising water levels. Yet these two species demonstrated different growth rates when grown under different water regime amplitudes and at different elevations. Growth of *T. procerum* did not respond to either amplitude or elevation, but its RGR remained negative. This suggests that another factor(s) was limiting the growth of *P. australis, T. domingensis* and possibly *T. procerum*, a factor that varies with water level.

Cyperus gymnocaulos had significantly increased plant performance (p <.0001) with increased nutrient loading rates but this effect was significantly reduced under a fluctuating water regime (p =0.0007). Remarkably, under a fluctuating regime, *P. australis* had a significant reduction in performance with increased nutrient loading rates (p =0.0013), whereas *T. domingensis* performance was significantly limited (p =0.034) even with increased nutrient loading rates. *T. procerum* too had increased plant performance with increased nutrient loading rates but this effect was reduced under a fluctuating regime. The morphological response by *T. procerum* demonstrates that it is mainly limited by the nutrient loading rates and not the water regime. However, it was significantly limited/reduced by its increased turnover rates caused by a stochastic fluctuating water regime. Illustrating that in fact the effects of nutrient enrichment on *T. procerum* were independent of water regime but bearing in mind that water regime is the primary factor determining the productivity of this species. For those species with higher elevation preferences, e.g. *C. gymnocaulos*, or low elevation preference, e.g. *T. procerum*, the effects of nutrient loading are independent of water regime, whereas those species with an intermediate elevation preference, e.g. *P. australis* and *T. domingensis* the effects of nutrient loading are largely dependent on the water regime.

Amphipoda and Trichoptera selectively fed on succulent semi-emergent macrophytes across sites of average to excellent ecological condition (31-64% to 65-97% of diet), depending on availability. These semi-emergent macrophytes contained the lowest C:N ratio (≈10:1), closest to that of their consumers (≈5:1) and therefore the highest nutritional content. In degraded riverine reaches, there were limited food resources available, hence course particulate organic matter (CPOM) formed the main dietary components of Amphipoda (20-53% of diet) even though it had the highest C:N ratio (≈40:1). At site VP. 1, filamentous algae was the main dietary component of Trichoptera (48-64% of diet) due to its availability and its low C:N ratio (≈14:1) in comparison to the other primary sources available. The imbalanced consumer-resource nutrient ratios in these degraded riverine reaches are likely to impose constraints on the growth and reproduction of their aquatic shredder communities with probable knock-on effects at higher trophic levels.

The installation of environmental flows to restore and promote aquatic / riparian plant communities, which in turn would benefit higher trophic organisms, is a viable and realistic management option along selected reaches. Those selected reaches contain a significant aquatic / riparian seed bank and with sufficient physical habitat remaining to promote their germination and establishment. However, the imposition of environmental flows as a control measure to prevent the colonisation and dominance of particular species (*T. domingensis* and *P. australis*) was deemed to be redundant as a management technique given the limited water resources available.

Foreword

This thesis has been prepared as a serious of chapters in a format that will be suitable for future publication in scientific journals. To maintain the sense of individual chapters, this has inevitably led to some repetition between chapters.

CHAPTER 1.

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1 General Introduction

Healthy, self-sustaining river systems provide important ecological and social goods and services upon which human life depends (Postel and Richter 2003). The number and magnitude of anthropogenic stressors that threaten these services is growing rapidly (Giller *et al.* 2004) , raising concerns over their sustainability. These stressors are both internal, such as direct pollution and geomorphic engineering of the river channel, and external, for example through land-use change in the catchment (Giller 2005).

Urban and agricultural activities contribute to the demise and degradation of river ecosystems, primarily by altering their capacity to perform critical ecosystem functions and services (Allan 2004; Allan *et al.* 1997). In addition, anthropogenic activities can adversely effect structural diversity with in river systems, as well as reduce water quality for human use (Moerke and Lamberti 2004). Freshwater habitats and organisms are threatened throughout the world (Palmer *et al.* 1997) which has resulted in species loss from freshwater systems being greater than any other system (Jenkins 2003). This has stimulated major restoration efforts worldwide (Giller 2005; Moerke and Lamberti 2004; Nakamura *et al.* 2006; Palmer *et al.* 2005). In the United States, for example, public and private organizations have spent about $15 billion (US) on more than 30,000 river and wetland restoration projects since 1990 (Bernhardt *et al.* 2005; Malakoff 2004) and in Japan more than 23,000 river restoration projects have been conducted during the last 15 years (Nakamura *et al.* 2006).

1.1 Deterioration of aquatic ecosystems

In Australia anthropogenic alterations of aquatic ecosystems can have detrimental ecological impacts not only on the inhabitants but also on the landscape itself (Harris 2001b; Thoms and Walker 1993; Walker 1985; Walker and Thoms 1993). Specific issues include: ecological degradation caused by river regulation, declining native fish populations, increasing stream salinity, loss of riparian and aquatic vegetation and invasion by exotic taxa, increased sedimentation because of poor catchment management, increases in the occurrence and severity of blue-green algal blooms, deterioration of the number and quality of floodplain wetlands and reduced in-stream habitat (Ladson *et al.* 1999).

As a result many rivers have been transformed from clear and macrophyte dominated systems to an alternate state, turbid and plankton dominated systems (Harris 2001b). The Darling, Murray, Napean, Hawkesbury, and Swan Rivers in Australia all show this switch to plankton dominated systems, but others, particularly the more ephemeral systems, either have a much reduced biodiversity or a substantial micro-benthos community (Burns and Walker 2000a; Burns and Walker 2000b; Sheldon and Walker 1997). This increased algal production may dominate the food webs of many rivers (Bunn and Davies 1999; Bunn *et al.* 2003; Harris 1999a) and these changes will have had, as yet, largely unquantified impacts on the dynamics of organic carbon cycles (Robertson *et al.* 1999) and food chain structure and function. Not surprisingly, these effects are probably no longer reversible without massive, and unrealistic, landscape rehabilitation (Folke *et al.* 2004; Harris 2001b; Scheffer *et al.* 2001).

1.2 Regulation of flows

Over half of the world’s accessible surface water is already appropriated by humans, and this is projected to increase to an astounding 70% by 2025 (Postel 1998). Water resource developments such as impoundments, diversion weirs, river abstraction and exploitation of aquifers, for the primary uses of irrigated agriculture, hydropower generation, industry and domestic supply, are responsible worldwide for unprecedented impacts to riverine ecosystems, most of which emanate from alterations to the natural hydrological regime (Rosenberg *et al.* 2000). A substantial body of evidence has accumulated supporting the natural flow paradigm (Poff *et al.* 1997), where the flow regime of a river, comprising the five key components of variability, magnitude, frequency, duration, timing, and rate of change, is recognized as central to sustaining biodiversity and ecosystem integrity (Rapport *et al.* 1998a; Rapport *et al.* 1998b; Richter *et al.* 1997; Rosenberg *et al.* 2000).

Flow regulations have changed the hydrology of rivers on three scales of temporal variation (Walker *et al.* 1995): the flood pulse (days to weeks), flow history (weeks to years) and the long term statistical pattern of flows, or water regime (decades or longer). It is this regulation that is widely acknowledged to be a major cause of deteriorating conditions in many rivers and floodplain ecosystems (Bunn and Arthington 2002; Kingsford 2000; Walker 1985; Walker *et al.* 1995). Bunn and Arthington (2002) review four key flow-related processes underlining the degradation of regulated rivers: habitat alterations and loss, disruption of life history processes and recruitment, loss of longitudinal and lateral connectivity, and susceptibility to invasions by exotic species. It is these processes, which have altered the natural distributions of species and the dynamics of aquatic populations and community structure, ecological interactions, and the transport of resources and energy through these altered systems (Arthington and Pusey 2003; Sparks 1995; Ward and Stanford 1995).

The water or flow regime is the primary factor influencing the composition and diversity of the plant communities that inhabit aquatic and riparian regions (Blanch *et al.* 1999b; Blanch *et al.* 2000; Boulton and Lloyd 1992; Brock 1994; Brownlow *et al.* 1994; Casanova and Brock 2000; Kingsford 2000; Lyte and Poff 2004; Maheshwari *et al.* 1995; Nicol *et al.* 2003; Poff *et al.* 1997; Rea 1992). A consequence of flow regulation and changing land use is that the floristic composition of aquatic habitats may alter (Blanch *et al.* 1999b; Blanch *et al.* 2000; Brock *et al.* 1999; Brownlow *et al.* 1994; Budelsky and Galatowitsch 2000; Froend and McComb 1994; Nicol *et al.* 2003; Rea 1992). Blanch *et al.* (1999b; 2000) showed that in the River Murray submerged macrophytes, with relatively low C : nutrient ratios, were restricted to weir pools whereas emergent species with much higher C : nutrient ratios dominated the majority of the river reaches. As many primary herbivores have C:N ratios of 5:1 (Evans-White *et al.* 2005) there is the possibility of a stoichiometric mismatch if their food source is restricted to carbon rich species. Similarly, Tibbetts and Molles (2005) compared nutrient ratios in cottonwoods in flood and non-flood sites on the Rio Grande, U.S.A. and suggested that these may impose a food quality constraint on the detritivores, illustrating just how an alteration of floristic composition alone without an alternation of states can impact on higher trophic levels.

1.3 Restoration approach

Restoration is defined as returning a site to a condition similar to the one that existed before it was altered, along with its predisturbance functions and related physical, chemical and biological characteristics (Middleton 1999). Restoration seeks to provide habitat and resources, to alter ecological processes – stimulating some and curtailing others, to moderate inputs and to favour some species and reduce others (Lake 2005). It can have two perspectives; one seeks to move away from a degraded state while the other seeks to approach some desired condition (Palmer *et al.* 2005). River restoration can be passive, where we simply allow natural hydraulic forces to reshape rivers slowly and reinstate the natural heterogeneity (Gillilan *et al.* 2005). Alternatively, we can apply specific and active measures more rapidly to modify channel form and structure or to reintroduce variations in stream flow (Giller 2005). Restoring rivers means not only dealing with their channels, but also dealing with their riparian zones (floodplains) and their catchments (Lake 2005).

Given the importance of freshwater systems in the provision of ecological services and diverse habitats for a huge range of species, there is a clear need for restoration that can maintain sustainable ecological services whilst reinstating ecosystem function and habitat range (Ehrenfeld 2000; Giller 2005). The restoration of a river or stream must be judged on whether the restoration is an ecological success (Palmer *et al.* 2005). Ecologically successful river restoration creates hydrological, geomorphological and ecological conditions that allow the restored river to be a resilient self-sustaining system, one that has the capacity for recovery from rapid change and stress (Walker *et al.* 2002).

In response to mounting environmental concerns, rivers and wetlands are now recognized as legitimate ‘users’ of water and jurisdictions must provide water allocations to sustain and where necessary restore ecological processes and the biodiversity of water-dependent ecosystems (ARMCANZ and ANZECC 1996). The re-introduction of variable stream flow regimes is proposed as a possible management tool to solve problems caused by flow regulations in the United States, Europe, Asia, Africa and Australia (Arthington and Pusey 2003; Bunn and Arthington 2002; Lake 2005; Leyer 2005; Poff *et al.* 1997; Puckridge *et al.* 1998; Richter *et al.* 1997; Rosenberg *et al.* 2000; Tharme 2003)

1.4 Instalment of Environmental flows

Recognition of the escalating hydrological alteration of rivers on a global scale and the resultant environmental and ecological degradation has led to the establishment of the science of environmental flow assessment (Tharme 2003). This area of science focuses on the water regime of a river, wetland or coastal zone to maintain ecosystems and their processes where there are competing water uses and where flows are regulated (Dyson *et al.* 2003). A rivers flow regime is now recognised as a “master variable” that drives variation in many other components of a rivers ecosystem, e.g. fish populations, floodplain forest composition, nutrient cycling, both directly and indirectly (Poff *et al.* 1997; Sparks 1995). A river’s natural flow regime is a cornerstone for determining ecosystem flow requirements and this is why an environmental flow prescription should always mimic natural flow characteristics as far as possible (Poff *et al.* 1997). The goal of environmental flows is to provide a flow regime that is adequate in terms of quantity, quality and timing for sustaining the health of the rivers and other aquatic ecosystems (Dyson *et al.* 2003). This raises two questions: How much water does a river need to remain ecologically sustainable? and How can this water be clawed back from other users? (Arthington and Pusey 2003).

In New Zealand, 30 – 75% of the natural mean annual flow was deemed sufficient to maintain the ecological standing of rivers in the Kapiti Coast district (Forlong 1994). In Australia, studies conducted in Queensland rivers suggest that around 80 – 92% of natural mean annual flow may be required to maintain a low risk of environmental degradation and some rivers in the Northern Territory are maintained at 80% of their natural flow. Whereas two-thirds of various flow indicators has been proposed as the restoration target for the River Murray, and 28% of the mean annual flow has been negotiated for the Snowy River in Victoria (Arthington and Pusey 2003). The Tennant or Montana method used calibration data from hundreds of rivers in the mid-Western states of the United States to specify minimum flows to protect a healthy river environment (Tennant 1976). Percentages of the mean annual flows are specified that provide different quality habitat for fish e.g. 10% for poor quality (survival), 30% for moderate habitat (satisfactory) and 60% for excellent habitat (Dyson *et al.* 2003). At least 25 countries have either applied this method as originally expounded by Tennant or in a modified form on the basis of various hydrological, geomorphological, ecological or catchment-based criteria (Dunbar *et al.* 1998). This method has become the most commonly applied hydrological methodology worldwide (Tharme 2003). A distinction may be made between the amount of water needed to maintain an ecosystem in close to pristine condition, and that which may be allocated to it (Dyson *et al.* 2003). Environmental flow assessment involves defining an appropriate flow to meet specific environmental objectives, so as to achieve a balance between environmental, social and economic conditions (Dyson *et al.* 2003).

1.5 The Project

The re-introduction of variable stream flow regimes is proposed as a possible management tool to solve problems caused by flow regulations (Arthington and Pusey 2003; Bunn and Arthington 2002; Lake 2005; Leyer 2005; Poff *et al.* 1997; Puckridge *et al.* 1998; Richter *et al.* 1997; Rosenberg *et al.* 2000; Tharme 2003). However, this is a very costly process and it is questionable whether the restoration of flows alone will result in any measurable improvement in the ecological functioning of those altered rivers (Robertson 1997). This present study will investigate the potential for environmental flows to stimulate macrophyte growth in four fragmented altered riverine systems and the ecological benefits that will stem from this action.

1.5.1 Implications for flow restoration

1.5.1.1 Current ecological health/condition (Chapter 2)

Efforts to restore river health that focus solely on reducing the impact of regulated flows may be nullified if land management practices are not considered as part of river ecosystem management (Robertson and Rowling 2000), particularly with regard to the restoration of aquatic and riparian plant communities. Before any restoration efforts are put in place, the current ecological health/condition of a river or stream needs to be established. Indicators of riverine health include: the biota present, water quality, hydrology, geomorphology and availability of physical habitat (Maddock 1999). Considerable evidence links the quality and quantity of physical habitat at a range of spatial scales and the structure and function of indigenous biological communities (Maddock 1999), hence it is a major determinant of aquatic community potential (Aadland 1993). Therefore, the physical habitat availability can be used to determine the restoration potential of aquatic and riparian plant communities. It is hypothesised that riverine reaches subjected to extensive land clearance, channelisation and regulation of flows will have significantly reduced physical habitat. This information can then be used to determine if restoration is warranted and if so, determine if restoration (via environmental flows) is a viable management option.

1.5.1.2 Aquatic and riparian seed bank (Chapter 3)

Anthropogenic alterations to aquatic ecosystems can have detrimental consequences, not only on the plant communities present but also on their seed banks (Boedeltje *et al.* 2002; Brock 1994; Brock 1999; Brock *et al.* 1999; Casanova and Brock 2000; Nicol *et al.* 2003; Peterson and Baldwin 2004; Warwick and Brock 2003). It is questionable whether there is still an aquatic and riparian seed bank remaining along severely degraded reaches. It is hypothesised that due to the impact of land clearance coupled with reduced flows, the flora present will be dominated by exotic, agricultural weeds resulting in a depauperate seed bank of aquatic and riparian species. Again the impact of environmental flows may be nullified if there is an inadequate aquatic and riparian seed bank.

1.5.1.3 Species productivity in relation to water regime (Chapter 4)

Knowledge of how vegetation parameters such as species productivity relate to water regime is valuable because even small changes in the hydraulic regime can have significant effects on the diversity and community structure of emergent macrophytes (Blanch *et al.* 1999a; Blanch *et al.* 1999b; Blanch *et al.* 2000; Brock and Casanova 1991; Brock and Casanova 1997; Maheshwari *et al.* 1995; Rea and Ganf 1994a; Rea and Ganf 1994b; Stromberg 2001). The current flow regimes would tend to favour those aquatic species that were either very tolerant of ‘dry’ conditions (e.g. *Cyperus* spp) and or generalist species such as *Typha* and *Phragmites*. The response of key species to the water regimes likely to result from the imposition of environmental flows is vital in understanding and predicting the responses of the present aquatic macrophytes communities to environmental management practices (Froend and McComb 1994). The species chosen for this study (*Cyperus vaginatus, Phragmites australis, Triglochin procerum* and *Typha domingensis*) naturally inhabit different zones along the elevation gradient ranging from deep water (*Triglochin procerum*) to fully exposed elevations high above the waters surface (*Cyperus vaginatus*). It is hypothesised that species will display similar tolerances to water depth and amplitude of water level fluctuations, tolerances that can be related to the elevation preference of each species.

1.5.1.4 Influence of water regime over nutrient loading (Chapter 5)

There is increasing concern as to the effects of nutrient loading into previously nutrient limited aquatic environments, particularly as most rivers are regulated (Puckridge *et al.* 1998). Anthropogenic nutrient loading into aquatic systems increases macrophyte production (Carr and Chambers 1998; Stevens *et al.* 2006); however, plant responses to nutrient supply may be influenced by the water regime, as variations in hydrology will affect nutrient dynamics (Baldwin and Mitchell 2000; Neill 1990; Spink *et al.* 1998). As flooding of the photosynthetic canopy will limit the capacity for the acquisition of carbon (Blanch *et al.* 1999a; Siebentritt 2003), it is hypothesised that under treatments of high nutrient loadings, excess resource availability, plant performance/productivity will not be reduced due to increasing fluctuations of water levels. It is further hypothesised that those more responsive faster growing species (e.g. *P. australis* and *T. domingensis*) shall be more constrained by the limited availability of nutrients rather than atmospheric carbon limitation (water regime), compared to those less responsive slower growing species (e.g. *C. gymnocaulos*), which will be compromised more by carbon limitation rather than nutrient availability. There are limited studies on the influence of water regime over the effects of nutrient loading on the growth of emergent macrophytes (Grace 1988; Neill 1990; Newman *et al.* 1998). However, this information is important in understanding the implications of restoring flow regimes to nutrient enriched aquatic environments and the effects this may have on the macrophytes communities present.

1.5.1.5 Consequence of catchment degradation (Chapter 6)

A consequence of changes in catchment primary production, river regulation, and irrigation is that the floristic composition of rivers may alter. These changes will have, as yet, largely unquantified impacts on the dynamics of organic carbon cycles (Robertson *et al.* 1999) and food chain structure and function (Harris 1999a; Hicks 1997; Ward and Stanford 1983). This poses the questions of what are the principal energy sources supporting the lower trophic level consumers in modified riverine systems? And do these energy sources alter across a gradient in catchment degradation? If there is a change in principal energy sources across a gradient in catchment degradation then what is the significance of these alterations for the higher trophic consumers. It is hypothesised that in excellent reaches (wooded or forested) allochthanous carbon sources would be the principal food source and aquatic macrophytes would play a minor role (Bunn 1993; Cummins *et al.* 1995; Hicks 1997; Vannote *et al.* 1980). It is further hypothesised that because the very poor reaches were devoid of riparian vegetation and had few macrophytes, the role played by these sources in the food web would become redundant and be replaced by a nutritively inferior alternative.

Anthropogenic alterations and modifications in catchments have resulted in their demise and degradation. Environmental flows are essential for their restoration, but as to where, how and why they should be prescribed in order to achieve their ecological objectives has yet to be determined. To determine if environmental flows have been ecologically successful will be a complex process. Like economic forecasting, ecological forecasting is notoriously difficult and imprecise (Tilman 2001). Assessing whether the environmental flows have had a beneficial effect on riverine health may take some time, as ecological processes can often only be measured over a series of growing seasons. For example the expected response time of riparian vegetation to restoration efforts may take 5 – 20 years in Pacific Northwest streams (Ronni *et al.* 2002). In the floodplain restoration of the Kissimmee River in Florida, the response times for macrophytes were put at 3 – 8 years (Trexler 1995), and the benefits of providing environmental flow allocations to the Snowy River, Australia is not expected to be fully realised until 2020 (Lake 2005).

1.6 Eastern Mount Lofty Ranges – area of focus

Lowland rivers, especially those of the Murray-Darling Basin in south-eastern Australia, have been very extensively degraded (Cullen 2005; Kingsford 2000), so much so that now there are very few rivers or portions of them that can be said to be intact. The area of focus for this study are four fragmented rivers in the Eastern Mount Lofty Ranges; the Angas River, the Finniss River, Tookayerta creek and Currency creek, just south-east of Adelaide, South Australia (Fig. 1.1). This region is one of South Australia’s wettest areas even though rainfall varies considerably over the entire region. On average the region receives 750 mm of rain per annum but the higher elevations of the region can receive up to 1,000 mm of rainfall per annum, where as on the southeastern lower plains, rainfall can be as low as 450 mm per annum. Most of the rainfall is received in the winter from cold frontal systems sweeping up from the Southern Ocean. Long-term rainfall records for the upper Finniss catchments indicate an overall decreasing trend in annual rainfall, with the decline being more pronounced in the last 20 years. They also indicate a trend of decrease and/or delay of rainfall in the month of June (Savadamuthu 2003). Similar trends of decreasing annual and June rainfall were observed in studies of the Barossa Valley, the Onkaparinga and Marne catchments, South Australia (Savadamuthu 2003). Summer daytime temperatures are quite variable due to closeness of the Southern Ocean and range from 23 – 30^{o}C depending on the wind direction. Cooler days are experienced when cold frontal systems sweep in from the southwest and hotter days occur when North/Northwest winds bring hot, dry air to the region from central South Australia.

The water resources of these catchments are vital to the region’s prosperity. In recent years, increasing anthropogenic developments have put much pressure on the available water, through the increased use of farm dams and ground water extraction. For example, the upper Finniss catchment has around 1,246 farm dams with an estimated total storage capacity of 5,822 ML (Savadamuthu 2003). The total volume of water held in farm dams in many sub-catchments has either exceeded or is nearing sustainable diversion limits set out in the Catchment Water Management Plan for the River Murray in South Australia (Savadamuthu 2003). Discharge in a number of important rivers and creeks are decreasing, in some places significantly because water is increasingly being diverted to dam storage and directly pumped or extracted from adjacent wells (DWLBC 2003a). Flow is not only being reduced in these rivers (Fig. 1.2) but the timing of the flows (‘wet period’) is also being dramatically altered in recent times (Fig. 1.3). In the upper Finniss dams have potentially reduced the median summer flows by 72% and median winter flows by 7%. Though summer flows constitute only 2-3% of the annual flows, they are critical to the water dependent ecosystems, particularly at a time when these aquatic systems are highly stressed, i.e. the late summer, early autumn period (Fig. 1.3) (Savadamuthu 2003). Results of modelling also indicate that the current farm dams of the upper Finniss have significantly reduced the low to median daily flows, which are critical in sustaining catchment ecosystems (Savadamuthu 2003).

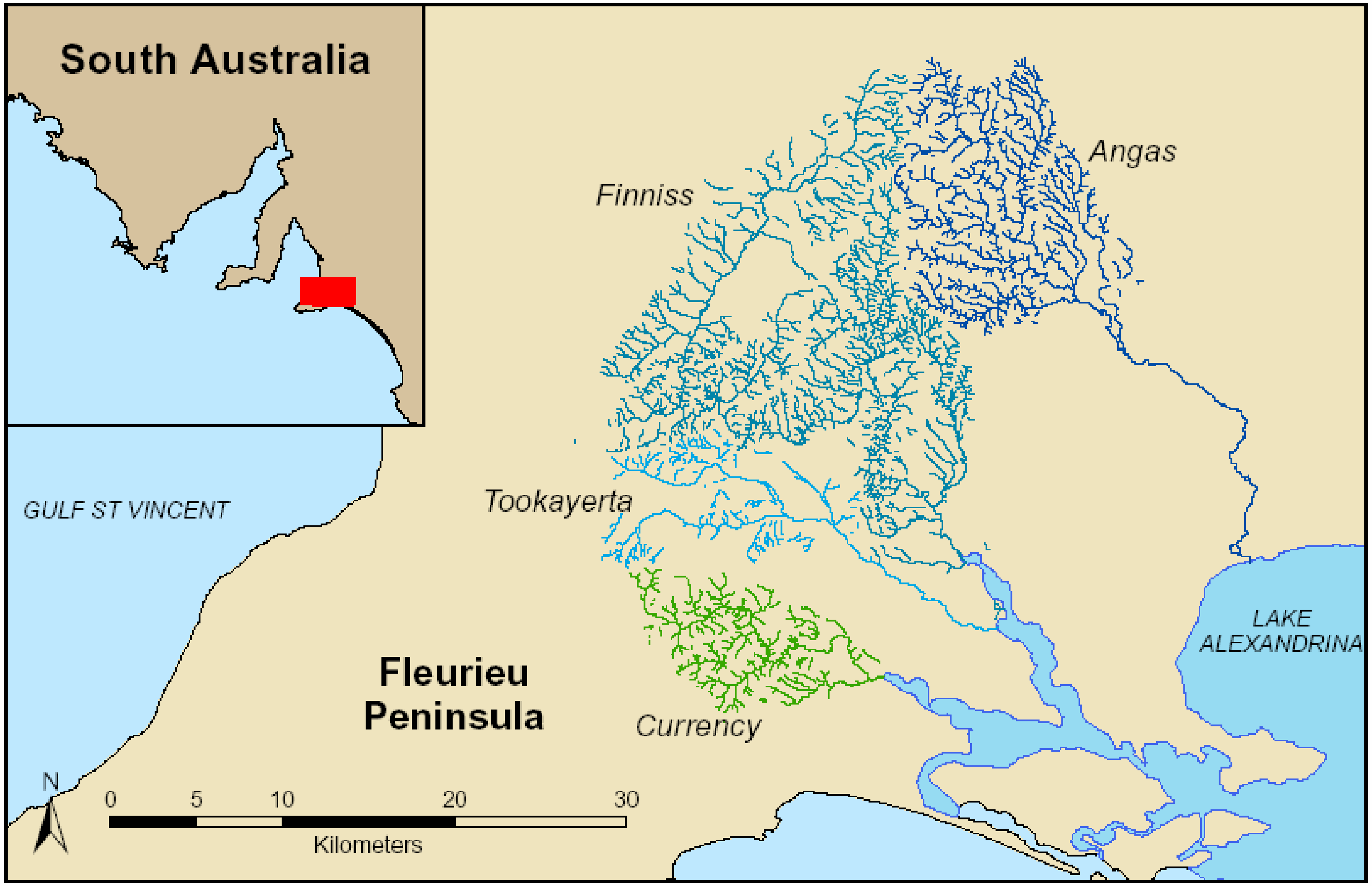

Figure 1.1: Location of the four study catchments in the Eastern Mt. Lofty Ranges in South Australia.

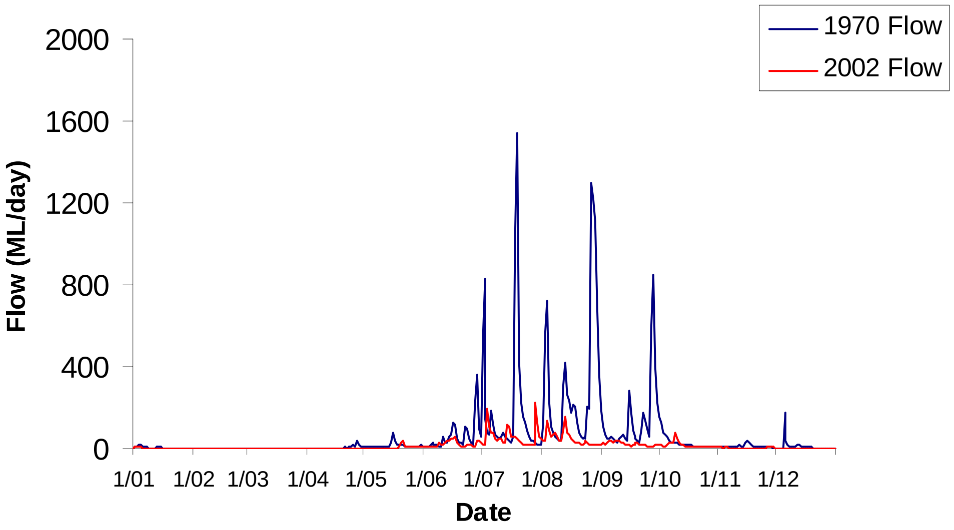

Figure 1.2: Comparison of discharge through the Finniss River at a location 4 km East of Yundi, (35°19′ S, 138°40′ E) for the years 1970 and 2002. Total discharge in 1970 was 24.2GL and in 2002 was 5.8GL.

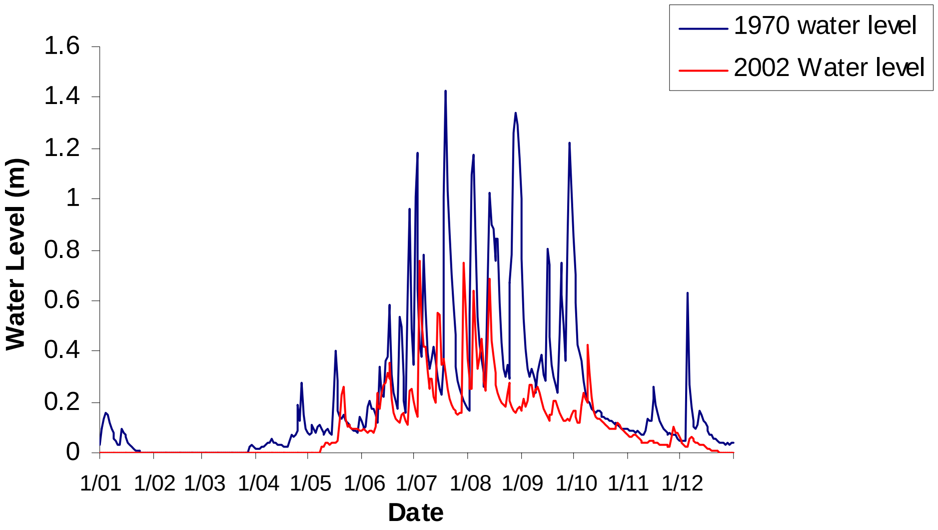

Figure 1.3: Comparison of variations in water level on the Finniss River at a location 4 km East of Yundi, (35°19′ S, 138°40′ E) for the years 1970 and 2002.

This region has also undergone extensive alterations in catchment primary production. The major land uses in this region include broad scale grazing, intensive grazing, vines, horticulture and floriculture, with limited protected areas. Extensive irrigation is assumed to be predominantly for viticulture and horticulture and to a lesser degree for intensive grazing (Savadamuthu 2003), which has severely impacted the ecology of these catchments.

CHAPTER 2.

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2 Assessing the ecological condition of riverine reaches and their restoration potential: Implications for Environmental Flows

2.1 Introduction

The ecological health/condition of a river or stream is a fundamental and increasingly important water management issue in Australia (Bunn *et al.* 1999; CSIRO 1992; Fairweather 1999). Since European settlement the vast majority of Australian catchments have been modified and altered (Lake 2005). Specific issues include; channelisation caused by catchment clearance and flow regulation (Poff *et al.* 1997; Sparks and Spink 1998), declining native fish populations (Harris and Silveira 1997), increased stream salinity (Peck *et al.* 1983), displacement of riparian and aquatic vegetation by exotic taxa (Baron *et al.* 2002; Merritt and Cooper 2000; Pettit *et al.* 2001), increased sedimentation (Erskine 1994), increased occurrence and severity of algal blooms (Baron *et al.* 2002), deterioration in number and quality of floodplain wetlands (Wasson *et al.* 1996), and the significant loss of riparian and in-stream habitat due to channelisation and catchment clearance (Biggs 1996; Maddock 1999). These have all contributed to the demise and degradation of Australia’s rivers and streams (Brierley *et al.* 1999; Harris 1999a; Harris 2001b; Thoms and Walker 1993; Walker 1985; Walker *et al.* 1997; Walker and Thoms 1993).

The provision of water allocations (environmental flows) from water storages at the expense of irrigation supplies (Arthington and Pusey 2003; EPA 1997; Norris and Thoms 1999) is a very costly process, particularly as South Australia is in a drought period. It is questionable whether the restoration of flows alone without the alteration of land management practices will result in any measurable improvement in the ecological functioning of those rivers (Robertson 1997). Therefore, before any restoration efforts are put in place, the current ecological condition of a river or stream needs to be established. This information can then be used to determine if restoration is warranted and if so, determine if restoration (via environmental flows) is a viable management option.

Indicators of riverine health include: the biota present, water quality, hydrology, geomorphology and availability of physical habitat (Maddock 1999). Stream biotic composition is strongly influenced by physical habitat (Norris and Thoms 1999) as it is their living space, and is defined as the local physical, chemical and biological features that provides an environment for those biota (Jowett 1997). It is a spatially and temporally dynamic entity determined by the interaction of the structural features of the river channel and the water regime (Maddock 1999). Considerable evidence links the quality and quantity of physical habitat at a range of spatial scales and the structure and function of indigenous biological communities (Maddock 1999). It has been argued that if the physical habitat is in poor condition, one would expect the biological health of a river or stream to be effected adversely (Brookes and Shields 1996), hence it is a major determinant of aquatic community potential (Aadland 1993). The riparian zone too, through its connection with the main channel, will also have an influence on riverine health (Naiman and Decamps 1997; Norris and Thoms 1999). It has a significant effect on material fluxes between terrestrial and riverine ecosystems (Naiman and Decamps 1997), so direct changes associated with riparian removal can have a detrimental impact on riverine ecosystem function and health (Bunn *et al.* 1999). The ‘Index of Stream Condition’ (Ladson *et al.* 1999) was one of the first river condition assessment tools to include physical features beyond those of the main river channel, as it recognised the important influence of riparian zones in contributing to riverine health.

The increasing environmental impacts on rivers and streams has driven the need for physical habitat assessment methods that measure ecological condition and integrity (Boulton 1999; Boulton and Brock 1999; Fairweather 1999; Maddock 1999). This information is vital in identifying those catchments/sub catchments for which restoration via environmental flows is a viable management option. In addition such tools can be used to assess the present river or stream health along selected reaches so their physical habitat availability can be compared before and after the restoration has taken place, and the effectiveness of the schemes can be appraised. It is important to recognize that the term habitat implies some biological significance, and that it is not simply an identifiable physical feature (Maddock 1999).

The purpose of this study was to identify those riverine reaches of sufficient ecological condition (physical habitat remaining and land management practices in place) that upon the addition of environmental flows would promote aquatic and riparian plant communities, resulting in their improved ecological structure and functioning. Water (Environmental flows) is a very valuable and vital resource in South Australia and therefore its allocation as environmental flows must be justified, particularly as South Australia is in a drought period. An assessment tool has been developed that will determine the ecological condition of selected reaches with the specific objectives of: i) determining the level of degradation across each surveyed catchment, ii) identifying the site parameters responsible for the ecological condition, iii) identifying those riverine sections that could benefit ecologically from the addition of environmental flows, and iv) in fragmented systems, determining whether environmental flows should be applied to the whole system or limited to particular sections or sub-catchments.

2.2 Materials and Methods

2.2.1 Study area

The study area is comprised of 4 fragmented catchments in the Eastern Mount Lofty Ranges (EMLR), the Angas, the Finniss, Currency and Tookayerta creeks, just southeast of Adelaide, South Australia (Fig. 1.1). This region has undergone extensive agricultural development, clearing, with alterations in catchment primary production. The major land uses in this region include broad scale grazing, intensive grazing, vines, horticulture and floriculture, with limited protected areas (Savadamuthu 2003). This has resulted in an increased pressure on the available water resources, leading to flows in a number in important rivers and creeks decreasing, in some places significantly (DWLBC 2003a). The total volume of water held in farm dams in many of the sub-catchments in the EMLR has either exceeded or is nearing sustainable diversion limits set out in the Catchment Water Management Plan for the River Murray in South Australia (Savadamuthu 2003).

2.2.2 Index of Riverine Ecological Condition

Incorporating indicators of geophysical and biological properties and processes, are likely to provide reliable estimates of the ecological condition in riverine ecosystems (Boulton and Brock 1999; Fairweather 1999). The ecological condition assessment tool developed here is similar to that of Ladson *et al.* (1999) and Jansen and Robertson (2001). Ladson *et al.* (1999) described an index of stream condition based on 18 indicators that measured alterations to the hydrology (an assessment of flow), physical form (condition of the channel and physical habitat), streamside vegetation, water quality and biota (macroinvertebrate populations) of streams. Jansen and Robertson (2001) developed and tested an index for the rapid appraisal of the ecological condition of floodplain riparian habitats using a subset of indicators proposed by Ladson *et al.* (1999). The Index developed here chose a similar approach and was designed to reflect the ecological condition of fragmented riverine reaches. The design selected indicators to reflect functional aspects of the physical, community and landscape features of both the riparian and aquatic zones – the physical habitat availability and condition, and therefore different from that of Ladson *et al.* (1999) as the indicators Hydrology (based on change in volume and seasonality of flow from natural conditions) and Aquatic life (based on number of families of macroinvertebrates) were absent. The index was broken down into five subindices, each with a number of indicator variables, as shown in Table 2.1; i) Habitat (habitat availability and degree of disturbance), ii) Banks (bank and soil structure and stability), iii) Riparian Cover (riparian vegetation cover, structural complexity and dominance of natives vs. exotics), iv) Water/Soil Quality (soil and water quality) and v) Vegetation Structure (continuity and complexity of in channel vegetation). The estimates for each indicator were scored and weighted, then summed to give a score out of 10 for each subindex. Then the five subindices were summed to provide a total index score out of 50 for each surveyed reach.

2.2.3 Reach selection and Rapid Appraisal Survey

Riverine reaches were selected after viewing longitudinal aerial videography of each of the fragmented catchments (DWLBC 2003b), from their mouths where they enter Lake Alexandrina, to their headwaters. Reaches were selected on the basis of their apparent canopy cover, apparent riparian zone, whether they appeared fenced or not, and the proximity of agricultural land usage. Reach selection was broken down into three categories; i) reaches that appeared to have a good canopy cover, riparian zone, and were apparently surrounded by dense native scrub/bush (non-agricultural); ii) reaches that appeared to have a good canopy cover, riparian zone, possibly fenced, and were surrounded by agricultural land usage; iii) reaches that appeared to have a poor canopy cover, little or no riparian zone, unfenced, and subjected to agricultural usage. A total of 51 reaches were selected along the Finniss, 29 along the Angas, 22 along Currency Creek and 13 along Tookayerta Creek (Appendix 1). These reaches were assessed subsequently in the field using the index of riverine ecological condition assessment tool.

A single observer who had previously completed a training period for standardisation purposes conducted all surveys during the spring of 2004 when all four rivers were running high. Each of the surveyed reaches was a 100m longitudinal section, which was subsequently broken up into five 20m sections. Estimates were made through observation for each indicator (Table 2.1) along each 20m longitudinal section. The estimates were averaged across all five 20m sections to provide a final estimate of each indicator for the 100m longitudinal section. Final estimates were scored accordingly and weighted, and then summed to give a total score for each reach. Potential scores ranged from 0 (worst condition) to 50 (best condition). In order to summarize some of the results, the total ecological condition scores (TECS) were grouped into five categories: Very poor condition < 25; Poor condition $\geq 25 < 30$; Average condition $\geq 30 < 35$; Good condition $\geq 35 < 40$; Excellent condition ≥ 40. The flora present along each surveyed reach was recorded and later used in Indicator Species Analysis.

Table 2.1: Subindices (and their weighting in the final score) and indicators of the index of riverine ecological condition, the range within which each indicator was scored, and the method of scoring for each indicator.

Sub-index (100m)	Indicator	Range	Method of scoring	Score
Habitat. (10/50)	Width of riparian vegetation.	0-4	≥ 15m = 4, 5 - < 15m = 3 1 - < 5m = 2, 0 - < 1m = 1 ≤ 0m = 0	
	Fenced or not	0-4	≥ 50yr = 4, 15 - < 50yr = 3 5 - < 15yr = 2, ≤ 5yr = 1 Not fenced = 0	
	Underwater slope	0-4	0 – 5% = 4, 5 – 10% = 3 10 – 15% = 2, 15 – 20% = 1 ≥ 20% = 0	
	Grazing	0-2	No grazing evident = 2 Moderate grazing evident = 1 Extensive grazing evident = 0	
				/10
Banks. (10/50)	Bank stability	0-4	Extreme erosion/little veg = 0 Extensive erosion = 1 Moderate erosion, banks held by discontinuous veg cover = 2 Isolated patches of erosion, with good veg cover = 3 Stable banks with no undermining and good veg cover = 4	
	Aquatic wood debris	0-4	None = 0 Parts of trees and branches along 25% of the bank = 1 Few large intact trees along > 25% of the bank = 2 Many large intact trees along >25% of the bank = 3 Numerous large intact trees along >50% of the bank = 4	
	Soil structure	0-2	No structure = 0 Roots and voids present = 1 Roots and voids plus either soil organisms or horizons evident = 2	
				/10
Riparian cover (10/50)	Canopy cover	0-3	0 = absent, 1= 1-30%, 2 = 31-60%, 3 = >60%	
	Understorey cover	0-3	0 = absent, 1= 1-30%, 2 = 31-60%, 3 = >60%	
	Ground cover	0-3	0 = absent, 1= 1-30%, 2 = 31-60%, 3 = >60%	
	Number of layers	0-3	0 = no vegetation layers to 3 = ground, under & canopy cover	
	Native v's Exotic	0-3	>60% Native = 3, 31-60% Native = 2 1-30% Native = 1, < 1% Native = 0	

	vegetation cover			**/10**
Water and soil quality (10/50)	Conductivity (µS cm^{-1})	0-4	Mt. Valley Plain <50 <100 <100 = 4 <150 < 250 < 300 = 3 < 300 < 400 < 500 = 2 < 500 < 700 < 800 = 1 ≥ 500 ≥ 700 ≥ 800 = 0	
	pH	0-4	6.5 – 7.5 = 4 6.0 – 6.4 or 7.6 – 8.0 = 3 5.5 – 5.9 or 8.1 – 8.5 = 2 4.5 – 5.4 or 8.4 – 9.4 = 1 >9.5 or < 4.5 = 0	**/10**
Vegetation structure (10/50)	Submerged	0-3	0 = absent, 1= 1-30%, 2 = 31-60%, 3 = >60%	
	Emergent	0-3	0 = absent, 1= 1-30%, 2 = 31-60%, 3 = >60%	
	Riparian	0-3	0 = absent, 1= 1-30%, 2 = 31-60%, 3 = >60%	
	Number of layers	0-3	0 = no vegetation layers to 3 = ground, under & canopy cover	
				/10
				Total Score **/50**

2.2.4 Data Analysis

The contribution of the subindices and their indicators to the ecological condition of surveyed reaches were determined using PC-ORD multivariate analysis (McCune and Mefford 1999). Non-metric multidimensional scaling (NMS) was used to determine the indicators that were highly correlated with the ecological condition of each surveyed reach. Multi-response permutation procedures (MRPP) were used to detect any significant difference between the flora recorded along surveyed reaches and the TECS for those given reaches (McCune and Grace 2002). Indicator species analysis was used to determine which plant species (terrestrial or aquatic) were significant indicators of reach TECS. Bray-Curtis similarities (Bray and Curtis 1957; McCune and Grace 2002) were used to calculate the similarity matrix for all multivariate community analysis and Relative Euclidean similarities (McCune and Grace 2002) were used for all multivariate environmental (subindices indicator) analysis. Two-dimensional ordination solutions with stress lower than 20% were deemed acceptable (Clarke 1993). The significance level for all statistical tests was chosen at *p* = 0.05.

2.3 Results

2.3.1 Ecological condition scores

The Finniss was the only river to contain reaches in excellent ecological condition (4 in total – see Table 2.2). The Angas on the other hand contained no reaches with an ecological condition score of higher than average; the majority of its reaches were classified to be in either poor or very poor ecological condition. Tookayerta and Currency both contained reaches ranging in ecological condition from very poor to good.

Table 2.2: Summary of Total Ecological Condition Scores (TECS) for surveyed reaches in each of the four catchments. In brackets is the percentage value of that score in relation to the total number of sites surveyed in that catchment.

Catchment	TECS = 1 Very Poor Condition	TECS = 2 Poor Condition	TECS = 3 Average Condition	TECS = 4 Good Condition	TECS = 5 Excellent Condition
Finniss	16	11	12	8	4
	(31%)	(22%)	(23%)	(16%)	(8%)
Currency	5	5	8	4	0
	(23%)	(23%)	(36%)	(18%)	(0%)
Tookayerta	3	2	2	6	0
	(24%)	(15%)	(15%)	(46%)	(0%)
Angas	15	9	5	0	0
	(52%)	(31%)	(17%)	(0%)	(0%)

All subindex scores increased with the increasing ecological condition of reaches, but some subindices contributed less than others (Fig. 2.1). For instance, soil and water chemistry varied little between sites, regardless of the total ecological condition score, where as the subindex habitat (width of riparian vegetation, fenced, grazing and underwater slope) appears to contribute significantly to the total ecological condition score.

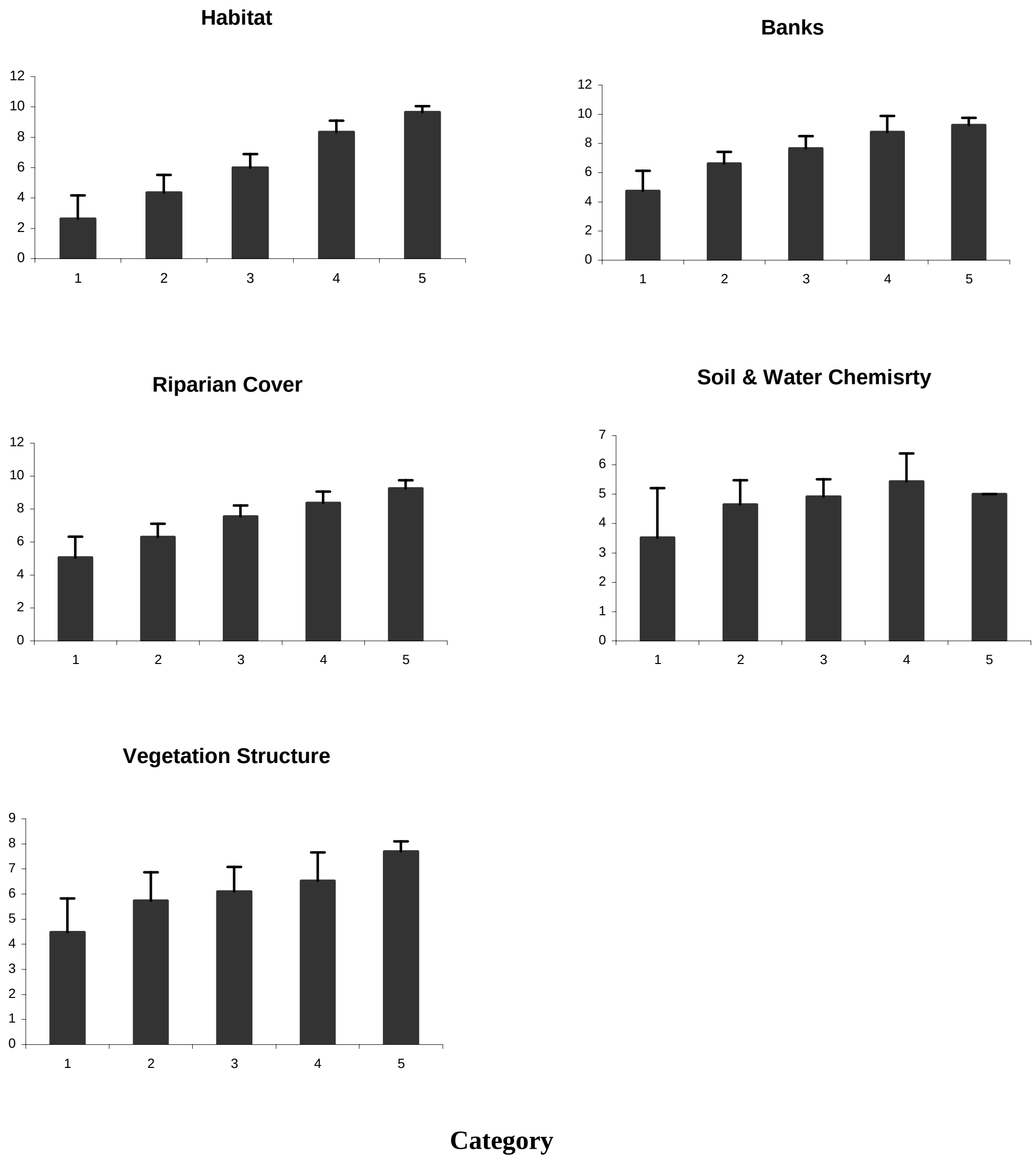

Figure 2.1: Mean scores for each subindex (Habitat, Banks, Riparian Cover, Soil & Water Chemistry and Vegetation Structure) for all sites in each category (1 = very poor, 2 = poor, 3 = average, 4 = good, 5 = excellent) based on the TECS (n = 115). Error bars show standard deviations.

2.3.2 Comparison of important indices among rivers

2.3.2.1 The Finniss

Analysis of the Finniss catchment using NMS and based upon the environmental features distinguished among the reaches (Fig. 2.2). Those reaches that had a TECS of 4 or 5 (good or excellent) were highly correlated ($R^2 = 0.650$) with the following vectors (subindex indicators): width of riparian vegetation, bank stability, aquatic wood, fenced, grazing, and canopy cover. However, those reaches with a TECS of 1 or 2 (very poor or poor) were negatively correlated with those vectors, and were rather more dispersed.

A closer analysis of the ordination and the grouping of sites according to their similarity based upon the subindices indicator scores revealed that the main grouping (site 1 to site 46A) each had a TECS of between 31 to 41.6 (average to excellent), with similarly high scores for the subindices habitat, banks and riparian cover. There was a sub-group (site 7 to site 40) within this group, which were strongly associated, with each reach having a TECS of 36.4 to 41.6 (good to excellent) and very similar high scores for the subindex indicators: width of riparian vegetation, fenced, underwater slope, grazing, bank stability, aquatic wood, canopy cover, understorey, submerged and riparian.

Sites 9 to site 48 each had a TECS of between 26.7 and 33.2 (poor to average) and had very similar scores for the subindex indicators: underwater slope, grazing, bank stability, aquatic wood, ground cover, understorey, native vs. exotic and riparian. Sites 15, 32 and 43 each had a TECS of from 26.8 to 29.7 (poor), with very similar subindex indicator scores for grazing, canopy cover, submerged and riparian. The remaining groupings of sites were all distinct. However, each scored relatively low for each of the subindex indicators, with TECS of between 26.4 to 15.4 (poor to very poor). The groupings were based on similar if not identical scorings for specific indicators, all of which made the groupings distinct but generally in a degraded to very degraded condition. Site 12 and site 30 were single reach groupings, which were not fenced and heavily grazed up to the waters edge. They were both unique and very degraded.

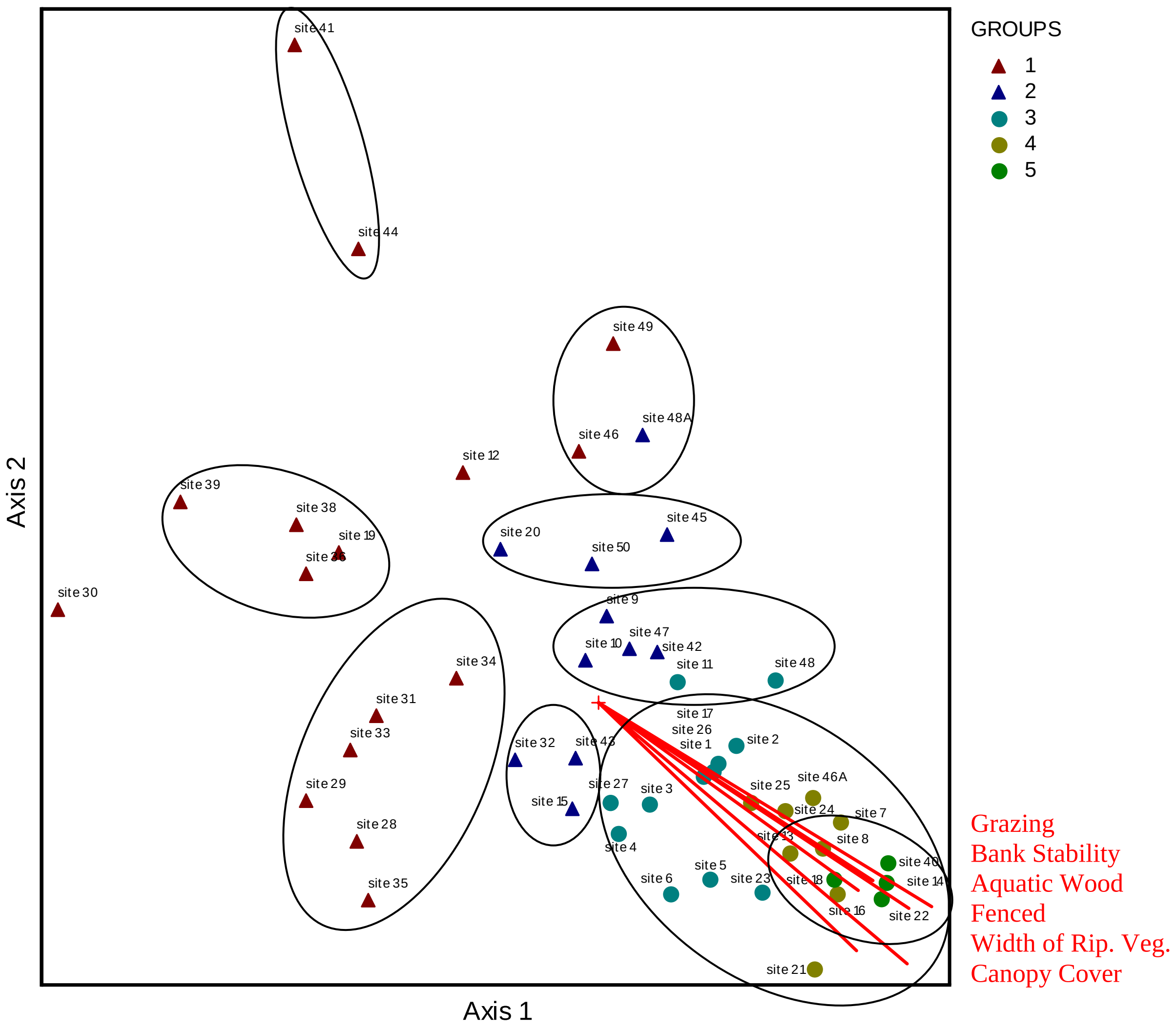

Figure 2.2: Non-metric multidimensional scaling (NMS) ordination of data for the Finniss catchment in each category (1 = very poor, 2 = poor, 3 = average, 4 = good, 5 = excellent) based on the subindices indicator scores for each site (n = 51). Final Stress = 14%, R^2 = 0.650.

A total of 52 species of flora were recorded along reaches through out the Finniss catchment (Appendix 2). An MRPP indicated that there was a significant difference ($p <$ 0.0001) among the species recorded along each reach and the TECS for those reaches. Indicator species analysis showed that pasture grasses were a significant indicator (p = 0.0010) of reaches with a TECS of 1 (very poor), along with *Rorippa nasturtium-aquaticum* (p = 0.0030). *Baumea juncea*, *Teline monspessulana* and *Pteridaceae esculentum* were significant indicators (p = 0.0230, 0.0080 and 0.0300 respectively) of reaches with a TECS of 4 (good).

2.3.2.2 The Angas

In the Angas catchment those surveyed reaches with TECS of 2 or 3 (poor or average) were highly correlated (R^2 = 0.50) with the vectors bank stability, submerged, soil structure, width of riparian vegetation, grazing, and fenced, based on a NMS analysis (Fig. 2.3). Separation of the vectors in-line with axes 1 and 2 indicates that those vectors in-line with axis 1 (Fenced, Grazing and Width of riparian vegetation) were the primary determinant of the ordination (R^2 = 0.696), and those vectors in-line with axis 2 (Bank stability, soil structure and submerged) were a secondary determinant (R^2 = 0.202).

A closer analysis of the ordination and the groupings of the sites revealed that site 1 and site 3 both had a TECS of 28.7 and 23.8 (poor and very poor) respectively, with the same low scores for the subindex indicators: fenced, bank stability, understorey cover, ground cover, native vs. exotic, submerged, and emergent. Site 2 is a unique single reach group, which is not fenced and is subjected to grazing, with excellent submerged and ground cover, but scores very poorly in all other aspects, with a TECS of 19.8 (very poor).

In the next grouping of sites (site 10 to site 28) each reach had a TECS ranging between 26.6 and 34.2 (poor and average), and had very similar high scores for the subindex indicators: width of riparian vegetation, soil structure, ground cover, and pH, with similar low scores for fenced, understorey cover, native vs. exotic, E.C, and submerged. The two reaches in the next grouping (site 16 and site 26) were very similar, each having a TECS of 25.7 and 29.4 respectively (poor). Both reaches scored the same low values for the subindex Habitat and for the subindex indicators: bank stability, understorey cover, native vs. exotic and riparian. Both reaches also scored the same high values for the subindex indicators; soil structure, ground cover, and emergent.

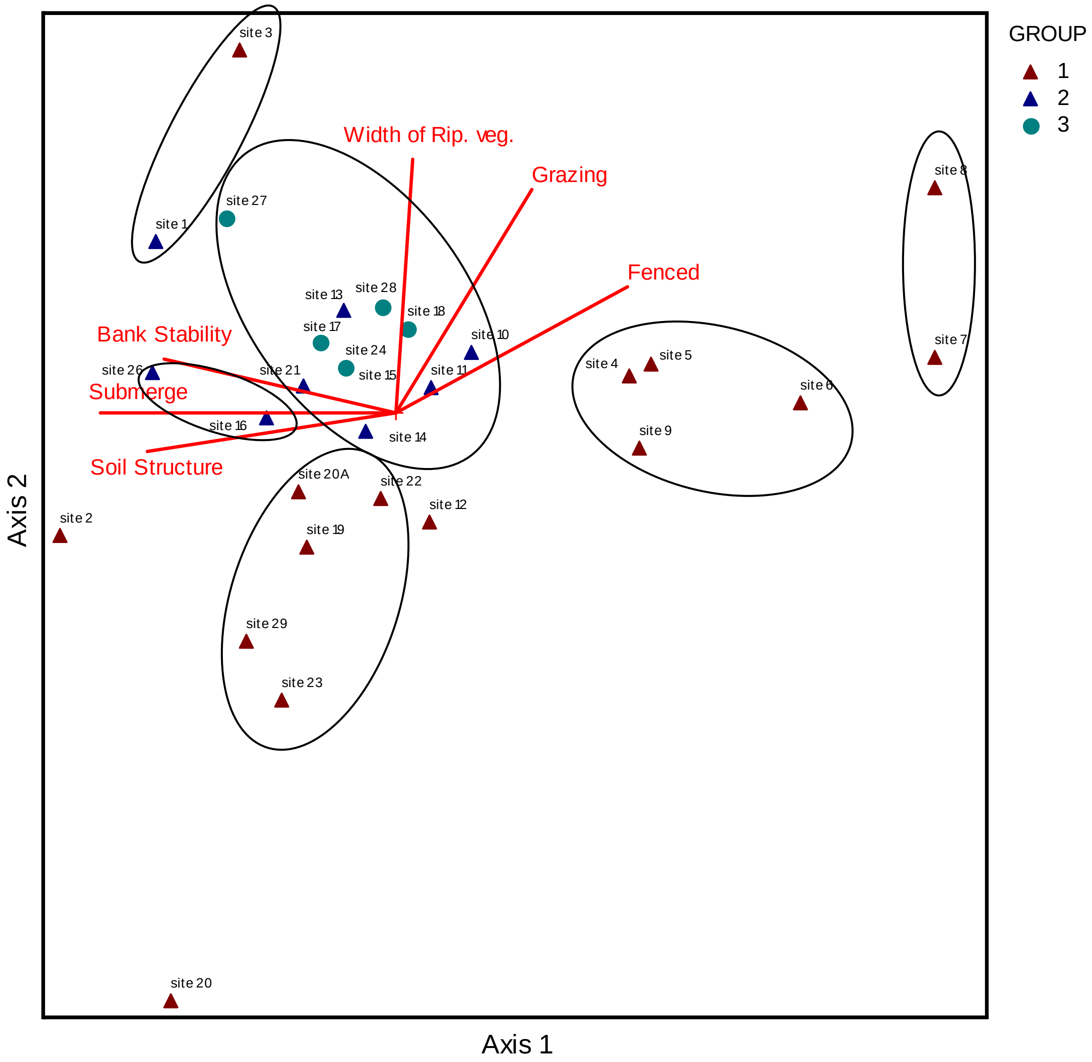

Figure 2.3: Non-metric multidimensional scaling (NMS) of data for the Angas catchment in each category (1 = very poor, 2 = poor, 3 = average), based on the subindices indicator scores for each site (n = 29). Final Stress = 13%. R^2 = 0.50.

Site 12 was a single reach group with a TECS of 21.4 (very poor). This reach was in very poor condition, scoring very poorly in all aspects except for the subindex indicators: emergent and ground cover. The reaches in the grouping of sites 19 to site 29 each had a TECS of between 18.8 to 23.7 (very poor), and had very similar low scores for the subindex indicators: fenced, grazing, bank stability, canopy cover, understorey cover, submerged and riparian. But similar high scores for pH, soil structure and ground cover. In general, all of the reaches in the grouping of sites 4 to site 9 scored poorly in all aspects and had identical poor scores for the subindex indicators; width of riparian vegetation, fenced, underwater slope, grazing and submerged. Sites 7 and site 8 scored extremely low in all aspects, with identical low scores for the subindex indicators: width of riparian vegetation, fenced, grazing, bank stability, soil structure, understorey cover, ground cover, native vs. exotic, submerged, emergent and riparian. Site 20 scored lowest in all aspects and was in extremely poor condition with a TECS of 13.7 (very poor).

A total of 52 species of flora were recorded along reaches through out the Angas catchment (Appendix 2). An MRPP revealed that there was a significant difference (p = 0.0055) among the species recorded along each reach and the TECS of those reaches. Indicator species analysis identified *Cotula coronopifolia* as a significant indicator (p = 0.0240) of reaches with a TECS of 3.

2.3.2.3 Currency creek

Analysis of Currency creek indicates that those reaches with a TECS of 3 or 4 (average or good) (Fig. 2.4) are highly correlated (R^2 = 0.55) with the vectors fenced, grazing, width of riparian vegetation, bank stability, and aquatic wood. Those reaches with a TECS of 1 or 2 (very poor or poor) were negatively correlated with those vectors and were dispersed.

A closer analysis of the ordination and the groupings of the sites based on subindices indicator scores revealed that site 1 was in poor condition (TECS of 27) scoring low in most aspects, but high in the subindex indicators of bank stability, ground cover and emergent. This site has a wide channel with dense reed beds along its banks, some understorey cover but no canopy cover. Site 12 was also degraded (TECS of 21.6), scoring poorly in all aspects. This site was fenced but was heavily grazed with no canopy or understorey cover.

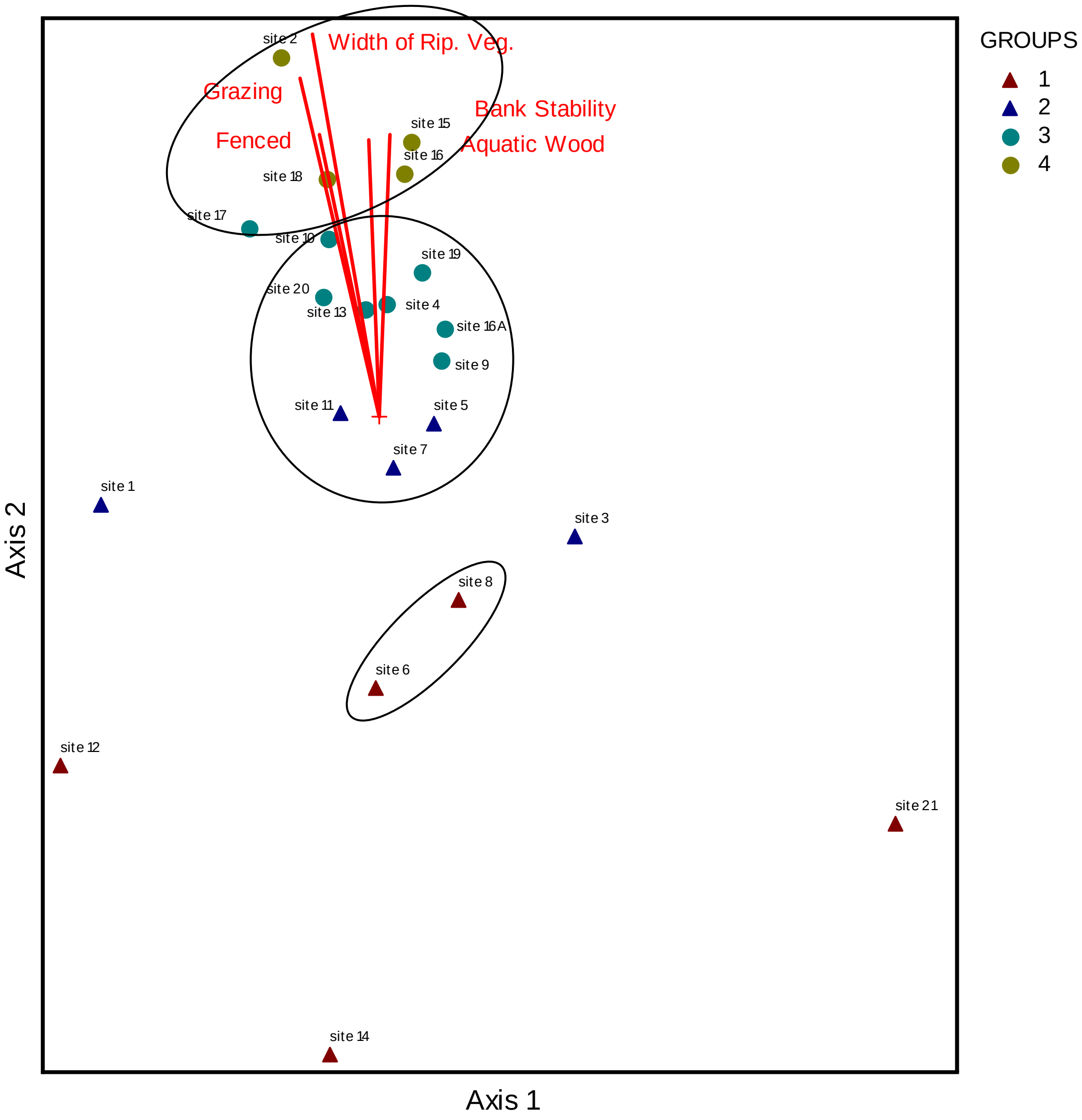

Figure 2.4: Non-metric multidimensional scaling (NMS) ordination of data for Currency creek catchment in each category (1 = very poor, 2 = poor, 3 = average, 4 = good) based on the subindices indicator scores for each reach, (n = 22). Final Stress = 9.6%, R^2 = 0.55.

Sites 2 to site 18 each had a TECS of average to good, ranging from 33.4 to 38.4, and had similar high scores for the subindices of Habitat, Banks and Vegetation structure. Each reach in this grouping also had identical high scores for the subindex indicators; width of riparian vegetation, grazing, soil structure, pH, submerged, emergent and riparian. Sites 4 to site 20 were the largest group made up of reaches with a TECS of between 27.3 to 33.8 (poor to average). Each reach in this group had very similar scores for the subindex indicators of grazing, bank stability, aquatic wood, soil structure, ground cover, pH, submerged, emergent and riparian. Site 3 was a single reach group in poor condition (TECS of 25.1), scoring poorly in all aspects, apart from the subindex indicators of canopy cover and aquatic wood. Both reaches along site 6 and site 8 were in very poor condition (TECS of 22.4 and 23.9, respectively) with identical low scores for the subindex indicators of width of riparian vegetation, grazing, aquatic wood, soil structure, canopy cover, understorey cover, native vs. exotic, and all of the indicators for the subindex Vegetation structure. Site 14 was the lowest scoring reach in all aspects. It was a very degraded reach (TECS of 16.5) being heavily grazed with no canopy or understorey cover, heavily eroded and channelised. Site 21 was again in a very poor condition (TECS of 17.9), scoring very poorly in all aspects, being grazed up to the waters edge; however, it had good submerged cover (31-60%).

There was a total of 48 species of flora recorded (Appendix 2) along Currency creek. An MRPP determined that there was no significant difference among the species recorded along each reach and the TECS for those reaches. Indicator species analysis identified *Cladium procerum* and *Plantago lanceolata* as significant indicators (p = 0.0190 and 0.0070, respectively) of reaches with a TECS of 4.

2.3.2.4 Tookayerta creek

An NMS analysis of Tookayerta creek catchment (Fig. 2.5) identified reaches with a TECS of 3 or 4 (average or good) to be highly correlated ($R^2 = 0.70$) with the vectors understorey cover, fenced, grazing, width of riparian vegetation, number of layers, aquatic wood, and canopy cover. The reaches with a TECS of 1 or 2 (very poor or poor) were negatively correlated with those vectors and were more dispersed.

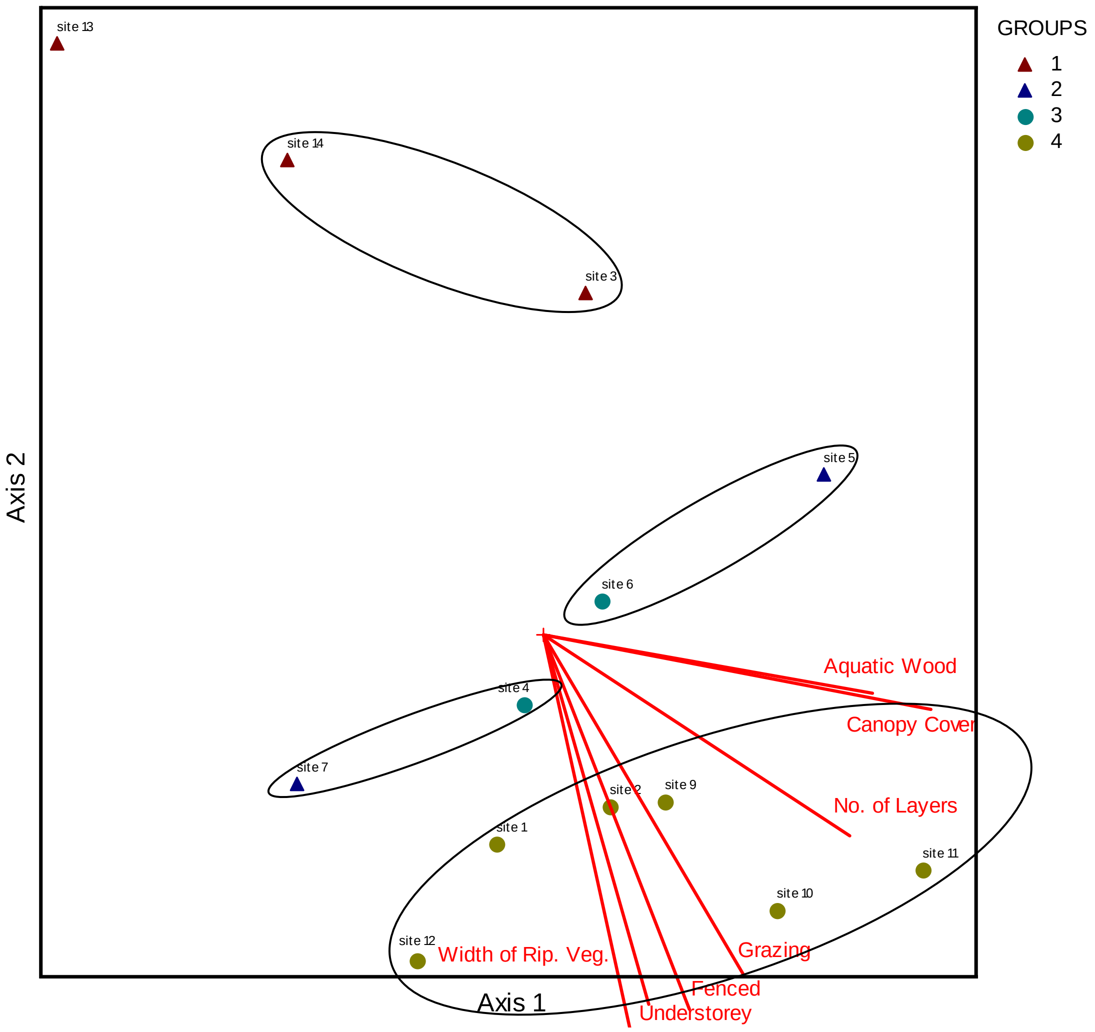

Figure 2.5: Non-metric multidimensional scaling (NMS) ordination of data for Tookayerta creek catchment in each category (1 = very poor, 2 = poor, 3 = average, 4 = good) based on the total index of site condition (n = 13). Final Stress = 6%, R^2 = 0.70.

A closer analysis revealed that the grouping of sites 1 to site 12, which was based on subindices indicator scores, showed each to have a TECS of good, ranging from 36.8 to 38.6. Each reach recorded a very similar high result for the indicators of width of riparian vegetation, fenced, grazing, bank stability, understorey cover, ground cover, emergent, riparian, and identical low scorings for submerged. Sites 4 and 7 were degraded (TECS of 30.5 and 28.0, respectively), but not severely. Both reaches had identical scores for the subindex indicators of width of riparian vegetation, bank stability, soil structure, understorey cover, ground cover, native vs. exotic, submerged, and emergent.

The two reaches that were very different were site 5 and site 6, with a total index condition score of 28.2 and 32.1 (poor and average), respectively. Each site scored identical scores for the subindex indicators of width of riparian vegetation, fenced, underwater slope, bank stability, aquatic wood, soil structure, ground cover, pH, and submerged. Both sites 3 and 14 were degraded (TECS of 22.3 and 24.6) and scored identical low scores for the subindex indicators: width of riparian vegetation, fenced, underwater slope, bank stability, aquatic wood, canopy cover, ground cover, native vs. exotic, submerged, and riparian. Site 13 was the most degraded site recorded along Tookayerta creek (TECS of 18.8 – very poor). This site was not fenced, grazed both sides with no canopy or understorey cover, scoring very poorly in all aspects.

There were 44 species of flora recorded along reaches of Tookayerta creek (see Appendix 2). An MRPP determined that there was a significant difference (p = 0.032) among the species recorded along each reach and the TECS for those reaches. However, Indicator species analysis determined that no individual species was a significant indicator of a reach TECS.

2.3.2.5 *Combined analysis*

An analysis of all 115 surveyed reaches (Fig. 2.6) identified those reaches with a TECS of 3, 4 or 5 (average to excellent) to be strongly correlated (R^2 = 0.50) with the vectors grazing, fenced, riparian, width of riparian vegetation, aquatic wood, and bank stability. Reaches from each of the four catchments with a TECS of 1 or 2 (very poor or poor) were negatively correlated with those vectors and dispersed.

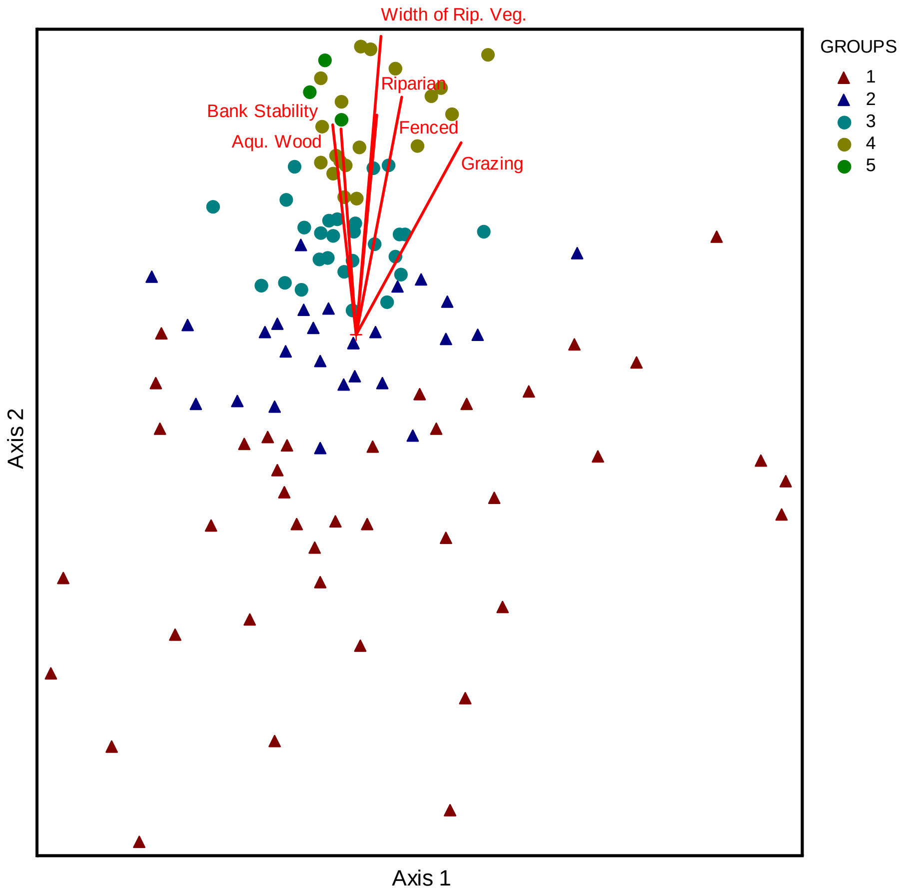

Figure 2.6: Non-metric multidimensional scaling (NMS) of data for all four catchments in each category (1 = very poor, 2 = poor, 3 = average, 4 = good, 5 = excellent) based on the subindices indicator scores for each site, (n = 115). Final Stress = 16.4%, R^2 = 0.50.

2.4 Discussion

2.4.1 Index of riverine ecological condition

Indices of ecological condition or integrity need to be benchmarked against relatively pristine reaches in order to provide a measure of variation from natural situations (Boulton 1999; Boulton and Brock 1999; Maddock 1999). The Finniss catchment contained four reaches that had not been or had been subjected to minimal anthropogenic alterations to allow for this benchmarking. These reaches provided excellent reference sites for establishing the scoring ranges of indicator variables. However, even the excellent reaches in relatively pristine ecological condition could not obtain a maximum score of 50. This was due to anthropogenic alterations in the upper Finniss catchment, which resulted in the increased water conductivity, erosion of underwater bank slope, loss of submerged vegetation, and the replacement of native taxa by exotic taxa (*Teline monspessulana* and *Pteridaceae esculentum* were significant indicators of reaches with a TECS of 4 (good) in those relatively pristine excellent reaches of the mid to lower catchment).

Indices for assessing the ecological condition, health or integrity of a river or riparian habitat (Jansen and Robertson 2001; Ladson *et al.* 1999) were employed to investigate the relationship between the river/riparian habitat and the land and water management practices associated with those habitats (Boulton 1999; Jansen and Robertson 2001; Ladson *et al.* 1999; Rapport *et al.* 1998b). But no such approach has been employed across the whole catchment scale for the purposes of determining the degree of catchment degradation and if restoration (via environmental flows) is a viable and practical management option, particularly in fragmented catchments. Nor have they been used to identify the main physical site parameters responsible for a river’s present condition. By identifying the main site parameters responsible for a rivers ecological condition, river restoration programs may then attempt to rectify those causative parameters. This will also allow for the river/stream health to be compared before and after the restoration program has taken place, and the effectiveness of the schemes can be appraised. The index of riverine ecological condition is a valuable rapid appraisal tool that allows for the coverage of numerous sites over large spatial scales. It is an index that may be applied to many catchments world wide, as long as precautions are taken to adjust the scoring of indicator variables against relevant reference sites (Boulton 1999; Brinson and Rheinhardt 1996; Maddock 1999).

2.4.2 Ecological condition, causative factors and restoration potential

The condition of each of the surveyed reaches was a function of the immediate and surrounding land use. For example, in the Finniss catchment site 18 (excellent condition) is beside site 19 (very poor condition) and likewise site 40 (again in excellent condition) and close to site 41 (again in very poor condition) (Appendix 1.). The condition of the reaches appears to be randomly distributed through out each catchment but is infact dependent on their immediate and surrounding land use.

Of the four catchments surveyed, each identified a unique set of site parameters (subindex indicators), which were strongly correlated with the ecological condition of the reaches in each of the catchments. This would suggest that each of the four catchments are unique and differ from each other. The indicator species analysis further supports this notion as each catchment had a different species as a significant indicator of a TECS for that catchment. However, when all 115 surveyed reaches were analysed together (Fig. 2.6), those reaches of average to excellent ecological condition were all strongly correlated with the subindex indicators: bank stability, riparian, grazing, fenced, aquatic wood, and width of riparian vegetation. This would indicate that these subindex indicators are the main site parameters determining the ecological condition of a riverine reach.

The indicators of aquatic wood and bank stability are functions of the channel morphology, which are directly influenced by the anthropogenic alterations in land use (clearing) and flow regulations (Boulton and Brock 1999; Brookes 1994; Brookes and Shields 1996; Harris 2001b; Merritt and Cooper 2000; Thoms and Walker 1993; Walker and Thoms 1993). Whereas the indicators of fenced, grazing, riparian and width of riparian vegetation are a direct function of the immediate and surrounding land management practices (Allan 2004; Allan *et al.* 1997; Baattrup-Pedersen *et al.* 2005; Bunn 1993; Molles *et al.* 1998; Robertson 1997; Robertson and Rowling 2000; Walker *et al.* 1997).

2.4.3 Implications for Environmental Flows

Livestock play a significant role in the demise and degradation of riparian and aquatic habitats (Jansen and Robertson 2001; Robertson and Rowling 2000), however, the condition of those habitats generally responds rapidly to the exclusion of livestock (Fleischner 1994; Robertson and Rowling 2000). Many of the factors that had a significant influence on the TECS of surveyed reaches: bank stability, width of riparian vegetation, soil structure, submerged, riparian, or understorey, would be dramatically improved with the removal and exclusion of stock. Unfortunately, other factors that also have a significant influence on the TECS of reaches are not so easily rectified. Aquatic wood, underwater slope and bank stability are a function of channel morphology and key structural habitat components (Ladson *et al.* 1999; O'Connor 1992), but with out massive and unrealistic bank reconstruction these factors are not reversible. Hence, restoration programs to restore river health via the restoration of flows should focus their efforts and limit the addition of environmental flows to reaches that are fenced, excluded from livestock, and which have not been too severely eroded and channelised (Jansen and Robertson 2001; Robertson 1997; Robertson and Rowling 2000). Such reaches still retain a physical habitat, and hence with the restoration of flows may promote aquatic and riparian plant communites, which would result in their improved ecological structure and functioning (Dyson *et al.* 2003; Mawhinney 2003).

This survey of ecological condition has highlighted those riverine reaches that would most benefit from environmental flows, along with reaches for which environmental flows would be of limited benefit due to the current land management practices in place (unfenced, subject to grazing and with relatively no riparian zone) (Appendix 1). In the EMLR the majority of the diverted water is held with in farm dams. This makes the application of environmental flows to limited riverine reaches more achievable. Flows may be released from selected farm dams (those farm dams in close proximity to selected reaches) and limited to those reaches with appropriate land management practices in place.

The exclusion of livestock and restoration of flows will not be enough to restore riverine ecosystems back to their Pre-European condition due to the permanently altered channel morphology and problems with exotic plants (Jansen and Robertson 2001; Robertson and Rowling 2000). However, the removal of stock and restoration of environmental flows would prevent further degradation and would significantly improve the ecological structure and functioning of these creeks.

CHAPTER 3.

3 Aquatic and riparian seed banks in the EMLR: the effects of anthropogenic changes in land use and flow regulations, and their restoration potential

3.1 Introduction

The seed bank is defined as the reserves of viable seed present in and on the soil surface (Roberts 1981) and associated litter (Simpson *et al.* 1989), which is capable of replacing adult plants (Baker 1989). The primary role of the seed bank is to ensure the continuation of the species after disturbance or natural mortality has reduced the extant vegetation and to preserve genetic diversity (Simpson *et al.* 1989). Seed banks contain seeds not only from the preceding year but may contain seeds from many previous years (Roberts 1981), especially species that develop seeds with long term viability (Thompson and Grime 1979). Species that inhabit environments subject to severe and unpredictable disturbances by cultivation, fire or large water level fluctuations generally form a large, persistent seed bank (Thompson 1992a).

In the majority of cases, plants growing under conditions of permanent inundation rarely produce seeds (particularly submergent species) and rely on asexual reproduction. They use propagules for propagation, population maintenance and in some cases dispersal (Sculthorpe 1967). In contrast, ecosystems that are subject to extreme desiccation may rely solely on seed for regeneration (Thompson 1992b). The seed bank strategies employed by species present in rivers and wetlands may reflect adaptations to a water regime (Leck and Brock 2000). Unregulated rivers and wetlands in Australia endure variable hydraulic regimes resulting in periods of wetting and drying, which varies seasonally and annually (Bayley 1995; Lyte and Poff 2004; Poff *et al.* 1997; Rea 1992; Thoms and Walker 1993; Walker 1985; Walker and Thoms 1993; Warwick and Brock 2003). Volder *et al.* (1997) reported how drought and flooding effected the flowering and seed production of the amphibious plant *Ranunculus peltatus*. *Triglochin procerum* produced 25,000 seeds m^{-2} in water a meter deep but only 300 seeds m^{-2} in shallow water (Rea and Ganf 1994c). Leck and Brock (2000) suggest that species from Australian temporary wetlands have adapted to persisting through “false starts”, where a favourable period for germination may be followed immediately by unfavourable conditions for growth and establishment, where the plants are unable to replenish the seed bank. Brock and Rogers (1998) reported that 10 of 16 species from an ephemeral floodplain in South Africa had persistent seed banks (adapted to false starts) and two species required a second wetting cycle to break dormancy. Hence, hydrology is one of the most important factors influencing the germination, establishment and seed production in species, from ephemeral rivers and wetlands (Brock 1991; Brock 1999; Brock and Casanova 1997; Casanova and Brock 1990; Mitsch and Gosselink 1993; Nicol *et al.* 2003; Pettit and Froend 2001; Volder *et al.* 1997).

An altered water regime will change the habitat template and so the biological character of a river or wetland must change accordingly (Walker and Thoms 1993). Species that had adapted to the natural water regime, had developed life history strategies; behavioural, physiological and morphological adaptations to enable their survival (Bunn and Arthington 2002; Lyte and Poff 2004). Therefore, anthropogenic alterations to that natural water regime can have detrimental consequences, not only on the plant communities present but also on the seed bank (Boedeltje *et al.* 2002; Brock 1994; Brock 1999; Brock *et al.* 1999; Casanova and Brock 2000; Nicol *et al.* 2003; Peterson and Baldwin 2004; Warwick and Brock 2003).

In addition to the altered water regimes, human induced pressures have lead to; increased stream salinity (Peck *et al.* 1983), displacement of riparian and aquatic vegetation by exotic taxa (Baron *et al.* 2002; Merritt and Cooper 2000; Pettit *et al.* 2001), increased sedimentation (Erskine 1994), deterioration in number and quality of floodplain wetlands (Wasson *et al.* 1996), and the significant loss of riparian and in-stream habitat due to channelisation and catchment clearance (Allan *et al.* 1997; Biggs 1996; Maddock 1999). As a consequence of these anthropogenic alterations along our rivers and streams, it is questionable whether there is an aquatic and riparian seed bank remaining. If not, then the restoration of aquatic and riparian plant communities back into these altered systems may have to take the form of species re-introduction. The current ecosystem practice to restore river ‘health’ of providing environmental flows may also be nullified if there is an inadequate seed bank remaining. The aim of this study is to assess the extent and significance of the aquatic and riparian seed bank in four catchments of the EMLR. It is hypothesised that those reaches subjected to severe anthropogenic alterations would contain a significantly reduced and altered aquatic and riparian seed bank. The specific objectives were: i) to assess the aquatic and riparian seed bank along four altered riverine catchments, ii) to determine if anthropogenic alterations have resulted in the reduction or loss of their aquatic/riparian seed banks, and iii) to determine if environmental flows would permit the re-establishment of native aquatic and riparian plant communities from seed banks, and if so, suggest where these environmental flows should be applied in order to optimise ecological outcomes.

3.2 Materials and Methods

3.2.1 Study area

The study area is comprised of 4 fragmented catchments in the Eastern Mount Lofty Ranges (EMLR), the Angas, the Finniss, Currency and Tookayerta creeks, just southeast of Adelaide, South Australia. This region has undergone extensive agricultural development, clearing, with alterations in catchment primary production. The major land uses in this region include broad scale grazing, intensive grazing, vines, horticulture and floriculture, with limited protected areas (Savadamuthu 2003). This has resulted in an increased pressure on the available water resources, leading to flows in a number in important rivers and creeks decreasing, in some places significantly, (DWLBC 2003a). The total volume of water held in farm dams in many of the sub-catchments in the EMLR has either exceeded or is nearing sustainable diversion limits set out in the Catchment Water Management Plan for the River Murray in South Australia (Savadamuthu 2003).

3.2.2 Catchment division

Each catchment was divided up into a number of reach sections depending on their geomorphology and natural history (M. Hammer, *pers. Comm.* 2004) (Fig. 3.1). Reach sections were chosen to represent the geological, hydrological, land use and vegetation gradient from the headwaters to the river mouth. The Angas was divided up into six reaches, the Finniss into seven, Tookayerta into four and Currency into 3 reaches (Fig. 3.1). The number of sections was dependent upon the river length. Section 1 in each catchment was chosen to represent that reach section where each of the rivers interacted with Lake Alexandrina. Upstream from the river mouth sections represented the lowland plains, the escarpment and the headwaters.

3.2.3 Material collection and preparation

Seed bank material was collected from the Angas on April 15th and 16th, 2004, and from the Finniss, Tookayerta creek and Currency creek, between May 2nd and May 5th, 2004. Within each reach section five independent sites were chosen on a basis of access. At each site sediment samples (10cm diameter by 5cm deep cores) were taken to represent sediments from the low and high water marks as well as three samples evenly spaced between these two points. Samples were only taken from banks where deposition occurred. A total of 500 samples were collected, five samples from each site. The samples were air dried in a greenhouse for 14 days until they had all reached constant weight. Because the focus of the work was at the level of the reach sections it was necessary to minimise the within reach section small-scale heterogeneity. To achieve this composite samples were formed by randomly mixing samples from each elevation within each section. This reduced the total number of samples from 500 to 100 and each river section was represented by 5 independent composite samples, e.g. the Angas consisted of 6 river sections with 5 independent composite samples representing each section and were designated 1A-E, 2A-E……6A-E.

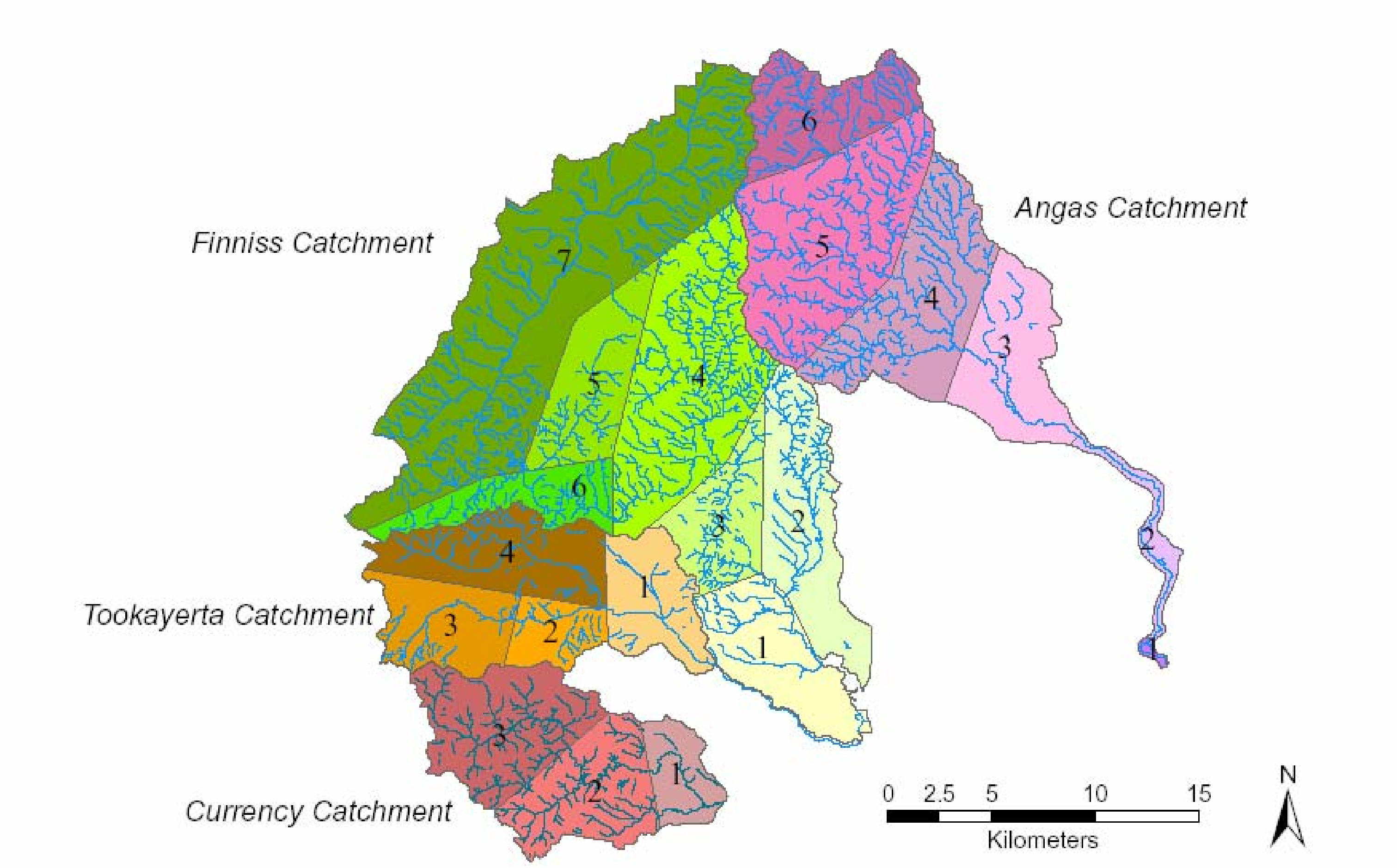

Figure 3.1: Catchment maps indicating the different stream sections for each catchment depending on their geomorphology and natural history for the longitudinal seed bank study.

3.2.4 Seedling emergence technique

The technique followed Nicol *et al.* (2003): 100 gram sub-samples from each of the composite samples representing the river sections were placed on top of 60-40 sandy loam in plastic trays (17 x 11 x 6.5cm), this gave a total of 100 samples. Samples were treated with a fungicide (Fongarid) and randomly arranged in a wet house at the University of Adelaide ($36^o56'$ S, $138^o36'$ E). Prior to the addition of the seed bank, Osmocote®, a slow release fertilizer (N: P: K = 17.4: 4.4: 8.8), was added to the sandy loam to give a nutrient loading equivalent to 100 g N m^{-2} yr^{-1}, which ensured there was no nutrient limitation. Five control trays consisting of sandy loam were placed amongst the experimental trays. An automated watering system ensured that the sediment remained water logged at all times.

Weekly germination counts were made over a 24-week period. All germinations were labelled unknown 1, unknown 2, etc. When seedlings were mature enough to survive re-potting they were removed and grown until identification was made to species level (Chambers *et al.* 1995; Cunningham *et al.* 1992; Gibbs and Gibbs 2001; Jessop and Toelken 1986; Romanowski 1998; Sainty and Jacobs 1981; Sainty and Jacobs 1994). Any seedlings that showed characteristics of any re-potted plant were named accordingly and removed. Any new germination that showed individual characteristics were removed, re-potted and labelled as a new unknown.

3.2.5 Functional Classification

Species were classified into four groups accordingly; Aquatic and Riparian Natives, Aquatic and Riparian Exotics, Terrestrial Natives and Terrestrial Exotics (Cunningham *et al.* 1992; Jessop and Toelken 1986; Sainty and Jacobs 1981; Sainty and Jacobs 1994).

3.2.6 Data analysis

Multi-response permutation procedures (MRPP) or non-parametric multivariate analysis of variance (NPMANOVA) were used to determine whether the species composition among reach sections were significantly different, but cannot give an indication of what caused the difference (McCune and Grace 2002). Differences in the species composition among the reach sections of each river were analysed using cluster analysis and indicator species analysis using PC Ord (Dufrene and Legendre 1997; McCune and Mefford 1999) and NPMANOVA was undertaken using the procedure described by Anderson (2001). Bray-Curtis (1957) similarities were used to calculate the similarity matrix for all multivariate analysis. The significance level for all statistical tests was chosen at $p = 0.05$.

Indicator species analysis (Dufrene and Legendre 1997) was used in the comparison of the seed bank species composition among reach sections to give an indication of which species characterise a particular reach section. This combines information on the species abundance in a particular group and the faithfulness of occurrence of a species in a particular group (McCune and Grace 2002). A perfect indicator of a particular group should be faithful to that group (always present) and exclusive to that group (never occurring in other groups) (McCune and Grace 2002). This test produces indicator values for each species in each group based on the standards of the perfect indicator. Statistical significance of each indicator value is tested by using the Monte Carlo (randomisation) technique where the real data is compared against 1,000 runs of randomised data (Dufrene and Legendre 1997). For this study, the groups were assigned according to reach sections; therefore this procedure was used for hypothesis testing (planned comparisons).

A species that is deemed not to be a significant indicator of a particular group is either (Dufrene and Legendre 1997):

Type A: Rare. The species is only found in one group but in low numbers. For example, one individual of a particular species was detected in the seed bank of one replicate of a particular reach section. This species is faithful and exclusive to the particular reach but present in such low numbers that it cannot be deemed a significant indicator with any confidence.

Type B: Widespread and abundant. The species is found in more than one reach section in high numbers. For example, a particular species is found in the seed bank of a number of reach sections in high numbers. This species is not faithful or exclusive to either reach section and it cannot be deemed a significant indicator of either.

Type C: Widespread and rare. The species is found in more than one reach section in low numbers. For example, one individual of a particular species is found in several replicates of a number of sections. This species is not faithful or exclusive to a particular section and it cannot be deemed a significant of that reach section.

The category to which a non-significant species fits can be determined by examination of the raw data. A species that is not a significant indicator is not necessarily ecologically unimportant. Widespread species could be generalists that can survive in a wide range of conditions and rare species could potentially require conservation (Nicol 2004).

Seed bank density was analysed using one-way ANOVA to determine any significant differences in the total number of seeds m^{-2} for each river section.

3.3 Results

A total of 81 species were recorded in the seed banks of the four rivers, unfortunately 8 species were unable to be identified to species level due to a power outage and automated watering system shutdown at the University of Adelaide during the Christmas closure period of 2004. The 8 unidentified species were made up of 5 sedges, 1 grass species and 2 unknown species. Table 3.1 shows the number of species recorded in seed bank of each river and the number of species recorded in each of the following categories: Aquatic and Riparian Natives, Aquatic and Riparian Exotics, Terrestrial Natives, Terrestrial Exotics, and the 8 unidentified species.

Table 3.1: The number of species recorded in each of the seed banks of the Angas, Finniss, Tookayerta creek and Currency creek in each of the categories: Aquatic and Riparian Natives, Aquatic and Riparian Exotics, Terrestrial Natives, Terrestrial Exotics, Unidentified Sedges, Unidentified Grass and Unknown Species.

Category	Stream				Total in each category
	Angas	Finniss	Tookayerta	Currency	
Aquatic & Riparian Natives	12	9	7	8	**16**
Aquatic & Riparian Exotics	4	1	2	2	**6**
Terrestrial Natives	12	9	10	7	**18**
Terrestrial Exotics	18	21	13	13	**33**
Total	46	40	32	29	**73**
Unknown Sedges	4	5	4	5	**5**
Unknown Grass	1	0	0	0	**1**
Unknown Species	0	2	2	1	**2**
Grand Total	51	47	38	35	**81**

3.3.1 Species Composition

3.3.1.1 River Angas

The majority of the River Angas sections contained seed banks that were significantly different from each other (NPMANOVA: $df = 5$, $F = 3.7587$, $P = 0.0002$). The only reach sections that were not significantly different from each other were sections 2 & 3 and sections 5 & 6 (Table 3.2). A cluster analysis (Fig. 3.2) illustrates the significant differences among each of the reach sections, particularly the uniqueness of sections 1 and 4, based on the seed bank species composition for each section. It also suggests similarities between sections 2 & 3 and sections 5 & 6.

Galenia secunda was a significant indicator of section 2 and exclusive to sections 2 & 3, and while not a significant indicator (Type A), *Nicotiana glauca* was also exclusive to those sections (Table 3.3). *Rorippa nasturtium-aquaticum*, an exotic aquatic/riparian species, was a significant indicator ($P = 0.007$) of section 6 and exclusive to sections 5 and 6, and again while not a significant indicator (Type A), *Bromus sterilis* was only recorded in these sections.

Table 3.2: NPMANOVA statistics obtained from comparisons of seed bank species composition of each river section for the River Angas using Pair-Wise posteriori comparisons based on Bray-Curtis dissimilarities.

River sections	*P*
Sections 1 & 2	**0.0072**
Sections 1 & 3	**0.0074**
Sections 1 & 4	**0.0088**
Sections 1 & 5	**0.0092**
Sections 1 & 6	**0.0086**
Sections 2 & 3	0.0596
Sections 2 & 4	**0.0086**
Sections 2 & 5	**0.0066**
Sections 2 & 6	**0.0070**
Sections 3 & 4	**0.0246**
Sections 3 & 5	**0.0096**
Sections 3 & 6	**0.0178**
Sections 4 & 5	**0.0102**
Sections 4 & 6	**0.0074**
Sections 5 & 6	0.3468

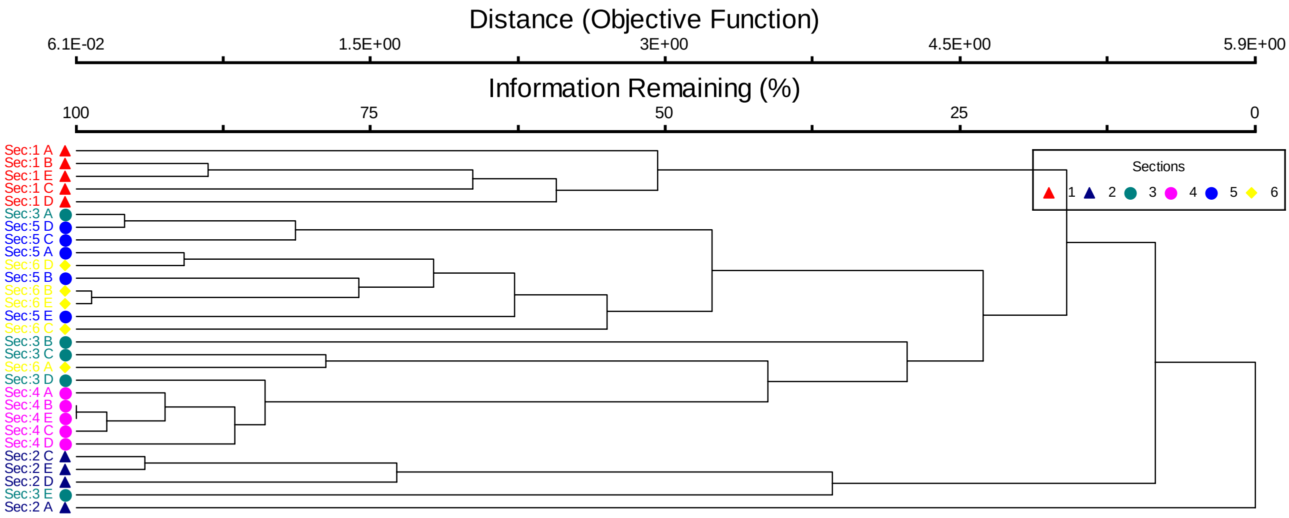

Figure 3.2: Cluster analysis depicting the similarity between the seed bank species composition and each of the reach sections of the River Angas.

A total of 51 species were recorded in the seed bank of the River Angas. An MRPP showed a significant difference ($A = 0.1973$; $P < 0.0001$) between the species recorded at each reach section. Out of a total of 51 species recorded in the seed bank, only 20 species (4 unknown sedges) were classified as aquatic and riparian (Table 3.3); and out of those 20 species, only 12 could be confirmed as native aquatic and riparian species. *Crassula helmsii* and *Isolepis fluitans* were widespread and rare (Type C), each occurring in a number of reach sections. *Callitriche stagnalis, Sarcocornia, Najas tenuifolia, Elacholoma hornii* and *Juncus sp"A"* were all rare (Type A), exclusive to one or two sections in very low densities. *Typha domingensis* was widespread and abundant (Type B), recorded in numerous sections and in high densities. *Juncus bufonius* was a significant indicator ($P = 0.017$) of section 5, recorded there in high abundance but also being recorded in sections 1, 4 and 6 in low densities. *Cyperus vaginatus* was a significant indicator ($P = 0.001$) of section 4, recorded there in high abundance but also being recorded in lower densities in reach sections 3 and 5. *Gratiola peruviana* was a significant indicator ($P = 0.005$) of section 1, recorded there in relatively high densities, while also recorded in lower densities in sections 4 and 5. *Myriophyllum simulans* was a significant indicator ($P = 0.017$) of reach section 1 being exclusive to that section in all replicates. The other 4 unknown sedges were considered to be rare or widespread and rare (Table 3.3).

Table 3.3: Indicator species analysis comparing the seed bank species composition between reach sections of the Angas to provide an indication of which species characterise a particular reach section (Type A, B or C denotes why the species was not a significant indicator) and functional classification of the species present (* denotes naturalised). Sections in bold indicate the species is a significant indicator of that section, *** denotes species recorded in the seed bank but not recorded in the vegetation community during the ecological condition survey (Chapter 2).

Species	Sections	*P*	Functional Classification
Callitriche stagnalis	1 & 6	1 (Type A)	Aquatic / Rip. Native
Crassula helmsii	1, 2 & 5	0.673 (Type C)	Aquatic / Rip. Native
Cyperus vaginatus	3, **4** & 5	0.001	Aquatic / Rip. Native
Elacholoma hornii ***	5	0.13 (Type A)	Aquatic / Rip. Native
Gratiola peruviana	**1**, 4 & 5	0.005	Aquatic / Rip. Native
Isolepis fluitans	1, 3, 5 & 6	0.325 (Type C)	Aquatic / Rip. Native
Juncus bufonius L. ***	1, 4, **5** & 6	0.017	Aquatic / Rip. Native
Juncus sp"A" ***	5	1 (Type A)	Aquatic / Rip. Native
Myriophyllum simulans ***	**1**	0.017	Aquatic / Rip. Native

Najas tenuifolia R. Br. ***	3	1 (Type A)	Aquatic / Rip. Native
Sarcocornia ***	1	0.133 (Type A)	Aquatic / Rip. Native
Typha domingensis	1, 3, 4 & 6	0.173 (Type B)	Aquatic / Rip. Native
Cotula coronopifolia	1	0.141 (Type A)	Aquatic / Rip. Exotic*
Cyperus eragrostis	5	1 (Type A)	Aquatic / Rip. Exotic
Myriophyllum aquaticum ***	**1**	0.014	Aquatic / Rip. Exotic
Rorippa nasturtium-aquaticum	5 & **6**	0.007	Aquatic / Rip. Exotic
Atriplex muelleri	1 & 5	0.284 (Type A)	Terrestrial Native
Bromus tectorum	3 & 4	0.388 (Type A)	Terrestrial Native
Euphorbia terracina L.	2	1 (Type A)	Terrestrial Native
Galenia secunda	**2** & 3	0.018	Terrestrial Native
Hemarthria uncinata	**1** & 4	0.005	Terrestrial Native
Lolium perenne	1, 2, 3, 4 & 5	0.06 (Type C)	Terrestrial Native
Medicago polymorpha L.	2 & 4	1 (Type A)	Terrestrial Native
Nicotiana glauca	2 & 3	1 (Type A)	Terrestrial Native
Phalaris paradoxa	1,2,3,4,5 & 6	0.146 (Type B)	Terrestrial Native
Picris echioides	1, 3 & 5	0.723 (Type C)	Terrestrial Native
Scaevola aemula	3, **4** & 5	0.036	Terrestrial Native
Trifolium glomeratum	1 & 4	0.369 (Type A)	Terrestrial Native
Anagallis arvensis	3, 4 & 6	0.676 (Type C)	Terrestrial Exotic
Arctotheca calendula	3 & 4	1 (Type A)	Terrestrial Exotic
Brassica juncea	3	1 (Type A)	Terrestrial Exotic
Bromus sterilis	5 & 6	0.388 (Type A)	Terrestrial Exotic
Conya albida	3	0.168 (Type A)	Terrestrial Exotic
Echium plantagineum	4	1 (Type A)	Terrestrial Exotic
Ehrharta longiflora Sm.	3, 4, 5 & 6	0.065 (Type C)	Terrestrial Exotic
Foeniculum vulgare Miller	4	1 (Type A)	Terrestrial Exotic
Heliotropium europaeum L.	2	1 (Type A)	Terrestrial Exotic
Melilotus indica	1 & 2	1 (Type A)	Terrestrial Exotic
Oxalis pes-caprae	2, 3 & 4	1 (Type A)	Terrestrial Exotic
Plantago coronopus	**1** & 2	0.001	Terrestrial Exotic*
Plantago lanceolata	3	1 (Type A)	Terrestrial Exotic
Plantago major	4 & **5**	0.01	Terrestrial Exotic*
Sonchus asper	3	1 (Type A)	Terrestrial Exotic
Sonchus oleraceus	2	1 (Type A)	Terrestrial Exotic
Stellaria media	1 & 2	1 (Type A)	Terrestrial Exotic
Trifolium campestre Schreb.	5	1 (Type A)	Terrestrial Exotic
Sedge A	3, 4, 5 & 6	0.821 (Type C)	Aquatic / Rip. Unknown
Sedge T2	6	1 (Type A)	Aquatic / Rip. Unknown
Sedge T3	4	1 (Type A)	Aquatic / Rip. Unknown
Sedge T4	6	0.128 (Type A)	Aquatic / Rip. Unknown
Grass 7	3	0.14 (Type A)	Unknown

Myriophyllum aquaticum, an exotic aquatic/riparian species, was a significant indicator (*P* = 0.014) of reach section 1, exclusive to this section. The other significant indicator species from the seed bank of the Angas were *Galenia secunda, Plantago coronopus, Plantago major*, *Hemarthria uncinata* and *Scaevola aemula*, each being a terrestrial species, either native or exotic. All of the other species recorded, aquatic and riparian exotic, terrestrial native and exotic, were each either rare or widespread and rare in abundance (Table 3.3).

3.3.1.2 River Finniss

Reach sections of the River Finniss contained seed banks that were significantly different from each other (NPMANOVA: *df* = 6, *F* = 3.9436, *P* = 0.0002) apart from sections 1 & 3, 1 & 4 and 3 & 4 (Table 3.4). A cluster analysis (Fig. 3.3) illustrates the similarities and differences between each reach section based on the seed bank species composition for each section. Sections 2, 5, 6, and 7 each contained a number of species classified as rare (Type A) and exclusive to each of those sections (Table 3.5). Whereas sections 1, 3, and 4 each share in common a number of species classified as rare and widespread (Type C), and sections 3 and 4 both contained *Senecio* spp. and *Solanum nigrum,* which was classified as rare (Type A) and exclusive to those two sections.

Table 3.4: NPMANOVA statistics obtained from comparisons of seed bank species composition of each river section for the River Finniss using Pair-Wise posteriori comparisons based on Bray-Curtis dissimilarities.

River sections	***P***
Sections 1 & 2	**0.0104**
Sections 1 & 3	0.6238
Sections 1 & 4	0.0592
Sections 1 & 5	**0.008**
Sections 1 & 6	**0.0292**
Sections 1 & 7	**0.0072**
Sections 2 & 3	**0.0062**
Sections 2 & 4	**0.0074**
Sections 2 & 5	**0.0056**
Sections 2 & 6	**0.0076**
Sections 2 & 7	**0.0088**
Sections 3 & 4	0.0506
Sections 3 & 5	**0.008**
Sections 3 & 6	**0.0084**
Sections 3 & 7	**0.0102**
Sections 4 & 5	**0.0078**
Sections 4 & 6	**0.0172**
Sections 4 & 7	**0.0216**
Sections 5 & 6	**0.0192**
Sections 5 & 7	**0.0076**
Sections 6 & 7	**0.0064**

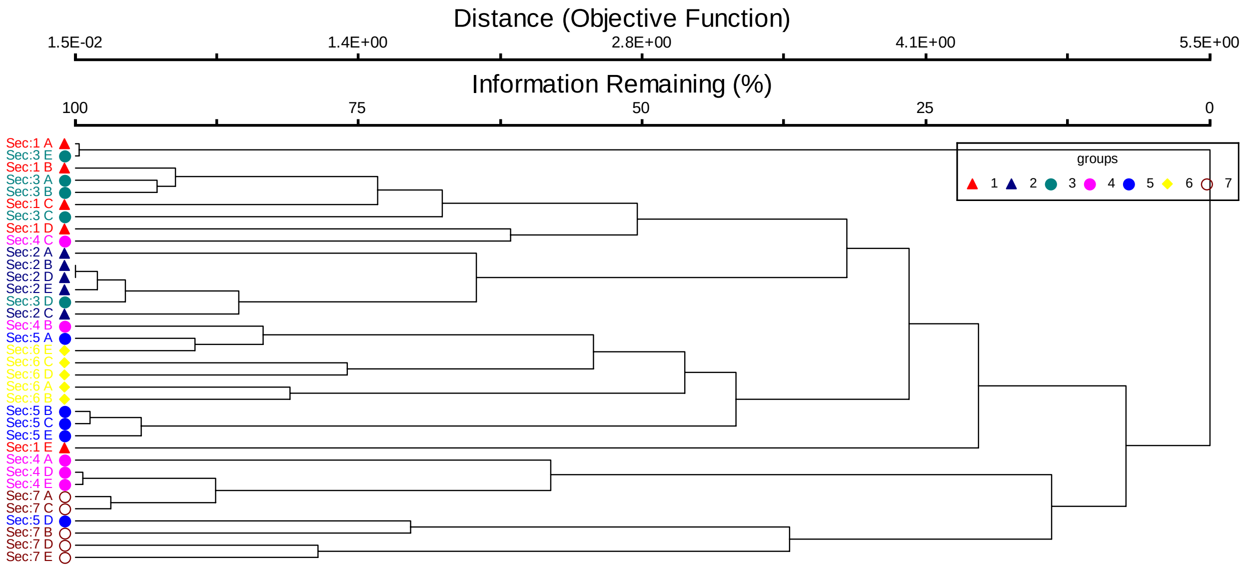

Figure 3.3: Cluster analysis depicting the similarity between the seed bank species composition and each of the reach sections of the River Finniss.

A total of 47 species germinated from the seed bank of the Finniss soil samples. An MRPP showed a significant difference (*A* = 0.2077; *P* < 0.0001) between the species recorded at each river section. Out of a total of 47 species recorded, only 15 species including 5 unknown sedges were classified as aquatic and riparian (Table 3.5). Out of those 15 species, only 9 could be confirmed as native aquatic and riparian species. Indicator species analysis (Table 3.5) shows that of the 9 aquatic and riparian native species recorded, five (*Crassula helmsii, Callitriche stagnalis, Ricciocarpus natans, Crassula sieberana* and *Eucalyptus camaldulensis*) were classified as rare, each being exclusive to the seed banks of one or two reach sections in very low densities. *Isolepis fluitans* was widespread and rare, recorded in the seed banks of sections 2, 3, 5, 6 and 7 in very low densities. *Juncus bufonius* was a significant indicator (*P* = 0.04) of section 2, recorded there in high abundance, but also occurred in lower densities in sections 1, 3, 4, 5, 6 and 7. *Cyperus vaginatus* was also a significant indicator (*P* = 0.001) of section 2, due to its high abundance in this section, but also occurred in lower densities in sections 1, 3, 4, 5, 6 and 7. *Typha domingensis* was a significant indicator (*P* = 0.025) of section 6, but also occurred in lower densities in section 4. The 4 unknown sedges, sedge T2 and sedge T3 were considered to be rare and widespread being recorded in a number of river sections in low densities. Sedge T4 was a significant indicator (*P* = 0.032) of section 7 due to its high abundance in this section, but was also recorded in lower densities in sections 1, 2, 3, 4, 5 and 6. As was sedge T5 a significant indicator (*P* = 0.021) of section 7, also due to its high abundance in this section, but was also recorded in lower densities in sections 1, 2, 3, 4, 5 and 6.

Table 3.5: Indicator species analysis comparing the seed bank species composition between reach sections of the Finniss to provide an indication of which species characterise a particular reach section (Type A, B or C denotes why the species was not a significant indicator) and functional classification of the species present (* denotes naturalised). Sections in bold indicate the species is a significant indicator of that section, *** denotes species recorded in the seed bank but not recorded in the vegetation community during the ecological condition survey (Chapter 2).

Species	Sections	*P*	Functional Classification
Callitriche stagnalis	5, 6 & 7	1 (Type A)	Aquatic / Rip. Native
Crassula helmsii	6	0.136 (Type A)	Aquatic / Rip. Native
Crassula sieberana ***	1, 2 & 6	1 (Type A)	Aquatic / Rip. Native
Cyperus vaginatus	1,**2**,3,4,5,6 & 7	0.001	Aquatic / Rip. Native
Eucalyptus camaldulensis	3	0.197 (Type A)	Aquatic / Rip. Native
Isolepis fluitans	2, 3, 5, 6 & 7	0.415 (Type C)	Aquatic / Rip. Native
Juncus bufonius L. ***	1,**2**,3,4,5,6 & 7	0.04	Aquatic / Rip. Native

Ricciocarpus natans ***	7	1 (Type A)	Aquatic / Rip. Native
Typha domingensis	4 & **6**	0.025	Aquatic / Rip. Native
Cotula coronopifolia	5	1 (Type A)	Aquatic / Rip. Exotic*
Bromus tectorum	1	1 (Type A)	Terrestrial Native
Centipeda minima	7	0.105 (Type A)	Terrestrial Native
Galenia secunda	7	0.118 (Type A)	Terrestrial Native
Lolium perenne	2 & 6	1 (Type A)	Terrestrial Native
Medicago arabica	4	1 (Type A)	Terrestrial Native
Phalaris paradoxa	1,2,3,4,5,6 & 7	0.806 (Type C)	Terrestrial Native
Picris echioides	2, 4, 6 & 7	0.824 (Type C)	Terrestrial Native
Rumex brownii	6	0.126 (Type A)	Terrestrial Native
Scaevola aemula	1, 3, 4, 6 & 7	0.243 (Type C)	Terrestrial Native
Anagallis arvensis	**4**, 5 & 6	0.027	Terrestrial Exotic
Apium graveolens	4	1 (Type A)	Terrestrial Exotic*
Bromus sterilis	1, **5** & 7	0.003	Terrestrial Exotic
Centaurium erythraea	4 & 5	0.07 (Type A)	Terrestrial Exotic
Conya albida	7	1 (Type A)	Terrestrial Exotic
Ehrharta longiflora Sm.	2, 4, 5 & 6	0.573 (Type C)	Terrestrial Exotic
Hypochoeris glabra	7	1 (Type A)	Terrestrial Exotic
Lamium amplexicaule	1	1 (Type A)	Terrestrial Exotic
Malva parviflora	4	1 (Type A)	Terrestrial Exotic
Plantago lanceolata	**2**, 3 & 7	0.001	Terrestrial Exotic
Plantago major	2, 4, 5, 6 & **7**	0.036	Terrestrial Exotic*
Rumex crispus	2	0.305 (Type A)	Terrestrial Exotic
Senecio spp.	3 & 4	1 (Type A)	Terrestrial Exotic
Solanum nigrum	3 & 4	1 (Type A)	Terrestrial Exotic
Sonchus asper	2 & 4	1 (Type A)	Terrestrial Exotic
Sonchus oleraceus	2, 3 & 5	1 (Type A)	Terrestrial Exotic
Teline monspessulana	7	1 (Type A)	Terrestrial Exotic
Trifolium campestre Schreb.	2, 5 & 7	1 (Type A)	Terrestrial Exotic
Trifolium dubium	7	1 (Type A)	Terrestrial Exotic
Trifolium subterraneum	5	1 (Type A)	Terrestrial Exotic
Vicia sativa	5	1 (Type A)	Terrestrial Exotic
Sedge A	1, 2, 3 & 6	0.148 (Type C)	Aquatic / Rip. Unknown
Sedge T2	2, 4, 5 & 7	0.195 (Type C)	Aquatic / Rip. Unknown
Sedge T3	1,2,3,4,5,6 & 7	0.422 (Type C)	Aquatic / Rip. Unknown
Sedge T4	1,2,3,4,5,6 & **7**	0.032	Aquatic / Rip. Unknown
Sedge T5	1,2,3,4,5,6 & **7**	0.021	Aquatic / Rip. Unknown
Unknown Spp.5	1 & **7**	0.001	Unknown
Unknown species 10	2 & 3	1 (Type A)	Unknown

Other significant indicator species from the seed bank of the Finniss were *Plantago lanceolata, Plantago major,* Unknown Spp. 5, *Bromus sterilis* and *Anagallis arvensis*, 4 being terrestrial species and 1 an unknown species. All of the other species recorded in the seed bank of the Finniss were either rare or widespread and rare in abundance (Table 3.5).

3.3.1.3 *Currency creek*

The sections of Currency creek were all significantly different (Table 3.6) from each other (NPMANOVA: *df* = 2, *F* = 2.8022, *P* = 0.0004). The cluster analysis (Fig. 3.4), illustrates the dissimilarities between each stream section based on the seed bank species composition. Each of its reach sections contained a number of species that were exclusive to that one section and classified as rare (Type A) species (Table 3.7).

Table 3.6: NPMANOVA statistics obtained from comparisons of seed bank species composition of each river section for Currency creek using Pair-Wise posteriori comparisons based on Bray-Curtis dissimilarities.

River sections	***P***
Sections 1 & 2	**0.016**
Sections 1 & 3	**0.008**
Sections 2 & 3	**0.0098**

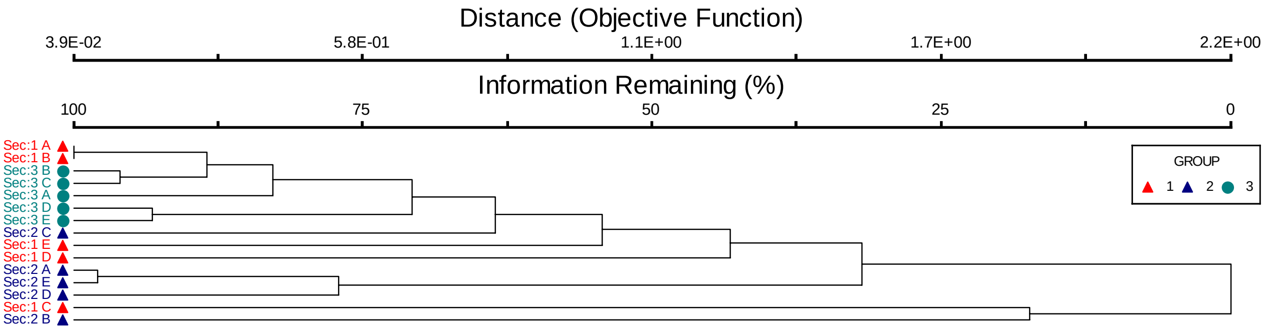

Figure 3.4: Cluster analysis depicting the similarity between the seed bank species composition and each of the reach sections of Currency creek.

A total of 35 species were recorded in the seed bank of Currency creek. An MRPP showed a significant difference (*A* = 0.09788; *P* = 0.0052) between the species recorded in the seed bank of each section. Table 3.7 - shows that out of a total of 35 species recorded, only 15 species including 5 unknown sedges were classified as aquatic and riparian. Out of those 15 species, only 8 could be confirmed as native aquatic and riparian species. Indicator species analysis (Table 3.7) shows that of those 8 aquatic and riparian species recorded, *Persicaria decipiens, Gratiola peruviana* and *Crassula sieberana* were all rare, each exclusive to one stream section in very low densities. *Crassula helmsii*, *Callitriche stagnalis* and *Cyperus vaginatus* were all widespread and rare, and *Isolepis fluitans* was widespread and abundant. *Juncus bufonius* was a significant indicator (*P* = 0.042) of section 1, recorded there in abundance, but also recorded in sections 2 and 3 in lower densities. The 5 unknown sedges were considered to be rare or widespread and rare, apart from sedge A, which was a significant indicator of section 1. The only other indicator species was *Phalaris paradoxa* (Terrestrial native species), which was a significant indicator of section 2. All of the other species recorded in the seed bank of Currency were either rare or widespread and rare in abundance (Table 3.7).

Table 3.7: Indicator species analysis comparing the seed bank species composition between reach sections of Currency creek to provide an indication of which species characterise a particular reach section (Type A, B or C denotes why the species was not a significant indicator) and functional classification of the species present (* denotes naturalised). Sections in bold indicate the species is a significant indicator of that section, *** denotes species recorded in the seed bank but not recorded in the vegetation community during the ecological condition survey (Chapter 2).

Species	Sections	*P*	Functional Classification
Callitriche stagnalis	2 & 3	0.305 (Type C)	Aquatic / Rip. Native
Crassula helmsii	1 & 2	0.53 (Type C)	Aquatic / Rip. Native
*Crassula sieberana ****	1	1 (Type A)	Aquatic / Rip. Native
Cyperus vaginatus	1 & 2	0.196 (Type C)	Aquatic / Rip. Native
Gratiola peruviana	3	1 (Type A)	Aquatic / Rip. Native
Isolepis fluitans	1, 2 & 3	0.418 (Type B)	Aquatic / Rip. Native
Juncus bufonius L. ***	**1**, 2 & 3	0.042	Aquatic / Rip. Native
Persicaria decipiens	2	0.286 (Type A)	Aquatic / Rip. Native
*Berula erecta ****	1	0.29 (Type A)	Aquatic / Rip. Exotic
Cotula coronopifolia	1, 2 & 3	0.633 (Type C)	Aquatic / Rip. Exotic*
Atriplex muelleri	1	1 (Type A)	Terrestrial Native
Atriplex semibaccata	2	1 (Type A)	Terrestrial Native
Galenia secunda	1 & 3	0.242 (Type C)	Terrestrial Native
Lolium perenne	2	1 (Type A)	Terrestrial Native
Phalaris paradoxa	**2**	0.024	Terrestrial Native
Scaevola aemula	1	0.07 (Type A)	Terrestrial Native
Trifolium glomeratum	1, 2 & 3	1 (Type C)	Terrestrial Native
Anagallis arvensis	1 & 2	1 (Type C)	Terrestrial Exotic
Arctotheca calendula	3	1 (Type A)	Terrestrial Exotic
Centaurium erythraea	1	0.275 (Type A)	Terrestrial Exotic
Conya albida	1	1 (Type A)	Terrestrial Exotic
Ehrharta longiflora Sm.	1, 2 & 3	0.161 (Type C)	Terrestrial Exotic
Oxalis pes-caprae	3	1 (Type A)	Terrestrial Exotic

Plantago coronopus	3	0.28 (Type A)	Terrestrial Exotic*
Plantago lanceolata	1 & 2	0.722 (Type C)	Terrestrial Exotic
Rumex crispus	2	1 (Type A)	Terrestrial Exotic
Solanum nigrum	1	1 (Type A)	Terrestrial Exotic
Sonchus oleraceus	1	1 (Type A)	Terrestrial Exotic
Stellaria media	1	0.281(Type A)	Terrestrial Exotic
Vicia sativa	1	1 (Type A)	Terrestrial Exotic
Sedge A	**1**	0.004	Aquatic / Rip. Unknown
Sedge T2	3	0.08 (Type A)	Aquatic / Rip. Unknown
Sedge T3	1, 2 & 3	0.081(Type C)	Aquatic / Rip. Unknown
Sedge T4	1 & 3	0.205 (Type C)	Aquatic / Rip. Unknown
Sedge T5	1 & 3	0.727 (Type C)	Aquatic / Rip. Unknown
Unknown Spp.5	2	0.287 (Type A)	Unknown

3.3.1.4 Tookayerta creek

Table 3.8 - shows that the only reach sections not to be significantly different from each other along Tookayerta creek were sections 3 & 4 (NPMANOVA: *df* = 3, *F* = 6.8833, *P* = 0.0002). A cluster analysis (Fig. 3.5) illustrates the similarities between sections 3 & 4 and the dissimilarities between each of the other sections based on the seed bank species composition. Sections 1 and 2 were distinct and unique. Section 1 contained *Galium murale* and *Plantago coronopus*, which were significant indicators of this section and exclusive to this section. Section 2 contained a number of rare species that were exclusive to this section, *Crassula Sieberana*, *Galenia secunda*, *Rumex crispus* and *Trifolium cernuum*. And both sections 1 and 2 contained significantly fewer seeds m^{-2} in comparison to sections 3 and 4 (Fig. 3.9).

Table 3.8: NPMANOVA statistics obtained from comparisons of seed bank species composition of each river section for Tookayerta creek using Pair-Wise posteriori comparisons based on Bray-Curtis dissimilarities.

River sections	***P***
Sections 1 & 2	**0.0084**
Sections 1 & 3	**0.0092**
Sections 1 & 4	**0.0096**
Sections 2 & 3	**0.0084**
Sections 2 & 4	**0.0142**
Sections 3 & 4	0.4778

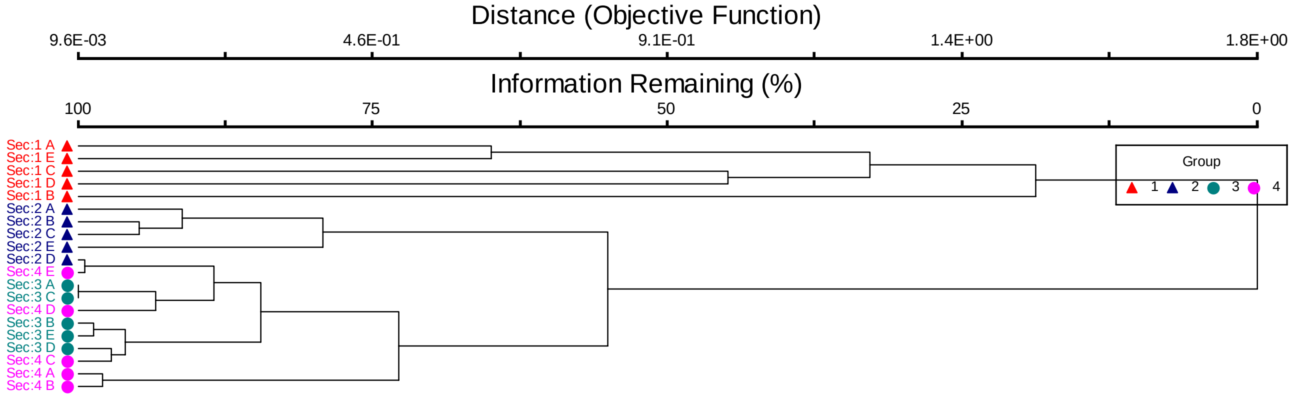

Figure 3.5: Cluster analysis depicting the similarity between the seed bank species composition and each of the reach sections of Tookayerta creek.

A total of 38 species were recorded in the seed bank of Tookayerta creek. An MRPP showed a significant difference (*A* = 0.3976; *P* = 0.000098) between species recorded in each reach section. Table 3.9 - shows that out of a total of 38 species recorded only 13 species (4 unknown sedges) were classified as aquatic and riparian; and out of those 13 species, only 7 could be confirmed as native aquatic and riparian species. Indicator species analysis (Table 3.9) showed that of the 7 native aquatic and riparian species, *Typha domingensis* and *Crassula sieberana* were rare in abundance. *Juncus bufonius* was considered abundant and widespread, recorded in all sections in relatively high densities. *Persicaria decipiens* was a significant indicator (*P* = 0.018) of reach section 3, but was also recorded in section 4. *Callitriche stagnalis* was a significant indicator (*P* = 0.029) of reach section 3, while also recorded in sections 2 and 4. *Cyperus vaginatus* was a significant indicator (*P* = 0.039) of section 2, while also occurring in sections 3 and 4, and *Isolepis fluitans* was a significant indicator (*P* = 0.015) of reach section 3, but recorded in section 2 also. The 4 unknown sedges, sedge T2 and sedge T4 were considered widespread and rare; sedge T3 was considered widespread and common, and sedge T5 was a significant indicator (*P* = 0.031) of reach section 1, but was also recorded in sections 2, 3 and 4. The two exotic aquatic and riparian species were rare or rare and widespread (Table 3.9).

Table 3.9: Indicator species analysis comparing the seed bank species composition between reach sections of Tookayerta creek to provide an indication of which species characterise a particular reach section (Type A, B or C denotes why the species was not a significant indicator) and functional classification of the species present (* denotes naturalised). Sections in bold indicate the species is a significant indicator of that section, *** denotes species recorded in the seed bank but not recorded in the vegetation community during the ecological condition survey (Chapter 2).

Species	Sections	*P*	Functional Classification
Callitriche stagnalis	2, **3** & 4	0.029	Aquatic / Rip. Native
Crassula sieberana ***	2	1 (Type A)	Aquatic / Rip. Native
Cyperus vaginatus ***	**2**, 3 & 4	0.039	Aquatic / Rip. Native
Isolepis fluitans	2 & **3**	0.015	Aquatic / Rip. Native
Juncus bufonius L. ***	1, 2, 3 & 4	0.138 (Type B)	Aquatic / Rip. Native
Persicaria decipiens	**3** & 4	0.018	Aquatic / Rip. Native
Typha domingensis	1	0.578 (Type A)	Aquatic / Rip. Native
Berula erecta ***	1	0.23 (Type A)	Aquatic / Rip. Exotic
Isolepis prolifera ***	1 & 2	1 (Type C)	Aquatic / Rip. Exotic
Atriplex lindleyi	4	1 (Type A)	Terrestrial Native
Centipeda minima	1, 3 & 4	0.195 (Type C)	Terrestrial Native
Galenia secunda	2	1 (Type A)	Terrestrial Native
Lolium perenne	4	1 (Type A)	Terrestrial Native
Medicago polymorpha L.	4	1 (Type A)	Terrestrial Native
Phalaris paradoxa	1, 2, 3 & 4	1 (Type C)	Terrestrial Native
Portulaca oleracea	4	1 (Type A)	Terrestrial Native
Rumex brownii	3	1 (Type A)	Terrestrial Native
Scaevola aemula	1	0.219 (Type A)	Terrestrial Native
Trifolium glomeratum	4	1 (Type A)	Terrestrial Native
Anagallis arvensis	1, 2, 3 & 4	0.558 (Type C)	Terrestrial Exotic
Arctotheca calendula	1	1 (Type A)	Terrestrial Exotic
Bromus sterilis	1 & 4	0.214 (Type C)	Terrestrial Exotic
Conya albida	1	0.188 (Type A)	Terrestrial Exotic
Ehrharta longiflora Sm.	2, 3 & 4	0.859 (Type C)	Terrestrial Exotic
Galium murale	**1**	0.034	Terrestrial Exotic
Plantago coronopus	**1**	0.038	Terrestrial Exotic*
Polygonum aviculara	3	1 (Type A)	Terrestrial Exotic

Rumex crispus	2	1 (Type A)	Terrestrial Exotic
Senecio spp.	2 & 4	0.37 (Type C)	Terrestrial Exotic
Teline monsoessulana	1 & 2	0.22 (Type C)	Terrestrial Exotic
Trifolium cernuum	2	1 (Type A)	Terrestrial Exotic
Trifolium subterraneum	3	0.198 (Type A)	Terrestrial Exotic
Sedge T2	1, 2, 3 & 4	0.07 (Type C)	Aquatic / Rip. Unknown
Sedge T3	1, 2, 3 & 4	0.053 (Type B)	Aquatic / Rip. Unknown
Sedge T4	1, 2, 3 & 4	0.093 (Type C)	Aquatic / Rip. Unknown
Sedge T5	**1**, 2, 3 & 4	0.031	Aquatic / Rip. Unknown
Unknown Spp.5	3	1 (Type A)	Unknown
Unknown species 10	1,2 & 4	0.2790 (Type C)	Unknown

The other significant indicator species from the seed bank were *Plantago coronopus* and *Galium murale*, both exotic terrestrial species and both significant indicators of section 1. All of the other species recorded were either terrestrial natives or exotics, and were each either rare or widespread and rare (Table 3.9).

3.3.2 Seed Bank Density

Seed density between each of the rivers sampled and in particular between differing river sections varied substantially (Figs. 3.6 – 3.9). Along the Angas section 2 had a significantly reduced seed bank with an average of 3,920 ± 3,268 seeds m^{-2}; where as all the other sections had in excess of 10,000 seeds m^{-2} (Fig. 3.6). On the Finniss, the sub catchments - sections 2 and 7 had significantly higher numbers of seeds m^{-2} (49,840 ± 23,006 and 48,580 ± 27765, respectively) in comparison to sections 1, 3, 4, 5 and 6 along the main channel (Fig. 3.7).

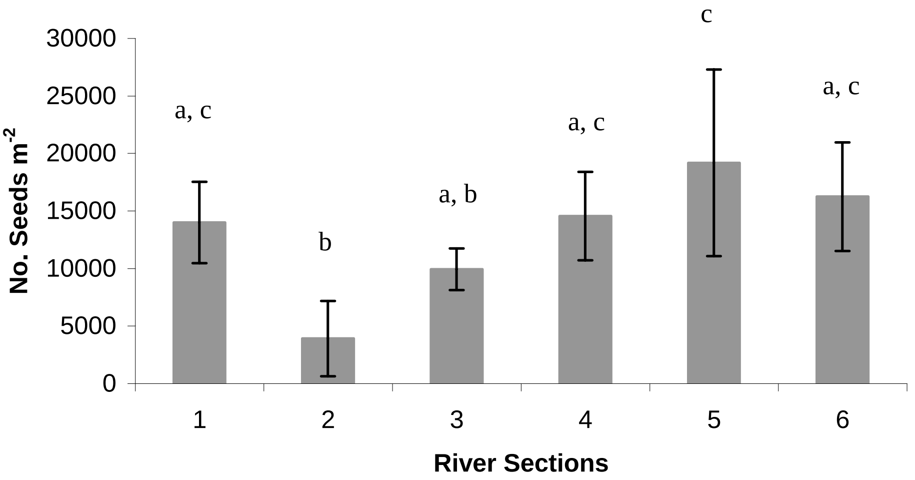

Figure 3.6: Total number of seeds m^{-2} along the River Angas. Means that are not significantly different ($p \leq 0.05$) using one-way ANOVA and Tukey HSD post hoc test are followed by the same letter. Error bars show standard deviations.

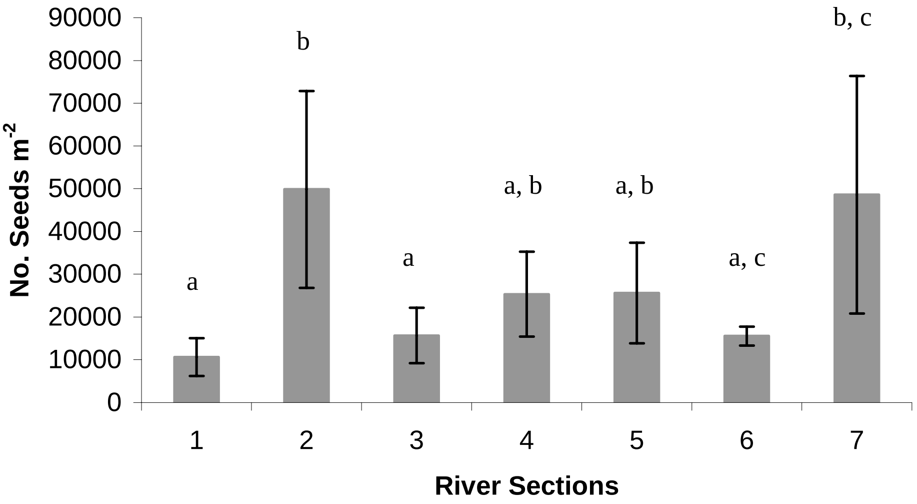

Figure 3.7: Total number of seeds m^{-2} along the River Finniss. Means that are not significantly different ($p \leq 0.05$) using one-way ANOVA and Tukey HSD post hoc test are followed by the same letter. Error bars show standard deviations.

Currency creek had relatively similar numbers of seeds m^{-2} for each section (Fig. 3.8) and comparable with numbers from the Angas and Finniss rivers. Tookayerta creek had significantly reduced numbers of seeds m^{-2} in its low land sections (sections 1 and 2), but sections 3 and 4 contained the highest numbers of seeds m^{-2} of any of the river sections sampled (Fig. 3.9).

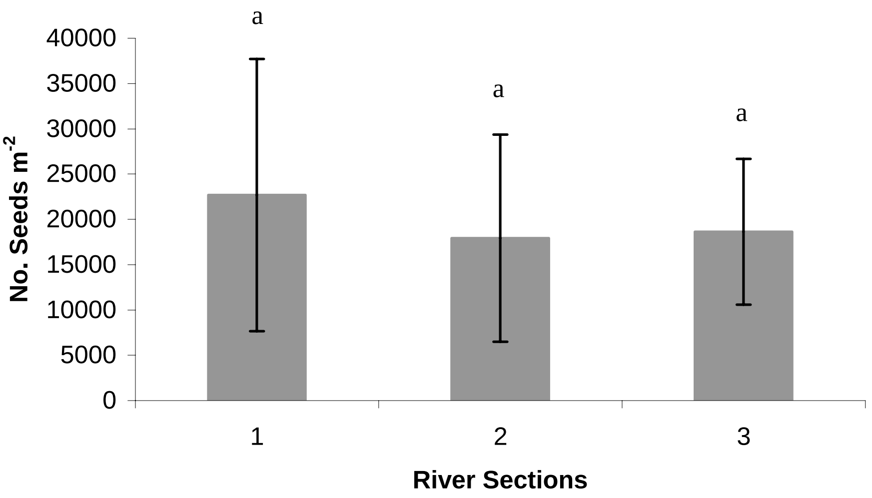

Figure 3.8: Total number of seeds m^{-2} along Currency creek. Means that are not significantly different ($p \leq 0.05$) using one-way ANOVA and Tukey HSD post hoc test are followed by the same letter. Error bars show standard deviations.

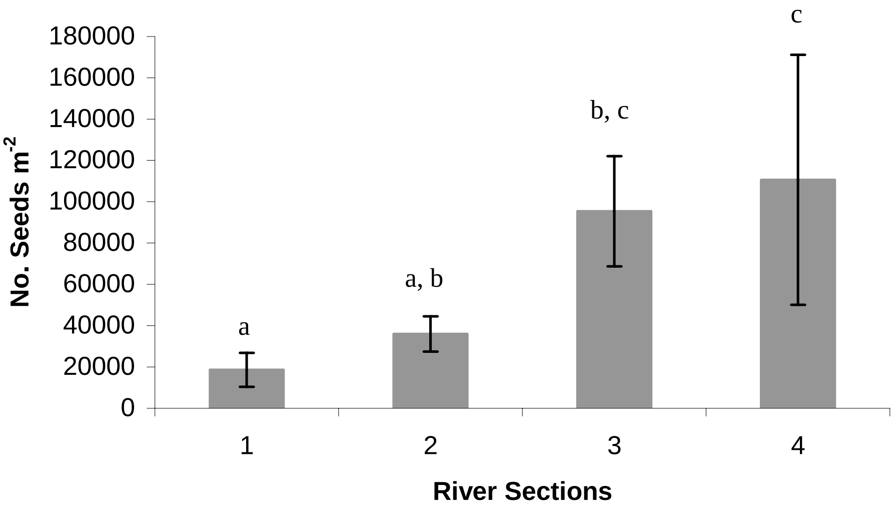

Figure 3.9: Total number of seeds m^{-2} along Tookayerta creek. Means that are not significantly different ($p \leq 0.05$) using one-way ANOVA and Tukey HSD post hoc test are followed by the same letter. Error bars show standard deviations.

3.4 Discussion

3.4.1 Aquatic and riparian seed banks

Generally, the seed banks along each the four catchments were of comparable density and species richness to those of other Australian rivers and wetlands (Nicol 2004; Nicol *et al.* 2003; Pettit and Froend 2001). There was a greater density of seeds m^{-2} and a greater species richness, along each reach section compared to the Blackwood River (with a total of 45 species and an average of 1318 $\pm$ 535 seeds m^{-2}) and the Ord River (with a total of 32 species and an average of 652 $\pm$ 291 seeds m^{-2}) in Western Australia (Pettit and Froend 2001). The density (ranging from 4,000 to 110,000 seeds m^{-2}) and richness (ranging from 13 to 20 species) of aquatic and riparian species recorded along each reach section were comparable to those recorded in Bool and Hacks Lagoons, southern Australian wetlands (Nicol *et al.* 2003). The seed bank densities were different to some overseas rivers such as the Vindel River (Sweden) where 189,181 seeds m^{-2} were detected in the strandlines following a spring flood (Nilsson and Grelsson 1990) and the Nyl River floodplain in South Africa where 1,300 seeds m^{-2} were detected (Brock and Rogers 1998).

The species richness may have been comparable to other Australian studies (Britton and Brock 1994; Brock *et al.* 2003; Finlayson *et al.* 1990), however, out of a total of 81 species recorded, 51 were classified as terrestrial. Of these, the majority were either rare or widespread and rare; occurring in low abundance, in a limited number of riverine sections (Tables 3.3, 3.5, 3.7 and 3.9) with the exception of *Phalaris paradoxa* (Table 3.3). This high proportion of terrestrial species is due to the fact that this region has undergone extensive agricultural development, clearing, with alterations in catchment primary production (DWLBC 2003a; DWLBC 2003b; Savadamuthu 2003). What is of greater concern is the number of exotic species (both aquatic and terrestrial) recorded in the seed banks of each river. The Angas had a total of 22 exotic (43% of 51 species recorded in total), the Finniss had 22 (47% of 47 species recorded in total), Tookayerta creek had 15 (39% of 38 species recorded in total) and Currency creek had 15 exotics (43% of 35 species recorded in total) (Table 3.1). These numbers are significantly higher in comparison to other Australian studies; Nicol *et al.* (2003) reported seven exotic species (25% of 28 species recorded in total) in the seed bank of a seasonal southern Australian wetland, Brock and Casanova (1997) found eleven exotics (18% of 60 species recorded in total) and

Casanova and Brock (2000) identified 12 exotic species (17% of 72 species recorded in total) from the seed banks of northern New South Wales temporary wetlands. The susceptibility of an area to invasion by exotic species has been attributed to a number of factors (Hobbs and Huenneke 1992), however the alterations of natural flow regimes and alterations in catchment primary production have coincided with the invasions of many rivers and floodplain systems by exotic plant species (Erskine *et al.* 1999; Sher *et al.* 2000).

Species richness may have been underestimated in this study as the seedling emergence technique was used with only one wetting cycle (continuously water logged). Brock and Rogers (1998) reported on two species that required a second wetting cycle to break dormancy. Therefore species may have gone undetected in this study. In future studies to determine the species richness of the seed bank more than one wetting may be required (sensu Brock and Rogers 1998; Leck and Brock 2000).

3.4.2 The impact and extent of catchment degradation on the aquatic and riparian seed banks

The plant communities and seed banks present in ephemeral rivers and wetlands at any one time reflect local conditions rather than longer term evolutionary events (Brock and Rogers 1998). The anthropogenic alterations to water regimes and catchment primary production in these systems, have changed the vegetation structure and composition and hence the seed bank composition and dynamics (Brock and Casanova 1997; Poiani and Johnson 1989). This was demonstrated not only by the high proportion of terrestrial species present (63% of all species recorded), but more so by the relatively high proportion of exotic (both aquatic and terrestrial) species present in the seed bank of each catchment.

3.4.2.1 The Angas

There was an aquatic and riparian seed bank remaining along the Angas but it was significantly reduced and limited to particular riverine sections. Only *Typha domingensis* was abundant and widespread, where as *Juncus bufonius* L, *Cyperus vaginatus*, *Gratiola peruviana*, both *Myriophyllum* sp., and *Rorippa nasturtium-aquaticum* were significant indicators of stream sections 5, 4, 1, 1, and 6, respectively (Table 3.3). The remaining aquatic and riparian species were either rare or widespread and rare in abundance. Of the 20 species classified as native or exotic aquatic and riparian species, known and unknown; 10 were recorded in the seed bank of river section 1, 1 in section 2, 5 in section 3, 6 in section 4, 10 in section 5, and 8 were recorded in the seed bank of section 6 (Table 3.3). This would suggest that sections 2, 3 and 4 had been impacted more severely than sections 1, 5 and 6. This is also consistent with the number of seeds m^{-2} for each of the river sections (Fig. 3.6).

3.4.2.2 The Finniss

Juncus bufonius, Cyperus vaginatus, Typha domingensis and sedge T4 were significant indicators of stream sections 2, 2, 6 and 7, respectively, while the other aquatic and riparian species were either rare or widespread and rare. Of the 15 species classified as native or exotic aquatic and riparian species, known and unknown; 7 were recorded in the seed bank of section 1, 9 were recorded in section 2, 8 were recorded in section 3, 7 from section 4, 9 from section 5, 11 from section 6, and 9 from section 7. There was no significant difference in the numbers of aquatic and riparian species recorded in each section, and even though sections 2 and 7 had significantly higher numbers of seeds m^{-2} (Fig. 3.7), there is no section or sections with a significantly reduced aquatic and riparian seed bank.

3.4.2.3 Currency Creek

Juncus bufonius and sedge A were recorded as significant indicators of section 1 and *Isolepis fluitans* was widespread and abundant. The other aquatic and riparian species were each classified to be either rare or widespread and rare. Of the 15 aquatic and riparian species recorded, 10 were recorded in the seed bank of section 3, 8 from section 2, and 10 from section 1. There was no significant difference in the numbers of aquatic and riparian species or the numbers of seed m^{-2} recorded in each section; hence no section has been more severely impacted than any of the others by catchment degradation.

3.4.2.4 Tookayerta Creek

Persicaria decipiens, Callitriche stagnalis, Cyperus vaginatus, Isolepis fluitans and sedge T5 were recorded as significant indicators of creek sections 3, 3, 2, 3 and 1, respectively, while *Juncus bufonius* was abundant and widespread. Both *Typha domingensis* and *Crassula sieberana* were recorded as rare in abundance. Of the 13 species classified as aquatic and riparian, 8 were recorded in section 1, 10 in section 2, 9 in section 3, and 8 in section 4. Again there was no significant difference in the numbers of aquatic and riparian species recorded in each section, and even though sections 3 and 4 have significantly higher numbers of seeds m^{-2} (Fig. 3.9), in fact the highest of any river section, there was no section or sections with a significantly reduced aquatic and riparian seed bank.

3.4.3 Ecological condition as indicated by the seed bank

This study provides evidence that long-lived, species-rich seed banks, which are not depleted by germination, give ephemeral rivers the resilience necessary to withstand a range of environmental fluctuations (Brock and Rogers 1998). However, the impact of human induced alterations has been quite severe along selected reaches of each of these four catchments resulting in their very poor ecological condition (Chapter 2). There was no aquatic or riparian species, which could be used as an indicator of ecological condition across sections of all catchments, i.e. indicators of sections with a high proportion of reaches of average to excellent ecological condition. However, indicator species analyses revealed pasture grasses to be a significant indicator of reaches in very poor condition ($p = 0.0010$) along the Finniss and *Baumea juncea* of those reaches in good condition ($p = 0.0230$). Along the Angas, *Cotula coronopifolia* was an indicator of those reaches in average condition ($p = 0.0240$) and along Currency creek, *Cladium procerum* was an indicator of those reaches in good condition ($p = 0.0190$). There was a terrestrial species that may be used as indicators of degradation. The Angas catchment was in the over-all poorest ecological condition relative to the other catchments (Chapter 2), where *Phalaris paradox* was widespread and abundant. *Phalaris paradox* was a significant indicator of section 2 of Currency creek, which contained no reach with a TECS of higher than average in comparison to its other sections. This study also validates the index of ecological condition to a certain degree, but due to the differences in scale used in both studies it is not entirely appropriate to say with complete certainty that there is a strong correlation between the ecological condition of riverine sections and the seed bank composition of those sections (Chapter 2). However, it is worth while noteing that along the Angas sections 2 and 3 recorded the lowest diversity and density of aquatic and riparian species across all sections and catchments. These sections only contained reaches with an ecological condition of poor to very poor. There were no other sections in any of the other three catchments with a significantly reduced diversity or density of aquatic and riparian species present in their seed banks that may be correlated with ecological condition of those sections (Appendix 1).

3.4.4 Management implications: Restoration potential of aquatic and riparian communities

In order to suggest those riverine sections that would have an increased chance of promoting aquatic and riparian plant communities from the addition of environmental flows, this study should be taken in conjunction with the ecological condition of each of those riverine sections (physical habitat availability) (Chapter 2).

The Angas River was in the over-all poorest ecological condition relative to the other catchments. The imposition of environmental flows should be limited to reaches of average ecological condition within sections 4, 5, and 6 (Appendix 1). These reaches contain sufficient physical habitat with adequate aquatic / riparian seed banks remaining that upon the installation of environmental flows would promote aquatic / riparian plant communities. When compared with the Finniss catchment, it is apparent that each of the Finniss's riverine sections (Fig. 3.1) was comprised of reaches with a physical habitat ranging in ecological condition from very poor to excellent (Appendix 1). This suggests that along each of the Finniss sections environmental flows would promote aquatic and riparian plant communities. Giles creek (section 2) and Bull creek (upper part of section 4) are exceptions as both contain reaches ranging in condition from very poor to poor. However, even though these sections are more ecologically degraded, they still contain aquatic and riparian species in their seed banks in sufficient numbers, and therefore with the aid of environmental flows may promote the germination and establishment of those plant communities.

The riverine sections of Currency and Tookayerta creeks both contained reaches ranging in ecological condition from very poor to good, with a similar richness of aquatic and riparian species and similar numbers of seeds m^{-2} present in their seed banks. In terms of promoting aquatic and riparian plant communities in these altered catchments, it is apparent that all reaches of average or greater ecological condition, located in any of the sections along Currency and Tookayerta creeks would benefit ecologically from the installation of environmental flows.

Table 3.10: The number of aquatic and riparian species recorded both during the ecological condition survey (Chapter 2) and this seed bank study.

Catchment **No. of Species:**	**Finniss**	**Angas**	**Currency**	**Tookayerta**
Aquatic and riparian species recorded in the extant vegetation	33	37	32	27
Aquatic and riparian species recorded in the seed bank	15	20	15	13
Aquatic and riparian species recorded in the extant vegetation but not in the seed bank	26	28	24	25
Aquatic and riparian species recorded in the seed bank but not present in the extant vegetation	3	7	3	5

There were 24 to 28 other aquatic and riparian species recorded in the extant vegetation of each catchment but not recorded in their seed banks (Table 3.10). There were also a number of species (3 to 7) found in each catchments seed bank that were not recorded in the extant vegetation of those catchments (Table 3.10). The discrepancy between the extant species and the potential communities are most likely as a result of anthropogenic alterations to water regimes and catchment primary production (Brock 1999; Brock and Casanova 1997; Brock *et al.* 1999; Casanova and Brock 2000). A species of particular interest is *C. sieberana*, recorded in the seed banks of the Finniss, Currency creek and Tookayerta creek, which is on the State endangered plant species list (Armstrong *et al.* 2003). *C. helmsii* also recorded in the seed banks of the Angas, Finniss and Currency creek is considered rare in the Mt. Lofty Ranges (Seaman 2002). This adds further support to the prescription of environmental flows to not only maintain the present aquatic and riparian plant communities, but also to enhance the germination and establishment of those species present in the seed bank which are not apparently present in the extant vegetation community.

CHAPTER 4.

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4 The influence of water level fluctuations on the growth of emergent macrophytes: Implications for management as control measures

4.1 Introduction

Water regime has been defined as the sum of water depth, rate and amplitude of flooding or drawdown, timing, frequency and duration of flooding or drawdown. A water regime can encompass both predictable and unpredictable changes over time. The time-scale of changes can vary from days to years. The response of emergent macrophytes to water depth has been well studied (Grace 1988; Grace 1989; Hellings and Gallagher 1992; Ostendorp 1991; Vretare *et al.* 2001; Waters and Shay 1990). Macrophytes respond to increased depth by elongating leaves to maintain an emergent canopy, sometimes redeploying resources from below-ground parts (Blanch *et al.* 1999a; Cooling 1996; Grace 1988; Grace 1989; Rea and Ganf 1994d; Waters and Shay 1990). Severe submergence can lead to carbon starvation by reducing the availability of atmospheric carbon (Cížková-Koncalová *et al.* 1992) and a diminished light climate.

Water regime as distinct from instantaneously measured water depth, has been implicated as the primary factor influencing the composition, diversity and distribution (Blanch *et al.* 1999b; Blanch *et al.* 2000; Boar 2006; Boedeltje *et al.* 2002; Brownlow *et al.* 1994; Casanova and Brock 2000; Deegan *et al.* 2005; Nicol *et al.* 2003; Nielsen and Chick 1997; Peterson and Baldwin 2004; Rea and Ganf 1994d; Warwick and Brock 2003) of emergent macrophyte communities. In aquatic systems species that cannot tolerate any waterlogging, establish on the upper sections of the elevation gradient, whereas only species that can tolerate waterlogging and submersions will survive in the lower sections of the elevation gradient. In environments where water depth is not constant, ephemeral, plants tolerating or responding to fluctuations in water depth are favoured (Brock and Casanova 1997). This results in a species rich community when compared with the adjacent terrestrial and aquatic communities.

The altering of the natural water regime by damming and draining of a waterway often results in water levels becoming less variable through time and the edge plant community may be restricted or disappear completely (Brock and Casanova 1991; Brock and Casanova 1997; Casanova and Brock 2000; Nielsen and Chick 1997). On the other hand the occurrence of low flows (low disturbance) due to the stabilising effect of dams and weirs has contributed to conditions favourable to fewer dominant species by the influence of water regime on competitive interactions (Brock and Casanova 1997; Deegan *et al.* 2005; Rea and Ganf 1994a; Rea and Ganf 1994c). This has lead to the establishment of dense littoral plants, such as extensive reed beds of *Phragmites australis* and cumbungi *Typha* spp along the River Murray, South Australia (Maheshwari *et al.* 1995).

Floods and droughts are important features of most running water ecosystems, but the alteration of natural flow regimes by recent human activities raises questions related to both evolution and conservation (Lyte and Poff 2004; Walker and Thoms 1993). This has resulted in water regime variation being considered a vital component in maintaining wetland and river function and diversity, in both Australia (Brock 1986; Brock 1991; Brock *et al.* 1999; Rea and Ganf 1994a) and else where around the world (Grace and Wetzel 1981; Grace and Wetzel 1982; Poff *et al.* 1997), even judged to be at least as important as changes in land use when it comes to its impacts on aquatic systems (Heggie and Skyring 1999).

Knowledge of how vegetation parameters such as species productivity relate to water regime is valuable because even small changes in the hydraulic regime can have significant effects on the diversity and community structure of emergent macrophytes (Blanch *et al.* 1999a; Blanch *et al.* 1999b; Blanch *et al.* 2000; Brock and Casanova 1991; Brock and Casanova 1997; Maheshwari *et al.* 1995; Rea and Ganf 1994a; Rea and Ganf 1994b; Stromberg 2001). This information is useful in understanding and predicting the responses of aquatic macrophytes to environmental management practices (Froend and McComb 1994).

The aim of this study was to determine how four species of emergent macrophyte would respond to a range of fluctuating water levels over a range of initial water depths (elevation). As flooding of the photosynthetic canopy, whether permanent or short-term as part of a fluctuating hydraulic regime, will limit the capacity for the acquisition of carbon (Blanch *et al.* 1999a; Siebentritt 2003), it is hypothesise both treatments will reduce plant performance. The species chosen for this study (*Cyperus vaginatus, Phragmites australis, Triglochin procerum* and *Typha domingensis*) naturally inhabit different zones along the elevation gradient ranging from deep water (*Triglochin procerum*) to fully exposed elevations high above the waters surface (*Cyperus vaginatus*). It is further hypothesised that species will display similar tolerances to water depth and amplitude of water level fluctuations, tolerances that can be related to the elevation preference of each species. The specific objectives were: i) to quantify the growth of macrophytes across gradients in depth and amplitude, ii) to quantify any morphological response by macrophytes to different amplitudes and depths, iii) compare the impact of depth and amplitude on plant performance, iv) determine whether any relationship exists between the natural elevation preference and tolerance to water level amplitude and water depth, and v) based upon these results predict changes at the community level, and relate this information to environmental management practices.

4.2 Materials and Methods

4.2.1 Study species

Four species were chosen for the experiment: *Cyperus vaginatus* R. Br., *Phragmites australis* (Cav.) Trin. ex Steud., *Triglochin procerum* R Br. and *Typha domingensis* Pers. All are rhizomatous perennials that form dense to monospecific stands. *T. procerum* relies less on clonal reproduction (as its lateral expansion is limited because its rhizomes are short) than on sexual reproduction to form large stands (Cunningham *et al.* 1992; Jessop and Toelken 1986). Locally, the species inhabit different zones along the elevation gradient with the sedge, *C. vaginatus*, inhabiting the highest point, usually 0 to 180 cm above the water surface, followed by *P. australis* and *T. domingensis*, which normally reside just above and just below the water surface, respectively, and *T. procerum* which prefers deep water, growing in water up to a depth of 120 cm (Table 4.1).

Table 4.1: Elevation distribution of the four study species in the EMLR.

Species	**Elevation relative to water surface** (cm)
C. vaginatus	0 to 180
P. australis	0 to 30
T. domingensis	-55 to 0
T. procerum	-120 to -50

4.2.2 Plant material

Adult *C. vaginatus* and *T. procerum* were collected from the River Angas, South Australia. *T. domingensis* and *P. australis* were collected from the Barker Inlet wetlands, South Australia. Approximately 90 specimens of each species were initially collected of similar size, maturity and biomass. The plant's below-ground reserves (tubers or rhizomes) and flowers were removed before being planted in plastic pots (23 × 23 × 20 cm) filled to a depth of 18 cm with sandy loam and topped with a 2 cm layer of cricket pitch clay to impede the diffusion of oxygen into the sediment and provide a more natural sediment redox potential. The slow release fertilizer Osmocote® was added to the sandy loam at a concentration equivalent to a loading rate of 100 g N m^{-2} $year^{-1}$. This loading rate has been demonstrated to be non-limiting in ponds experiments (Morris 1998). To ensure a non-limiting supply of micro-nutrients, 30 % of the fertilizer (by weight) was Osmocote Plus®. Plants were then placed in outdoor ponds and watered to saturation except for *T. procerum*, which was flooded by 50 cm.

Plants were allowed to establish for 11 weeks (22nd October, 2004 until 12th January, 2005). At the end of the establishment period only 48 specimens of *C. vaginatus* survived, which meant the number of replicates for this species, had to be reduced from the anticipated five to three. Twelve specimens of each species were randomly selected and harvested to measure initial biomass.

4.2.3 Experimental water regimes

The four fluctuating water levels chosen were: Static (water depth remained at 60 cm throughout the experimental period); 60 ± 15 cm (water depth ranged from 45 cm to 75 cm), 60 ± 30 cm (water depth ranged from 30 to 90 cm) and 60 ± 45 cm (water depth ranged from 15 to 105 cm) (Fig. 4.1), hereafter termed Static, ±15 cm, ±30 cm and ±45 cm, respectively. The regimes had corresponding drawdown/flooding rates of 0 cm day^{-1}, 1.5 cm day^{-1}, 3.0 cm day^{-1} and 4.5 cm day^{-1}. The average water depth for each treatment was 60 cm. Within each fluctuating water level, plants were grown at different elevations with the sediment surface 20, 40 and 60 cm from the bottom of the ponds (hereafter termed deep, intermediate and shallow, respectively). Each hydraulic regime was replicated in two ponds.

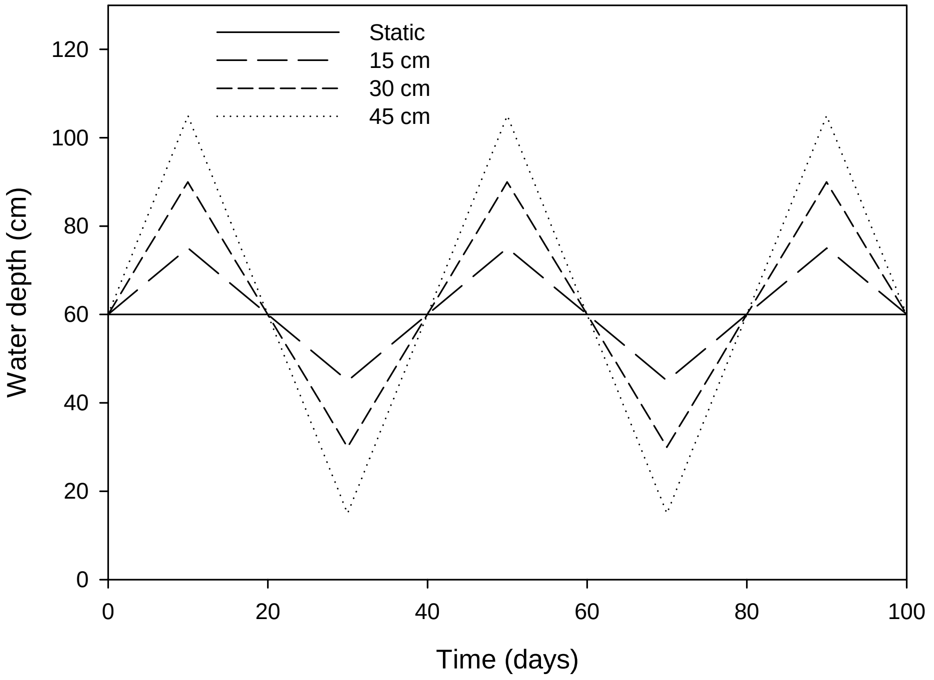

Figure 4.1: Experimental water regimes. In each pond, potted plants were placed at three elevations: sediment surface 20, 40 and 60 cm above the pond base.

4.2.4 Pond Experiment

Three replicates of *C. vaginatus* and five replicates of *P. australis*, *T. domingensis* and *T. procerum* for each elevation treatment (shallow, intermediate and deep) were distributed between the two replicate outdoor ponds (4.5 × 3.5 × 1.2 m deep) for each hydraulic regime. For those pots that would be completely exposed by the water level fluctuations (ie, shallow ±30 cm, shallow and intermediate ±45 cm), RibLock® columns (30 cm diameter, either 20 or 40 cm tall as appropriate) filled with sandy loam were used as a base. The columns allow water from the base of the pond to move into the plant pots thus maintaining minimal water supply even when the pots were otherwise completely above the waters surface (Nicol and Ganf 2000). The experiment ran for 100 days (13th January until 22nd April, 2005). The water level in each of the ponds was maintained manually.

Over the course of the experiment, a *T. procerum* specimen from the ±15 cm intermediate treatment died. Another specimen of *P. australis*, also from the ±15 cm intermediate treatment, failed to show any growth over the course of the experiment. Upon harvest it was found the belowground parts had rotted and the plant was excluded from the dataset.

4.2.5 Data Collection and Analysis

Each week through out the experimental period, the following data was collected: the leaf/stem length and the number of shoots per pot. At the conclusion of the experimental period, the plants were harvested, washed, and the fresh-weight determined. The plant material was then oven dried at 60 °C for seven days and the dry-weight measured.

There were no significant differences between the plants allocated to each treatment, based upon initial height and the number of stems/leaves per pot (Denton and Ganf 1994). No differences were apparent between growth in the two replicate ponds for each water regime, hence the pond dataum were pooled for subsequent analysis (Blanch *et al.* 1999a). Treatment comparisons were made using Three-way ANOVAs on log-transformed or Arcsine square-root transformed data, with water regime amplitude (static, ±15 cm, ±30 cm and ±45 cm), initial depth/elevation (deep, intermediate and shallow) and species as sources of effect.

4.2.6 Estimation of Relative Growth Rate and Emergent Surface Area

Relative Growth Rate (RGR) was calculated using the formula from Harper (Harper 1977):

$$\text{RGR (mg g}^{-1}\text{ day}^{-1}\text{)} = \frac{\ln Wf - \ln Wi}{\Delta t} \qquad (1)$$

where Wf and Wi are the final and initial plant dry-weight biomass (g) over Δt (days). Initial biomass was estimated from twelve replicates per species destructively harvested at the end of the establishment phase. Mean values of initial biomass were used in calculations of the RGR.

To estimate emergent surface area, the relationship between surface area and culm or leaf length was measured on a sub sample of one replicate from each treatment for each species. Surface area was measured on a Delta-T meter. The resulting linear regressions were significant for all species (all $p<0.0001$). For the sake of predictive accuracy, the regression was constrained to an intercept of zero. The regression slopes were 1.0439, 3.2770, 3.3331 and 2.1661 for *C. vaginatus, P. australis, T. procerum* and *T. domingensis*, respectively. As the regressions were constrained, the r^2 was not reported by the regression analysis. The r^2 values for unconstrained regressions were: 0.6955, 0.5856, 0.9502 and 0.7458, respectively.

4.3 Results

4.3.1 Species performance

4.3.1.1 Biomass

In comparison with deep or intermediate elevations the final biomass of *C. vaginatus* was greatest in shallow water irrespective of the amplitude of the water level fluctuations but it decreased with increasing amplitude (Table 4.2). In contrast, there was little difference in the average biomass of *P. australis* across either elevation or amplitude gradients. However, intermediate elevations across all amplitudes favoured the accumulation of biomass for this species, but the combination of deep water and high water level fluctuations was detrimental. For *T. domingensis* the influence of large fluctuations in water level had a more pronounced inhibitory effect across all elevations. *T. procerum* did not display any obvious trend or pattern.

Table 4.2: Comparison of total final biomass (dwt)(g) in four species of emergent macrophytes subjected to four water level amplitudes at three elevations. Mean (Std. Dev.), *n*=3-5.

		Amplitude			
Species	**Elevation**	**Static**	**± 15 cm**	**± 30 cm**	**± 45 cm**
C. vaginatus	**Deep**	38 (32.2)	31 (16.6)	12 (2.8)	17 (11.5)
	Intermediate	66 (26.5)	55 (23.7)	61 (35.7)	50 (23.8)
	Shallow	216 (83.1)	132 (7.7)	112 (4.9)	111 (42.2)
P. australis	**Deep**	249 (102.6)	207 (49.2)	237 (31.2)	112 (42.3)
	Intermediate	278 (98.0)	263 (51.7)	334 (65.0)	246 (27.9)
	Shallow	209.2 (34.0)	207 (82.4)	289 (92.3)	267 (22.5)
T. procerum	**Deep**	30.6 (18.5)	88 (72.9)	34 (22.8)	20 (18.1)
	Intermediate	33 (30.0)	30 (16.2)	31 (11.7)	25 (6.6)
	Shallow	38 (11.4)	23 (8.3)	19 (19.1)	14 (12.1)
T. domingensis	**Deep**	562 (96.6)	666 (107.8)	621 (157.3)	262 (181.8)
	Intermediate	639 (86.6)	699 (189.9)	472 (124.9)	245 (113.5)
	Shallow	573 (118.)	491 (131.7)	470 (66.0)	343 (114.4)

To quantify these observations, and to compare and contrast the preferences of the four species, a Three-way ANOVA was performed (Table 4.3). The significant interaction terms indicates that final biomass is dependent upon specifying species and elevation as well as species and amplitude. The species-elevation interaction lends support to the observation that species have different habitat requirements. For example, *C. vaginatus* prefers shallow elevations but is less tolerant of water level fluctuations. In contrast, *P. australis* and *T. domingensis* grew well, within their tolerance limits, irrespective of whether they are subjected to a static water level or to levels that fluctuate up to ± 30 cm, but are perhaps less tolerant of fluctuations of ±45 cm.

Table 4.3: Results of a Three-way ANOVA performed on various indicators of performance for four species of emergent macrophytes subjected to four water level amplitudes at three elevations.

Source	***p* value**					
	Final biomass (dwt)(g)	RGR (mg g^{-1} day^{-1})	Vegetative reproduction (shoots pot^{-1})	Final emergent surface area (cm^2)	Average emergent surface area (cm^2)	Leaf or stem length (cm)
Species	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**
Elevation	0.1933	**<0.0001**	**<0.0001**	**<0.0001**	**0.0004**	**<0.0001**
Amplitude	**<0.0001**	**<0.0001**	0.8668	0.8727	**0.0246**	**0.0014**
Species×Elevation	**0.0016**	**<0.0001**	**0.0008**	**<0.0001**	**<0.0001**	**<0.001**
Species×Amplitude	**<0.0001**	0.1166	0.8260	0.3681	**<0.0001**	0.1229
Elevation×Amplitude	0.2567	0.3417	0.2328	0.2197	0.8087	0.6933
Species×Elevation× Amplitude	0.1586	0.3402	0.0946	0.9245	**0.0141**	0.5249

Similarly, the significant interaction between species and amplitude (Table 4.3) reinforces the different habitat preferences of the species. For example, the biomass of *C. vaginatus* decreases as amplitude increases irrespective of elevation. And, irrespective of elevation, the biomass of *P. australis* and *T. domingensis* appears to be independent of amplitudes between Static and ±30 cm but they recorded their lowest biomasses at an amplitude of ±45 cm. However, the large variability associated with these data probably over-rides any significant three-way interaction.

4.3.1.2 Relative Growth Rate

Although the biomass data is useful for within species comparisons, it does not account for major differences between the initial sizes of the four species. To account for this, the initial and final biomasses were used to calculate RGR. As quantitative information on the loss of biomass during the experiment is not available, these values represent a net relative growth rate.

The RGRs generally reflect the patterns for final biomass. However, although the biomasses of *P.australis* and *T. domingensis* were generally higher than *C. vaginatus* (Table 4.2), the growth rate of *P. australis* was substantially lower than *C. vaginatus* that had maximum growth rates similar to those for *T. domingensis* (Table 4.4). The RGRs of *T.*

procerum were all negative, probably due to the fact that as water levels fell the exposed submerged leaves desiccated and died.

Table 4.4: Comparison of RGR (mg g^{-1} day^{-1}) in four species of emergent macrophytes subjected to four water level amplitudes at three elevations. Mean (Std. Dev.), *n*=3-5.

		Amplitude			
Species	**Elevation**	**Static**	**± 15 cm**	**± 30 cm**	**± 45 cm**
C. vaginatus	**Deep**	14.1 (9.2)	13.7 (6.0)	5.2 (2.5)	7.3 (7.1)
	Intermediate	21.8 (3.7)	19.7 (4.2)	20.2 (6.1)	18.7 (4.5)
	Shallow	33.5 (4.0)	29.1 (0.6)	27.4 (0.4)	26.9 (3.6)
P. australis	**Deep**	14.4 (3.4)	12.9 (2.4)	14.4 (1.4)	6.4 (3.7)
	Intermediate	15.5 (4.0)	15.3 (2.2)	17.7 (2.1)	14.8 (1.2)
	Shallow	13.1 (1.7)	12.4 (4.4)	16.0 (3.5)	15.6 (.8)
T. procerum	**Deep**	-10.1 (9.5)	-0.5 (10.0)	-12.9 (18.4)	-16.2 (10.7)
	Intermediate	-13.7 (17.9)	-8.8 (5.7)	-7.8 (3.7)	-9.9 (3.0)
	Shallow	-5.6 (3.1)	-10.7 (3.4)	-15.4 (8.7)	-19.4 (11.1)
T. domingensis	**Deep**	23.0 (1.7)	24.8 (1.6)	23.9 (2.6)	13.6 (7.2)
	Intermediate	24.4 (1.4)	25.0 (2.7)	21.1 (2.6)	14.0 (4.7)
	Shallow	23.2 (1.9)	21.5 (3.2)	21.3 (1.4)	17.8 (3.2)

The Three-way ANOVA (Table 4.3) again demonstrates that the four species require different conditions to optimise growth and that RGR is both species and elevation dependent. *C. vaginatus* has the highest RGR at shallow elevations, whereas for both *P. australis* and *T. domingensis* the highest RGRs occurred at intermediate or shallow elevations. The lowest RGRs were generally recorded for the ± 45 cm amplitude irrespective of species or elevation, with some exceptions (*C. vaginatus* – deep; *P. australis* – shallow; and *T. procerum* – intermediate) (Table 4.4).

4.3.1.3 Vegetative Reproduction

Vegetative reproduction (Table 4.5), or the number of shoots per pot, was highest for *P. australis*. Vegetative reproduction was independent of water level amplitude (Table 3). The general pattern of shoot production in *C. vaginatus* was for the greatest number to occur at shallow elevations. A similar trend was found for the recruitment of *T. domingensis*: shallow elevations encouraged shoot production, deep elevations reduced shoot production especially at ±45 cm. Despite the negative RGRs of *T. procerum*, shoot production was positive.

Table 4.5: Comparison of the final number of shoots per pot in four species of emergent macrophytes subjected to four water level amplitudes at three elevations. Mean (Std. Dev.), *n*=3-5.

		Amplitude			
Species	**Elevation**	**Static**	**± 15 cm**	**± 30 cm**	**± 45 cm**
C. vaginatus	**Deep**	1.4 (0.6)	1.5 (0.6)	1.1 (0.4)	1.6 (0.7)
	Intermediate	1.9 (0.6)	1.9 (0.7)	2.0 (0.5)	1.8 (0.9)
	Shallow	3.4 (1.5)	3.0 (1.2)	2.5 (0.8)	2.6 (0.9)
P. australis	**Deep**	20.5 (8.3)	20.6 (6.4)	19.8 (7.4)	18.6 (4.3)
	Intermediate	25.4 (10.6)	21.8 (15.2)	31.1 (10.6)	24.7 (5.6)
	Shallow	22.7 (6.0)	21.2 (7.9)	27.6 (9.1)	25.4 (11.1)
T. procerum	**Deep**	2.3 (0.7)	2.4 (1.2)	2.0 (1.2)	1.8 (0.6)
	Intermediate	1.4 (1.0)	1.6 (0.5)	2.4 (0.9)	2.8 (1.5)
	Shallow	3.2 (1.9)	1.9 (0.9)	1.8 (1.2)	1.9 (1.7)
T. domingensis	**Deep**	3.9 (1.0)	3.9 (1.1)	3.9 (1.7)	2.9 (1.5)
	Intermediate	4.7 (1.3)	4.6 (1.6)	3.9 (1.6)	4.1 (2.7)
	Shallow	5.3 (1.2)	5.0 (1.6)	4.6 (1.7)	4.1 (1.6)

The Three-way ANOVA demonstrates that the conditions optimal for shoot production differed between species and was dependent upon species as well as elevation (Table 4.3). For example, the greatest number of shoots was recorded in the shallow treatment for *C. vaginatus*, whereas for *P. australis* the greatest shoot production occurred in the intermediate and shallow treatments. Amplitude had no significant influence on shoot production (*p*=0.8668). *T. domingensis* recorded its lowest shoot production at the deeper elevations across all amplitudes. No obvious pattern or trend was apparent for *T. procerum*.

4.3.1.4 Leaf or Stem Length

All species recruited longer leaves or stems when growing in deep water compared with plants growing in shallow water (Table 4.6). However, leaf length was dependent upon both species and elevation (Tables 4.3) suggesting that species differed in their response to elevation. For example, *T. domingensis* and *T. procerum* had leaf lengths directly proportional to water depth with differences between elevation close to 20 cm irrespective of the amplitude of water level changes. *C. vaginatus* responded poorly and struggled to develop longer stems when grown in deep water. Stems lengths of deep plants were sometimes smaller than plants grown at intermediate elevations. For *P. australis* grown at deep elevations, again recruited longer stems.

Table 4.6: Comparison of final average leaf/stem length (cm) in four species of emergent macrophytes subjected to four water level amplitudes at three elevations. Mean (Std. Dev.), *n*=40-339.

		Amplitude			
Species	**Elevation**	**Static**	**± 15 cm**	**± 30 cm**	**± 45 cm**
C. vaginatus	**Deep**	52.2 (31.2)	46.8 (31.8)	41.9 (28.5)	49.4 (25.0)
	Intermediate	42.9 (29.1)	47.7 (29.4)	48.5 (31.7)	52.1 (28.8)
	Shallow	43.6 (24.4)	42.9 (25.2)	41.8 (26.5)	45.4 (24.9)
P. australis	**Deep**	140.0 (37.2)	133.1 (36.9)	147.4 (41.1)	131.5 (35.2)
	Intermediate	121.5 (45.8)	110.8 (35.5)	129.9 (37.7)	133.2 (40.1)
	Shallow	107.4 (35.0)	98.1 (34.7)	109.9 (38.1)	114.9 (35.4)
T. procerum	**Deep**	82.9 (18.8)	86.4 (19.3)	94.2 (23.2)	96.4 (22.9)
	Intermediate	61.6 (15.0)	67.6 (18.2)	64.7 (21.0)	79.1 (23.8)
	Shallow	35.0 (10.8)	44.2 (13.7)	51.2 (18.7)	48.1 (18.0)
T. domingensis	**Deep**	163.1 (36.4)	163.3 (38.4)	169.3 (37.6)	174.4 (47.6)
	Intermediate	139.6 (40.6)	131.9 (42.6)	137.3 (37.5)	149.4 (37.8)
	Shallow	117.9 (34.6)	111.7 (34.8)	122.7 (31.5)	128.5 (34.3)

Increasing amplitude of water level fluctuations resulted in a general though marginal increase in leaf or stem length (*p*=0.0014). However, increasing water regime amplitude did not always have a linear impact on leaf length. For example, when grown at intermediate and shallow water depths, *T. domingensis* and *P. australis* leaf lengths showed a decrease between the Static and ±15 cm water regime, then an incremental increase between the ±15 and ±45 cm water regimes. For *T. procerum*, leaf length generally increased across both elevation and amplitude. However, for *C. vaginatus* stem length remained relatively constant across both elevation and amplitude gradients (Table 4.6).

4.3.1.5 Emergent Surface Area

The emergent surface area can be presented as either final surface area (Table 4.7) or average surface area (averaged over the 100 days of the experimental period) (Fig. 4.2). The first was used to examine the response of plants to fluctuating water levels as it represents the accumulated response to changing water depth. The second can be used to examine the potential limitation for carbon acquisition that may constrain growth (assuming all species can only access atmospheric carbon).

The emergent leaf surface area of *T. procerum* may have been overestimated because emergent leaf length was calculated by subtracting the water depth above pot surface from total leaf length. Thus, the decumbent leaves of *T. procerum* may have little or no emergent area even when the leaf length is greater than the instantaneously measured water depth. Nevertheless, predicted emergent surface areas have not been modified.

Table 4.7: Comparison of the final emergent surface area per pot (cm^2) in four species of emergent macrophytes subjected to four water level amplitudes at three elevations. Mean (Std. Dev.), *n*=3-5.

		Amplitude			
Species	**Elevation**	**Static**	**± 15 cm**	**± 30 cm**	**± 45 cm**
C. vaginatus	**Deep**	89.7 (117.2)	36.5 (27.2)	0.0	0.0
	Intermediate	762.4 (456.5)	890.4 (439.9)	246.3 (163.4)	698.7 (171.7)
	Shallow	5141.7 (1731.2)	4672.7 (502.1)	1992.8 (136.4)	3194.4 (660.7)
P. australis	**Deep**	10371.1 (4501.3)	10464.2 (2672.6)	10146.3 (4727.7)	8274.4 (1582.9)
	Intermediate	12026.6 (4315.5)	9223.5 (5754.2)	16351.0 (3991.2)	11958.5 (849.4)
	Shallow	9083.2 (1487.3)	8612.0 (1570.6)	13256.2 (1805.5)	11592.1 (3500.4)
T. procerum	**Deep**	3592.3 (1058.6)	3802.4 (1419.9)	3533.9 (690.2)	2569.2 (1429.7)
	Intermediate	3695.3 (786.6)	2613.2 (528.1)	3839.1 (509.2)	4163.1 (1331.4)
	Shallow	2613.8 (1327.4)	2325.2 (848.6)	2865.8 (1906.0)	3003.1 (1914.0)
T. domingensis	**Deep**	11729.8 (2332.9)	11177.0 (3108.7)	10485.5 (4451.2)	8838.4 (3572.1)
	Intermediate	11488.5 (1980.0)	11603.7 (1994.2)	10174.9 (2239.5)	12426.0 (5385.2)
	Shallow	10112.5 (1165.1)	9679.3 (2159.3)	10415.8 (2134.6)	10128.1 (2060.8)

In general, *C. vaginatus* had lower final emergent surface areas than the other three species and *T. domingensis* the greatest. *C. vaginatus* grown at deep elevation with water levels that fluctuated by ±30 and ±45cm had no emergent leaf area at the final harvest unlike the other three species that had leaf lengths that could remain partially exposed even under the largest fluctuations in water level. The results of the ANOVA support the observed trends that the final emergent surface area was dependent upon species and elevation. Surprisingly, final emergent surface areas were independent of amplitude (Table 4.3).

To examine whether emergent surface area influenced growth, the average emergent surface area (averaged over the experimental period) was plotted against RGR (Fig. 4.2). These data suggests that in *C. vaginatus* the average emergent surface area was asymptotically related to (and therefore a determinant of) RGR ($p<0.0001$; $r^2=0.7196$; $F=87.276$; $n=36$; RGR ($mg\ g^{-1}\ day^{-1}$) = -5.096 + 4.313 × ln (Average emergent surface area (cm^2)). The RGR was independent of surface area in the remaining species ($p>0.05$). The relatively low emergent surface areas of *T. procerum* could signify that the assimilation of carbon was limiting performance but this more likely reflects the loss of above-ground material pursuant to draw-down in some treatments.

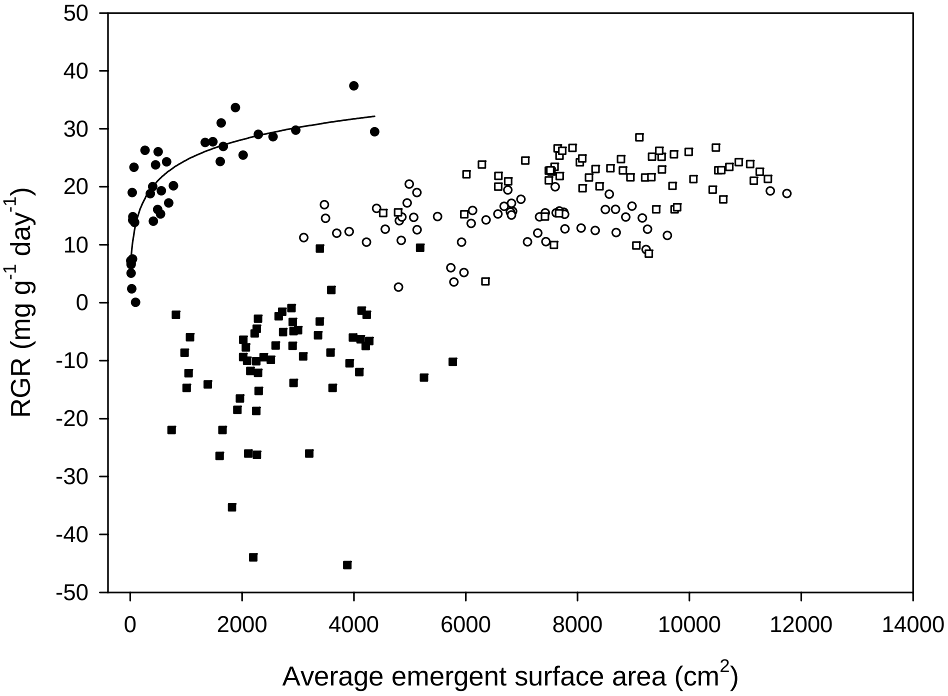

Figure 4.2: Relationship between RGR (mg g^{-1} day^{-1}) and average emergent surface area (cm^2)(averaged over the 100 days of the experiment) in four species of emergent macrophytes subjected to four water level amplitudes at three elevations. *C. vaginatus*: solid circle and solid line ($p<0.0001$; $r^2=0.7196$; $F=87.276$; $n=36$; RGR (mg g^{-1} day^{-1}) = -5.096 + 4.313 × ln (Average emergent surface area (cm^2)), *P. australis*: open circle, *T. procerum*, solid square, *T. domingensis*, open square.

4.3.2 Biomass Allocation

C. vaginatus had a higher proportion of biomass allocated to roots and rhizomes at shallow elevations and a higher allocation to shoots at deep elevations across all amplitudes except the ±45cm water level fluctuation (Table 4.8). *P. australis* allocated a greater proportion of biomass to shoots at intermediate elevations irrespective of amplitude of water level fluctuations (Table 4.9). No obvious trends were displayed by *T. domingensis* (Table 4.10) or by *T. procerum* (Table 4.11).

Table 4.8: Comparison of biomass allocation (%) in *C. vaginatus* subjected to four water level amplitudes at three elevations. Mean (Std. Dev.), *n*=3.

Tissue	Depth/Regime	Static	± 15 cm	± 30 cm	± 45 cm
Root	**Deep**	7.0 (3.6)	4.6 (2.3)	11.8 (6.0)	11.4 (5.7)
	Intermediate	12.0 (5.1)	8.3 (0.9)	12.5 (1.3)	6.8 (2.2)
	Shallow	36.0 (10.4)	27.2 (3.1)	20.3 (4.7)	16.0 (7.4)
Rhizome	**Deep**	11.9 (1.6)	17.7 (9.9)	12.2 (2.9)	30.0 (18.0)
	Intermediate	15.5 (1.3)	18.1 (4.1)	15.9 (5.1)	19.0 (5.7)
	Shallow	16.5 (0.7)	18.9 (3.5)	17.7 (4.2)	23.2 (9.2)
Shoot	**Deep**	81.2 (2.2)	77.8 (7.7)	75.9 (3.2)	58.6 (23.5)
	Intermediate	72.5 (3.9)	73.6 (5.1)	71.6 (6.3)	74.3 (6.5)
	Shallow	47.5 (10.1)	53.9 (1.3)	62.0 (2.3)	60.8 (10.8)
Flower	**Deep**	0	0	0	0
	Intermediate	0	0	0	0
	Shallow	0	0	0	0

Table 4.9: Comparison of biomass allocation (%) in *P. australis* subjected to four water level amplitudes at three elevations. Mean (Std. Dev.), *n*=4-5.

Tissue	Depth/Regime	Static	± 15 cm	± 30 cm	± 45 cm
Root	**Deep**	23.6 (5.4)	18.1 (3.6)	21.5 (4.0)	12.9 (6.9)
	Intermediate	18.1 (1.4)	19.4 (13.2)	18.2 (5.5)	17.9 (5.9)
	Shallow	16.7 (3.8)	16.8 (3.5)	22.2 (20.9)	18.3 (5.8)
Rhizome	**Deep**	18.7 (1.9)	22.3 (3.6)	25.5 (3.8)	29.2 (9.5)
	Intermediate	24.2 (4.0)	17.9 (10.5)	21.8 (4.6)	22.4 (4.6)
	Shallow	27.0 (4.0)	27.3 (5.4)	24.8 (4.2)	26.3 (6.0)
Shoot	**Deep**	56.3 (7.6)	59.3 (5.2)	52.3 (4.6)	57.9 (14.8)
	Intermediate	57.1 (4.8)	62.4 (21.3)	58.7 (6.9)	59.2 (7.1)
	Shallow	55.7 (7.1)	55.7 (7.0)	52.5 (21.3)	55.2 (5.2)
Flower	**Deep**	1.4 (1.0)	0.3 (0.3)	0.6 (0.5)	0
	Intermediate	0.6 (0.4)	0.3 (0.5)	1.4 (1.0)	0.5 (0.7)
	Shallow	0.5 (0.4)	0.2 (0.2)	0.5 (1.0)	0.1 (0.2)

Table 4.10: Comparison of biomass allocation (%) in *T. domingensis* subjected to four water level amplitudes at three elevations. Mean (Std. Dev.), *n*=5.

Tissue	Depth/Regime	Static	± 15 cm	± 30 cm	± 45 cm
Root	**Deep**	31.8 (2.7)	43.2 (12.8)	37.9 (9.0)	21.4 (8.7)
	Intermediate	33.6 (2.0)	38.0 (10.8)	31.1 (4.3)	36.1 (15.2)
	Shallow	32.4 (5.0)	34.5 (4.6)	32.8 (9.6)	21.3 (2.0)
Rhizome	**Deep**	6.8 (1.5)	6.8 (3.9)	7.7 (3.0)	4.5 (2.9)
	Intermediate	7.8 (1.6)	8.5 (2.5)	7.2 (5.7)	8.3 (4.4)
	Shallow	7.5 (3.7)	5.8 (3.2)	6.8 (3.4)	7.2 (3.7)
Shoot	**Deep**	61.4 (3.4)	50.0 (9.8)	54.4 (8.0)	74.2 (10.8)
	Intermediate	58.6 (2.8)	53.5 (10.7)	61.7 (8.1)	55.7 (15.2)
	Shallow	60.1 (5.5)	59.7 (6.1)	60.4 (9.2)	71.4 (5.0)
Flower	**Deep**	0	0	0	0
	Intermediate	0	0	0	0
	Shallow	0	0	0	0

Table 4.11: Comparison of biomass allocation (%) in *T. procerum* subjected to four water level amplitudes at three elevations. Mean (Std. Dev.), *n*=4-5.

Tissue	Depth/Regime	Static	± 15 cm	± 30 cm	± 45 cm
Root	**Deep**	32.0 (15.1)	60.2 (24.0)	39.8 (23.9)	47.8 (4.6)
	Intermediate	40.5 (20.8)	36.7 (11.8)	38.9 (14.6)	39.8 (12.7)
	Shallow	58.1 (9.1)	48.4 (7.6)	32.3 (10.7)	53.6 (12.5)
Rhizome	**Deep**	10.5 (12.5)	0.9 (1.4)	29.1 (40.0)	7.9 (9.1)
	Intermediate	20.5 (37.6)	13.3 (14.0)	12.4 (8.5)	15.8 (10.4)
	Shallow	13.6 (9.0)	23.0 (6.7)	27.5 (16.7)	22.7 (24.4)
Shoot	**Deep**	57.5 (17.5)	39.0 (22.9)	31.1 (17.8)	44.3 (8.9)
	Intermediate	39.0 (25.9)	50.0 (7.9)	47.6 (17.2)	44.4 (7.8)
	Shallow	28.3 (3.6)	28.6 (3.7)	40.0 (13.3)	23.7 (13.8)
Flower	**Deep**	0	0	0	0
	Intermediate	0	0	1.0 (2.3)	0
	Shallow	0	0	0.2 (0.3)	0

To quantify these observations, and to compare and contrast the proportion of biomass allocated to various structures for each species across four water level amplitudes at three elevations, a Three-way ANOVA was performed (Table 4.12). The significant interaction term indicates that the percentage of biomass allocated to roots and shoots were dependent upon specifying species and elevation. This interaction again lends support to the observation that species have different habitat requirements. For example, *C. vaginatus* prefers shallow elevations but tolerates to a certain extent deeper elevations and increasing water level fluctuations by placing a greater proportion of biomass into the above ground shoots. There is a suggestion that *P. australis* has a preference for intermediate elevations across all amplitudes through the higher proportion of biomass allocation to above ground shoots at this elevation. *T. domingensis* and *T. procerum* were less consistent in their response and tolerance to increasing amplitude of water level fluctuations with no obvious trends in biomass allocation to either above or below ground structures, in either species.

Table 4.12: Results of a Three-way ANOVA performed on biomass allocation (%) for four species of emergent macrophytes subjected to four water level amplitudes at three elevations.

Source	*p* value			
	Root	**Rhizome**	**Shoot**	**Flower**
Species	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**
Elevation	**0.0423**	0.0854	**0.0006**	0.5171
Species x Elevation	**0.0076**	0.2591	**0.0021**	0.5404
Amplitude	0.0756	0.1153	0.8322	0.4961
Species x Amplitude	0.6065	0.6329	0.2586	0.2332
Elevation x Amplitude	0.1385	0.4452	**0.0418**	0.2399
Species x Amplitude x Elevation	0.0504	0.6009	0.1045	0.2579

4.4 Discussion

4.4.1 Impact of Elevation and Amplitude of water level fluctuations on Leaf Length

All species recruited longer leaves or stems when growing in deep water compared with plants growing at shallow elevations (Grace 1988; Grace 1989; Hellings and Gallagher 1992; Ostendorp 1991; Vretare *et al.* 2001; Waters and Shay 1990). The response was mirrored in *T. domingensis*, which on average, had leaves that were close to 20 cm different between elevations. The relatively high capacity of *T. domingensis* to adjust leaf length has been cited as an adaptation allowing exploitation by this species of deep water (Grace 1989; Grace and Wetzel 1982), and this example of plasticity must presumably also serve *T. procerum*. The response was poorest in *C. vaginatus* where stem lengths showed a 9 cm difference across the elevation gradient. The ability for the different species to respond was consistent with the species' natural elevation preference with *C. vaginatus*, which prefers high elevations, adapting poorly compared with the other species. Average leaf lengths were also different between plants grown under different water regimes: plants growing under more highly fluctuating water regimes developed significantly longer leaves in comparison with plants growing under static conditions. In *T. domingensis* the difference in average leaf length between the static and ±45 cm water regime amounted to less than 11 cm. Given leaf lengths were at least 110 cm, a maximum increase in leaf length of just 11 cm seems at best marginal, and it is likely that plants were tailoring length in developing leaves to the more immediate perception of water depth rather than adjusting the length of mature leaves to water levels as they changed through time (Cooling *et al.* 2001; Rea and Ganf 1994a; Vretare *et al.* 2001). As such, plants experiencing a fluctuating water regime will always be "sub-optimally acclimatised" to the current water depth (Vretare *et al.* 2001). Further, as has already been observed, leaf or stem lengths were increased by increasing water regime fluctuation suggesting that a plant will not develop shorter leaves during a drawdown phase, but only longer leaves during a flooding episode. Thus, plants adapt leaf length more readily or quickly to increasing water levels, but may adapt only to a small degree, or slowly, to falling water levels (Edwards *et al.* 1981). Vretare *et al* (2001) showed that *P. australis* was unable to phenotypically adapt to cyclic changes in water level because the water level changed more quickly than the plant could respond by altering morphology.

4.4.2 Impact of Elevation and Amplitude of fluctuation on Biomass and Growth

It was expected that increasing amplitude of water level fluctuations would reduce growth by reducing the emergent surface area and therefore the capacity for the acquisition of atmospheric carbon in *P. australis, T. domingensis* and *C. vaginatus* but not in *T. procerum* due to the latter's probable ability to photosynthesis under water by accessing bicarbonate from the water column (Rea 1992) and is therefore uneffected by flooding events. Previous research has shown a linear relationship between growth and emergent surface area in the emergent macrophyte *Bolboscheonus medianus* (Blanch *et al.* 1999a). Hence any factor that reduces the emergent surface area could therefore reduce growth.

Elevation did not have a consistent effect on biomass among the four species such that the influence of elevation and amplitude of water level fluctuations cannot be separated as single factors. *C. vaginatus*, which has a high elevation preference, was strongly inhibited by increasing water depth. This is consistent with its preferred habitat at high elevations where the plant is unlikely to be top-flooded and has access to water and atmospheric CO_2. Leyer (2005) reported on 30 macrophyte species, which responded significantly to water level fluctuations. Species with high elevation preferences migrated to lower elevations where water level fluctuations were reduced (Leyer 2005). This would explain the wide distribution of *C. vaginatus* along the elevation gradient in the EMLR (Table 4.1). As the water level fluctuations reduced in this region *C. vaginatus* migrated to lower elevations where the soil moisture conditions were not as dry as the higher elevations, resulting in the greater distribution of this species. In contrast, species with a low elevation preference, such as *P. australis* and *T. domingensis*, were more tolerant to both depth and water level fluctuations (see Grace, 1989). However, the biomass and RGR of *T. domingensis* and *P. australis* were depressed when grown under the combination of deep elevation and a highly fluctuating water level (±45 cm). Between the static and ±45 cm amplitude treatments, growth of *T. domingensis* was inhibited by 52%. However, the growth of *P. australis* appeared to be enhanced by fluctuating water levels and only showed a severe drop-off in growth in the deep elevation, ±45 cm amplitude treatment. Other research has demonstrated positive or negative changes in biomass with elevation (Grace 1989; Hellings and Gallagher 1992; Vretare *et al.* 2001) and a similar response to amplitude has been documented for *P. australis* (Vretare *et al.* 2001) and the fen species *Phalaris arundinacea* and *Deschampsia cespitosa* (Kennedy *et al.* 2003).

4.4.3 How does a fluctuating water level constrain plant performance?

On the basis of previous research (Blanch *et al.* 1999a; Siebentritt 2003), it was hypothesised that fluctuating water levels would constrain growth by decreasing the emergent surface area of plants and thus the capacity for the acquisition of atmospheric carbon. In *C. vaginatus*, this was the case (Fig. 4.2); RGR and the average emergent surface area (and the implied rate of carbon acquisition) were closely related. Having low emergent surface areas in comparison with the other species, growth of *C. vaginatus* will be more prone to carbon limitation. It did however attempt to combat both increasing depth/elevation and amplitude of water level fluctuations, through the allocation of a greater proportion of biomass to the above ground shoots (emergent surface area). This was an attempt to maintain a sufficient average emergent surface area for the acquisition of atmospheric carbon.

RGR was independent of the average emergent surface area (and the implied rate of carbon acquisition) in *P. australis* and *T. domingensis* even when the photosynthetic canopy was partially inundated by rising water levels. This was probably due to the large size of both these species and hence their large emergent surface areas (Table 4.7) in comparison with *C. vaginatus*. Their large emergent surface areas must serve as an adaptation to protect against the stresses associated with growing in deep water or under conditions of fluctuating water levels. Yet these two species demonstrated different growth rates when grown under different water regime amplitudes and at different elevations. Further, the RGRs for *T. domingensis* and *P. australis* were quite low even when viewed as net RGRs (ie, the growth rate does not include a loss term). This suggests that another factor(s), as yet unidentified, was limiting the growth of *P. australis, T. domingensis* and possibly *T. procerum*, a factor that varies with water level. This could involve sediment chemistry (Baldwin and Mitchell 2000; Grace 1988; Ponnamperuma 1984) or aeration (van Eck *et al.* 2004; White and Ganf 2002; Yamasaki 1984).

4.4.4 Imposition of environmental flows as control measures in the EMLR

The results of this study can be correlated with the elevation distribution of these four species in local rivers and wetlands in the EMLR (Table 4.1). Surveys conducted on the Lower River Murray, South Australia, are highly relevant since the water level is controlled through a series of barrage weirs. The weirs are operated to maintain a highly stable pool water level (i.e. immediately above a weir)(±2.5 cm), but such control can lead to dramatic fluctuations in the water level immediately below the weir (commonly ±20 cm daily)(Walker *et al.* 1994). Thus, between weirs, there is a gradient in the degree of water level fluctuations. The results of field surveys along the Lower River Murray suggest different species have different preferred niches along this gradient in water level fluctuations: *Cyperus* sp. only occurred in reaches which experienced low flooding but high variability in water levels, *P. australis* was tolerant of a range of water level fluctuations, and *Typha* spp. was only found in areas of stable water levels immediately above the weir (Blanch *et al.* 1999b; Blanch *et al.* 2000; Walker *et al.* 1994). No observations were made on the distribution of *T. procerum*. The distribution of *T. domingensis* and *Cyperus* spp. is similar to the performance found in this pond experiment though the broad distribution of *P. australis* in the field would suggest it is more broadly tolerant of water depth and water regime than suggested by the pond experiment.

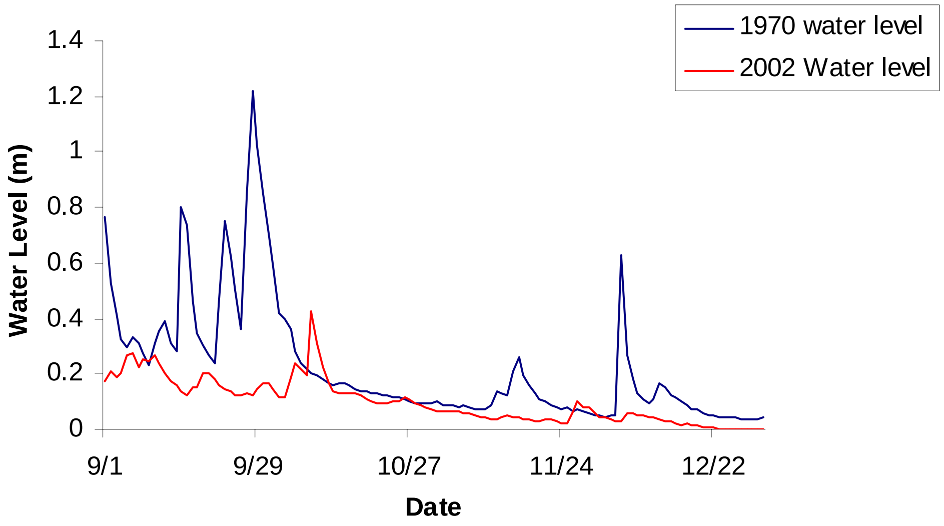

Figure 4.3: Comparison of variations in water levels on the Finniss River during spring/early summer at a location 4 km East of Yundi, (35^{o}19′ S, 138^{o}40′ E) for the years 1970 and 2002.

Given the close correspondence between field observations and the results of this study, it appears the results of this pond experiment can be extrapolated directly to both explain and predict the distribution of wetland plants in relation to water regime (Rea and Ganf 1994d) and in particular to the application of environmental flows. In the EMLR, a once highly fluctuating water regime (represented here by the 1970 water level) has now been replaced by a relatively stable water regime (represented here by the 2002 water level), particularly during the crucial spring months when the aquatic plant species in these systems are commencing growth (Fig. 4.3). The current water regime has similar water level fluctuations to the ±15 cm experimental treatment; therefore the macrophyte responses under this regime may be extrapolated to the field. Likewise, predictions regarding macrophyte responses to the installation of environmental flows with water level fluctuations of ±30 cm and ±45 cm may be extrapolated to the field from this pond experiment.

The stabilisation of natural fluctuating water regimes may have lead to the establishment of dense littoral species, such as *P. australis* and *T. domingensis* (Maheshwari *et al.* 1995) in the EMLR. However, the application of flows in the EMLR will be constrained to the amount of available water in local farm dams. In the upper Finniss catchment there is an estimated total storage capacity of 5,822 ML (Savadamuthu, 2003). To increase the water level by 45cm would require an additional 90ML of water per day (Savadamuthu, 2003). Therefore, there is a sufficient volume of water stored in the farm dams of the upper Finniss catchment to increase the water levels by ±45 cm over an extended period of time during the growing season (Figs. 1.2 and 1.3). However, due to the present drought conditions in South Australia, the anticipated environmental flow prescriptions are unlikely to provide flows that would result in water level fluctuations in excess of ±45 cm. *P. australis* and *T. domingensis* are too large (size) and too densely established to be negatively affected by the addition of flows to this region. In contrast, *C. vaginatus* even when grown at shallow elevations responds to amplitude in water level fluctuations, hence the spread of this species could be controlled by water level fluctuation, but not in this region due to limited water resources. The variation in the final biomass (Table 4.2) of *T. procerum* makes any general statement about this species very difficult. The ability of emergent macrophytes to withstand sub-optimal conditions was demonstrated in this pond study and others (tolerate 2-3 years of sub-optimal flooding before dying back) (Siebentritt 2003). Therefore, the imposition of environmental flows as a control measure to prevent or reduce the colonisation and dominance of particular species (e.g. *T. domingensis* and *P. australis*) is unlikely to succeed given the limited water resources available.

CHAPTER 5.

5 The effects of nutrient loading on emergent macrophytes and the influence of water regime: Implications for flow restoration

5.1 Introduction

Water regime is the primary factor determining floristic composition in aquatic systems (Boedeltje *et al.* 2002; Brownlow *et al.* 1994; Casanova and Brock 2000; Mitsch and Gosselink 1993; Nicol *et al.* 2003; Nielsen and Chick 1997; Peterson and Baldwin 2004; Warwick and Brock 2003). However, its effects may be influenced or modified by a number of additional factors (eg, nutrient loadings, light availability, salinity, competition), which play major roles in shaping the final distribution of plant species (Baldwin and Mitchell 2000; Barrat-Segretain and Elger 2004; Deegan and Harrington 2004; Deegan *et al.* 2005; Grace and Wetzel 1981; Howard and Mendelssohn 2000; James *et al.* 2006; Kennedy *et al.* 2003; Siebentritt and Ganf 2000; Siebentritt *et al.* 2005; Spence 1982).

Anthropogenic alterations to natural flow regimes have coincided with non-native plant invasions of many waterways and flood plains, where the occurrence of low, more constant flows (low disturbance) have contributed to conditions favourable to fewer dominant species (Erskine *et al.* 1999; Lonsdale 1993; McCosker 1994; Mitchell 1978; Sher *et al.* 2000). This may lead to the establishment of dense littoral plants, such as the extensive reed beds of *Phragmites australis* and cumbungi *Typha* spp along the River Murray, South Australia (Maheshwari *et al.* 1995). Increased nutrient loads have also had dramatic effects on the plant diversity and community structure in aquatic systems (Bedford *et al.* 1999; Levine *et al.* 1998; Paerl 1997; Peterson *et al.* 2001; Phillips *et al.* 1978; Tracy *et al.* 2003; Vitousek *et al.* 1997; Wigand *et al.* 1997). For instance, Levine *et al.* (1998) found that after two growing seasons nutrient loading reversed the hierarchy of species dominance observed under ambient marsh conditions. Altered hydrology together with nutrient loading are implicated in the expansion of *Typha domingensis* into areas previously dominated by *Cladium jamiaicense* (Newman *et al.* 1998) and *Eleocharis interstincta* (Newman *et al.* 1996) in the Everglades (USA).

Anthropogenic nutrient loading into aquatic systems increases macrophyte production (Carr and Chambers 1998; Stevens *et al.* 2006); however, plant responses to nutrient supply may be influenced by the water regime, as variations in hydrology will affect nutrient dynamics (Baldwin and Mitchell 2000; Neill 1990; Spink *et al.* 1998). The drying and re-flooding of sediments may increase or decrease plant nutrient uptake and/or their ability to use nutrients for growth (Neill 1990; Schat 1984). As a result, the effects of resource supply and water regime on plant growth may interact. Although Güsewell *et al.* (2003) found that the effects of nutrient enrichment were largely independent of water regime.

Pristine Australian forested catchments export little nitrogen or phosphorous into rivers, but as catchments are cleared, exports increase (Harris 2001a; Harris 2001b). There is increasing concern as to the effects of nutrient loading into previously nutrient limited aquatic environments, particularly as most Australian rivers are regulated (Puckridge *et al.* 1998). This regulation will alter the stoichiometry of the major elements, by altering residence time within a system (Harris 2001a), retaining these additional nutrients for longer periods, and may have as large an effect on the catchments as the nutrient loading itself (Harris 1999b). Current ecosystem management in Australia to restore river ‘health’ focuses on providing water allocations, ‘environmental flows’ from water storages (EPA 1997; Norris and Thoms 1999). But it is questionable whether restoration of flows alone will result in any measurable improvement in the ecological functioning of those rivers (Robertson 1997). Efforts to restore river health that focus solely on reducing the impact of regulated flows may be nullified if nutrient loading is not considered as part of river ecosystem management. There are limited studies on the influence of water regime over the effects of nutrient loading on the growth of emergent macrophytes (Grace 1988; Neill 1990; Newman *et al.* 1998). However, this information is vital in understanding the implications of restoring flow regimes to nutrient enriched aquatic environments and the effects this may have on the macrophytes communities present.

The purpose of this study was to examine the simultaneous effects of a fluctuating water level (natural water regime) and nutrient loadings on the performance of four species of emergent macrophyte. It is necessary to study the effect of these two stressors simultaneously, since the response of a species to one factor may be significantly influenced by the other (Nilsen and Orcutt 1996). Macrophytes respond to increased inundation by elongating leaves to maintain an emergent canopy, sometimes redeploying resources from below-ground parts (Blanch *et al.* 1999a; Cooling 1996; Grace 1988; Grace 1989; Rea and Ganf 1994d; Waters and Shay 1990). They respond to increased nutrient loading by increasing production (above-ground tissue) (Carr and Chambers 1998; Stevens *et al.* 2006), and reducing biomass allocation to below-ground root tissue (Aerts and Chapin III 2000). Severe submergence can lead to carbon starvation by reducing the availability of atmospheric carbon (Cížková-Koncalová *et al.* 1992). As flooding of the photosynthetic canopy will limit the capacity for the acquisition of carbon (Blanch *et al.* 1999a; Siebentritt 2003), it is hypothesised that under treatments of high nutrient loadings, excess resource availability, plant performance will not be reduced due to increasing fluctuations of water levels. It is further hypothesised that those more responsive faster growing species (e.g. *P. australis* and *T. domingensis*) shall be more constrained by limited availability of nutrients than atmospheric carbon limitation (water regime), compared to those less responsive slower growing species (e.g. *C. gymnocaulos*), which will be compromised more by carbon limitation rather than nutrient availability. The specific objectives were: i) to quantify the growth of macrophytes across gradients in nutrient loading rates and water regimes, ii) to quantify any morphological response by macrophytes to different nutrient loading rates and water regimes, iii) to compare the impact of nutrient loading rates and water regimes on plant performance at optimal species elevations, iv) to determine if increased nutrient loading would out-weigh the growth constrains of a fluctuating water regimes and v) to identify the implications of flow restoration to nutrient enriched aquatic environments.

5.2 Materials and Methods

5.2.1 Study species

Four species were chosen for the experiment: *Cyperus gymnocaulos* Steudel, *Phragmites australis* (Cav.) Trin. ex Steud., *Triglochin procerum* R Br. and *Typha domingensis* Pers. All are rhizomatous perennials that form monospecific stands. *T. procerum* relies less on clonal reproduction (as its lateral expansion is limited because its rhizomes are short) than on sexual reproduction to form large stands (Cunningham *et al.* 1992; Jessop and Toelken 1986). Locally, the species inhabit different zones along the elevation gradient with the sedge, *C. gymnocaulos*, inhabiting the highest point, usually 0 to 180 cm above the water surface, followed by *P. australis* and *T. domingensis,* which normally reside just above and just below the water surface, respectively, and *T. procerum* which prefers deep water, growing in water up to a depth of 120 cm (Table 5.1). All species are common throughout the Eastern Mount Lofty Ranges (EMLF) of South Australia.

Table 5.1: Elevation distribution of the four study species in Eastern Mt. Lofty Ranges.

Species	**Elevation relative to water surface**
C. gymnocaulos	0 to 180
P. australis	0 to 30
T. domingensis	-55 to 0
T. procerum	-120 to -50

5.2.2 Plant material

Adult *C. gymnocaulos* and *T. procerum* were collected from the River Angas, South Australia. *T. domingensis* and *P. australis* were collected from the Barker Inlet wetlands, South Australia. Approximately 90 specimens of each species were initially collected of similar size, maturity and biomass. The plant's below-ground reserves (tubers or rhizomes) and flowers were removed before being planted in plastic pots (23 × 23 × 20 cm) filled with a 2 cm base of cricket pitch clay, followed by 16 cm of sandy loam and topped with a 2 cm layer of cricket pitch clay to impede the diffusion of oxygen into the sediment, providing a more natural sediment redox potential and to impede the loss of nutrients to the surrounding water column. The above-ground material of *C. gymnocaulos* was cut back to 5 cm above the soil surface and that of *T. domingensis* and *P. australis* to 30 cm above the soil surface. Plants were then placed in outdoor ponds and watered to saturation except for *T. procerum*, which was flooded by 30 cm.

Specimens of *C. gymnocaulos* were collected and replanted on the 19th of October, 2005 and allowed to establish for 12 weeks (19th October, 2005 until 12th January, 2006). Specimens of *T. procerum*, *T. domingensis* and *P. australis* were collected and replanted between the 17th to the 21st of November, 2006, and allowed to establish for 8 weeks (21st November, 2005 until 12th January, 2006). From observations made on the length of time required for *C. gymnocaulos* to establish in comparison to the other species from the previous years pond experiment (Chapter 4), it was decided to provide *C. gymnocaulos* with a longer establishment period (4 weeks approx.). At the end of the establishment period six specimens of *T. domingensis* and twelve specimens each of *C. gymnocaulos, P. australis and T. procerum* were randomly selected and harvested to measure initial biomass. Six specimens of *T. domingensis* had died during the establishment period.

5.2.3 Experimental water regimes

Two water regimes were used for the pond experiment: stable and fluctuating. Ponds with a stable water regime had a constant water depth of 45 cm and ponds with a fluctuating water regime had a water depth fluctuating between 31 and 105 cm. To better emulate a natural fluctuating water regime, a stochastic pattern of flooding and drawdown was devised (Fig. 5.1). The water regime was based on a pre-regulation hydrograph of the Finniss River, South Australia (Savadamuthu 2003).

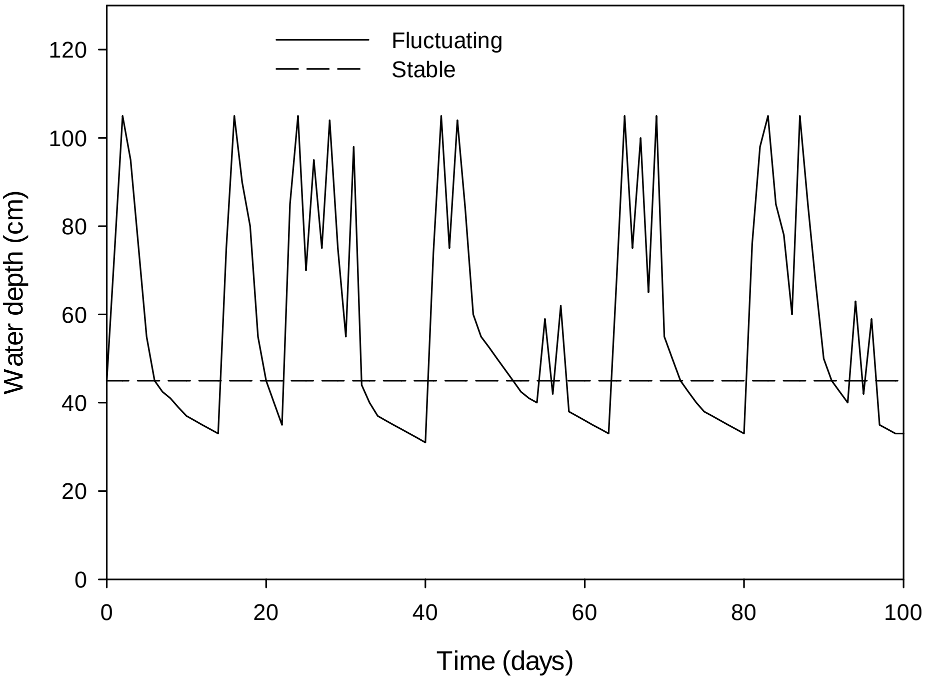

Figure 5.1: Experimental water regimes. In each pond, potted plants were placed at optimal species elevation; sediment surface for *T. procerum* was at 20 cm, for *T. domingensis* and *P. australis* was at 40 cm, and *C. gymnocaulos* at 60 cm above the pond base.

5.2.4 Nutrient loading rates

Nutrients were added to the pots at the end of the establishment phase to avoid any nutrient-dependent preconditioning. Several bores were manually drilled into the sediment and a slow release fertilizer Osmocote® was added to the sandy loam at 3 concentrations, equivalent to a loading rate of 0, 10 and 30 g N m^{-2} yr^{-1}. To ensure a supply of micronutrients, 30 % of the fertilizer (by weight) was Osmocote Plus®.

5.2.5 Pond Experiment

Each water regime was replicated between two separate outdoor ponds (4.5 × 3.5 × 1.2 m deep). Five replicates of each species for each nutrient loading were placed within each pond (giving a total number within each pond of 60 and a total number of replicates for each treatment of 10). Each species was placed at its preferred elevation: *C. gymnocaulos*: sediment surface at 60 cm, *P. australis* and *T. domingensis*: 40 cm, and *T. procerum*: 20 cm. (see Chapter 4). For those pots that would be completely exposed by the water level fluctuations (ie, *C. gymnocaulos* under fluctuating conditions), RibLock® columns (30 cm diameter, 40 cm tall) filled with sandy loam were used as a base. The columns allow water from the base of the pond to move into the plant pots thus maintaining minimal water supply even when the pots were otherwise completely above the waters surface. The experiment ran for 100 days (16th January until 15th April, 2006). The water level in each of the ponds was maintained manually.

Over the course of the experiment, four *T. domingensis* specimens died, three from the static 30 g N m^{-2} yr^{-1} treatment and one from the static 10 g N m^{-2} yr^{-1}.

5.2.6 Data Collection and Analysis

A tagging study was conducted over the course of the experiment to follow certain growth aspects of the plants. The leaves or stems of three randomly selected replicates from each treatment were tagged at the beginning of the experimental period. Every 10 days, new stems or leaves were tagged and the elongation and mortality of leaves monitored – net recruitment.

At the conclusion of the experimental period, the stem or leaf lengths were measured for each plant. The plants were then harvested, washed, and the plant material was then oven dried at 60 °C for seven days and the dry-weight measured.

There were no significant differences between the plants allocated to each treatment, based upon initial height and the number of stems/leaves per pot (Denton and Ganf 1994). No differences were apparent between plants under the same treatment in each of the replicates ponds for each water regime, hence the pond data was pooled for subsequent analysis (Blanch *et al.* 1999a). As species were placed at different elevations within ponds, each species was analysed separately, hence species was not used as a source of effect in the analyses (as in Chapter 4). Treatment comparisons were made using Two-way ANOVAs on log-transformed or Arcsine square-root transformed data, with water regime (fluctuating or stable) and nutrient loading (0, 10 or 30 g N m^{-2} yr^{-1}) as sources of effect.

5.3 Results

5.3.1 Species performance

C. gymnocaulos showed a significant increase in stem length (p <.0001) but a significant reduction in the final biomass (p = 0.0007) under a fluctuating water regime as opposed to the static regime (Table 5.2). There was also a significant reduction in each of the performance indicators across nutrient loading rates. As the nutrient load increased, plant performance increased under each water regime treatment. However, there was no significant interaction between water regime and nutrient loading rates on plant performance indicating that the effects of these two variables on plant performance were independent of each other.

Table 5.2: Comparison of indicators of performance for *C. gymnocaulos* subjected to two water regimes at three nutrient loadings using a Two-way ANOVA. Mean (Std. Dev.), n = 10.

		Water Regime		**ANOVA**	
Indicator	**Nutrient Loading**	**Static**	**Fluctuating**	Source	P value
Final Biomass (dwt)(g)	**0**	86 (27.6)	57 (10.1)	Water Regime	**0.0007**
	10	108 (23.4)	78 (16.7)	Nutrient Loading	**<.0001**
	30	172 (31.7)	109 (27.0)	Regime x Loading	0.6407
Leaf or Stem Length (cm)	**0**	47 (22.7)	55 (24.1)	Water Regime	**<.0001**
	10	52 (24.1)	56 (25.8)	Nutrient Loading	**0.0017**
	30	55 (27.3)	58 (25.3)	Regime x Loading	0.0996

For *P. australis* there was no effect of water regime or nutrient loading on plant performance, however, there was an interaction effect on total plant biomass ($F_{2,60} = 7.5$, $p = 0.0013$). Under the static regime the total biomass increased with nutrient enrichment, in contrast this decreased under the fluctuating regime (Table 5.3). Plants recorded their highest total biomass under a static regime at a loading rate of 30 mg g^{-1} day^{-1} and their lowest biomass under a fluctuating regime at a loading rate of 30 mg g^{-1} day^{-1}.

Table 5.3: Comparison of indicators of performance for *P. australis* subjected to two water regimes at three nutrient loadings using a Two-way ANOVA. Mean (Std. Dev.), n = 10.

		Water Regime		**ANOVA**	
Indicator	**Nutrient Loading**	**Static**	**Fluctuating**	Source	P value
Final Biomass (dwt)(g)	**0**	42 (11.5)	73 (48.9)	Water Regime	0.4093
	10	72 (18.6)	56 (23.5)	Nutrient Loading	0.1809
	30	104 (22.4)	37 (15.3)	Regime x Loading	**0.0013**
Leaf or Stem Length (cm)	**0**	81 (31.4)	90 (33.5)	Water Regime	0.1168
	10	83 (34.3)	86 (35.3)	Nutrient Loading	0.4030
	30	94 (36.9)	83 (28.4)	Regime x Loading	0.0858

The performance of *T. domingensis* (Table 5.4) increased with increased nutrient loading rates under a static regime. Under a fluctuating regime the plant performance remained relatively constant for each indicator irrespective of the nutrient loading rates. The significant interaction term between water regime and nutrient loading rate (*p* = 0.0344) for plant final biomass suggests that the effect of a fluctuating water regime is over-riding or limiting the effect of nutrient loading rates on plant final biomass. For stem length there was a significant effect of water regime (*p* <.0001) and nutrient loading rate (*p* = 0.0029) on plant performance. The significant interaction term between water regime and nutrient loading rate for stem length (*p* = 0.0003) again indicates that the effect of a fluctuating water regime is over-riding or limiting the effect of nutrient loading rate on plant performance.

Table 5.4: Comparison of indicators of performance for *T. domingensis* subjected to two water regimes at three nutrient loadings using a Two-way ANOVA. Mean (Std. Dev.), *n* = 6-10.

		Water Regime		**ANOVA**	
Indicator	**Nutrient Loading**	**Static**	**Fluctuating**	Source	*P* value
Final Biomass (dwt)(g)	**0**	89 (15.7)	90 (25.9)	Water Regime	0.9787
	10	120 (28.6)	92 (48.4)	Nutrient Loading	0.2622
	30	169 (14.3)	91 (52.9)	Regime x Loading	**0.0344**
Leaf or Stem Length (cm)	**0**	88 (28.6)	124 (36.2)	Water Regime	**<.0001**
	10	101 (31.3)	130 (41.8)	Nutrient Loading	**0.0029**
	30	108 (33.15)	125 (44.2)	Regime x Loading	**0.0003**

In *T. procerum* (Table 5.5) each of the indicators of plant performance increased with increased nutrient loading across both regimes, but the effect was more dramatic under a static regime. There was a significant effect of water regime on plant final biomass (*p* = 0.0260) and of nutrient loading rate on leaf length (*p* <0.0001).

Table 5.5: Comparison of indicators of performance for *T. procerum* subjected to two water regimes at three nutrient loadings using a Two-way ANOVA. Mean (Std. Dev.), *n* = 10.

		Water Regime		**ANOVA**	
Indicator	**Nutrient Loading**	**Static**	**Fluctuating**	Source	*P* value
Final Biomass (dwt)(g)	**0**	16 (4.9)	11 (5.5)	Water Regime	**0.0260**
	10	22 (6.5)	14 (5.7)	Nutrient Loading	0.0712
	30	26 (12.7)	12 (4.8)	Regime x Loading	0.7389
Leaf or Stem Length (cm)	**0**	60 (11.2)	69 (25.6)	Water Regime	0.1485
	10	62 (14.5)	79 (23.3)	Nutrient Loading	**<.0001**
	30	71 (16.9)	83 (26.7)	Regime x Loading	0.1932

5.3.2 Biomass allocation

C. gymnocaulos (Table 5.6) allocated a significantly higher proportion of biomass to the root tissue at lower nutrient loading rates (*p* = 0.0229) under a static regime. The same trend was observed under a fluctuating regime but significantly reduced (*p* = 0.0002). The proportion of biomass allocated to rhizome tissue was higher in those plants subjected to higher nutrient loading rates, but significantly reduced under a fluctuating regime (*p* = 0.0056) and the proportion of biomass allocated to above-ground parts was significantly higher in those plants subject to a fluctuating regime (*p* <.0001) (Table 5.6).

Table 5.6: Comparison of biomass allocation (%) in *C. gymnocaulos* subjected to two water regimes at three nutrient loadings using a Two-way ANOVA. Mean (Std. Dev.), *n* = 10.

		Water Regime		**ANOVA**	
Tissue	**Nutrient Loading**	**Static**	**Fluctuating**	Source	*P* value
Root	**0**	26.7 (11.6)	14.8 (2.7)	Water Regime	**0.0002**
	10	26.5 (6.7)	16.3 (3.8)	Nutrient Loading	**0.0229**
	30	21.5 (6.1)	11.4 (3.1)	Regime x Loading	0.9482
Rhizome	**0**	32.8 (8.6)	24.4 (7.5)	Water Regime	**0.0056**
	10	31.5 (6.6)	27.3 (6.2)	Nutrient Loading	0.0834
	30	34.2 (5.6)	31.7 (5.1)	Regime x Loading	0.3330
Shoot	**0**	40.5 (9.7)	60.8 (5.6)	Water Regime	**<.0001**
	10	42.0 (8.9)	56.5 (6.1)	Nutrient Loading	0.8077
	30	44.3 (8.0)	57.0 (6.3)	Regime x Loading	0.2629

P. australis (Table 5.7) allocated a significantly higher proportion of biomass to the root tissue in those plants subjected to lower nutrient loading rates ($p = 0.0255$) under a static regime and this trend was significantly reduced under a fluctuating regime ($p = 0.0005$). The significant interaction term ($p = 0.0433$) would indicate that the effect of water regime is contradicting the effect of nutrient loading at lower nutrient loading rates. There was a significantly higher proportion of biomass allocated to rhizome tissue under a static regime as opposed to a fluctuating regime ($p <.0001$). The proportion of biomass allocated to rhizome tissues was significantly reduced under a fluctuating regime ($p <.0001$). With regard to the proportion of biomass allocated to the above-ground parts, there was a significant interaction term ($p = 0.0175$) between water regime and nutrient loading rate indicating that the effect of a fluctuating water regime was contradicting the effect of nutrient loading rates under a static water regime (Table 5.7).

Table 5.7: Comparison of biomass allocation (%) in *P. australis* subjected to two water regimes at three nutrient loadings using a Two-way ANOVA. Mean (Std. Dev.), *n* = 10.

		Water Regime		**ANOVA**	
Tissue	**Nutrient Loading**	**Static**	**Fluctuating**	Source	*P* value
Root	**0**	13.1 (2.6)	8.2 (1.9)	Water Regime	**0.0005**
	10	12.3 (1.4)	10.2 (4.4)	Nutrient Loading	**0.0255**
	30	8.7 (1.5)	8.9 (3.5)	Regime x Loading	**0.0433**
Rhizome	**0**	28.9 (5.9)	18.5 (5.9)	Water Regime	**<.0001**
	10	28.1 (6.0)	20.2 (3.0)	Nutrient Loading	0.8477
	30	25.2 (4.8)	21.3 (3.4)	Regime x Loading	0.1137
Shoot	**0**	58.1 (5.7)	73.3 (7.0)	Water Regime	**<.0001**
	10	59.5 (6.4)	69.9 (6.3)	Nutrient Loading	0.2399
	30	66.2 (5.8)	69.9 (5.4)	Regime x Loading	**0.0175**

Again *T. domingensis* (Table 5.8) allocated a significantly higher proportion of biomass to the root tissue at lower nutrient loading rates ($p = 0.0077$) and this was significantly reduced ($p <.0001$) in those plants subjected to a fluctuating regime. There was a significant effect of water regime ($p <.0001$) on the proportion of biomass allocated to the above-ground parts. As the nutrient load increased the proportion of biomass allocated to shoot tissue increased and this increased significantly ($p <.0001$) under a fluctuating regime.

Table 5.8: Comparison of biomass allocation (%) in *T. domingensis* subjected to two water regimes at three nutrient loadings using a Two-way ANOVA. Mean (Std. Dev.), *n* = 6-10.

		Water Regime		**ANOVA**	
Tissue	**Nutrient Loading**	**Static**	**Fluctuating**	Source	*P* value
Root	**0**	38.7 (4.5)	21.9 (9.9)	Water Regime	**<.0001**
	10	34.2 (4.5)	19.0 (10.1)	Nutrient Loading	**0.0077**
	30	27.5 (4.6)	15.9 (5.0)	Regime x Loading	0.6910
Rhizome	**0**	7.4 (3.5)	6.1 (3.1)	Water Regime	0.3292
	10	9.9 (2.4)	5.2 (3.6)	Nutrient Loading	0.6794
	30	8.9 (2.0)	6.9 (4.2)	Regime x Loading	0.3517
Shoot	**0**	53.9 (6.2)	71.9 (12.3)	Water Regime	**<.0001**
	10	55.9 (5.7)	75.8 (9.7)	Nutrient Loading	0.0597
	30	63.7 (5.6)	77.3 (6.1)	Regime x Loading	0.5638

T. procerum (Table 5.9) allocated a significantly higher proportion of biomass to the root tissue at lower nutrient loadings (*p* <.0001) and under both a fluctuating and static regime. There was a significantly higher proportion of biomass allocated to the above-ground parts with increased nutrient loading rates (*p* <.0001) irrespective of water regime.

Table 5.9: Comparison of biomass allocation (%) in *T. procerum* subjected to two water regimes at three nutrient loadings using a Two-way ANOVA. Mean (Std. Dev.), *n* = 10.

		Water Regime		**ANOVA**	
Tissue	**Nutrient Loading**	**Static**	**Fluctuating**	Source	*P* value
Root	**0**	48.7 (7.9)	52.7 (14.5)	Water Regime	0.3597
	10	45.7 (7.5)	45.2 (12.0)	Nutrient Loading	**<.0001**
	30	30.8 (5.7)	38.2 (9.3)	Regime x Loading	0.4389
Rhizome	**0**	5.0 (6.9)	3.3 (3.7)	Water Regime	0.8156
	10	3.7 (4.4)	2.2 (2.2)	Nutrient Loading	0.9883
	30	4.3 (5.2)	2.1 (2.2)	Regime x Loading	0.9688
Shoot	**0**	46.3 (11.4)	44.0 (15.0)	Water Regime	0.6299
	10	50.6 (7.5)	52.6 (12.9)	Nutrient Loading	**<.0001**
	30	64.9 (8.7)	59.7 (9.5)	Regime x Loading	0.5862

5.3.3 Tagging Study

Net recruitment (net recruitment of stems/leaves during the experimental period) (Table 5.10) increased significantly for *C. gymnocaulos* with increased nutrient loading rates (*p* <.0001) across both water regimes, however, it was reduced under the fluctuating regime.

For *P. australis* there was no effect of either water regime or nutrient loading on net recruitment and the same was true for *T. procerum*. For *T. domingensis* there was a significant effect of water regime (*p* = 0.0430) and nutrient loading rate (*p* = 0.0204) on net recruitment. The significant interaction term between water regime and nutrient loading rates (*p* = 0.0211) indicates that the positive effect of increased net recruitment observed under a static regime with increased nutrient loading rates was being limited by the fluctuating regime.

Similar trends were observed in the gross recruitment (gross recruitment of stems/leaves during the experimental period) of each species (Table 5.11) except for *T. procerum*. Its gross recruitment was significantly affected by the interaction of water regime and nutrient loading rates (*p* = 0.0128), with higher recruitment at low nutrient loading rates under a fluctuating regime in comparison to the static regime, and lower recruitment at high nutrient loading rates under a fluctuating regime in comparison to the static regime.

Table 5.10: Comparison of net recruitment (recruitment – loss) for each species subjected to two water regimes at three nutrient loadings using a Two-way ANOVA. Mean (Std. Dev.), *n* = 6-10.

		Water Regime		**ANOVA**	
Species	**Nutrient Loading**	**Static**	**Fluctuating**	Source	*P* value
C. gymnocaulos	**0**	45.0 (4.6)	38.7 (10.0)	Water Regime	0.1824
	10	62.0 (3.0)	55.0 (1.7)	Nutrient Loading	**<.0001**
	30	86.0 (14.4)	67.0 (9.5)	Regime x Loading	0.7563
P. australis	**0**	9.7 (3.2)	7.7 (7.4)	Water Regime	0.2278
	10	9.0 (2.0)	7.3 (3.1)	Nutrient Loading	0.9354
	30	13.3 (3.1)	4.7 (0.6)	Regime x Loading	0.4375
T. procerum	**0**	-1.0 (3.6)	-1.3 (2.3)	Water Regime	0.9581
	10	1.3 (3.1)	-0.7 (3.2)	Nutrient Loading	0.3590
	30	4.3 (4.0)	-1.3 (1.5)	Regime x Loading	0.4069
T. domingensis	**0**	9.3 (1.5)	15.7 (5.0)	Water Regime	**0.0430**
	10	13.7 (3.8)	12.3 (3.1)	Nutrient Loading	**0.0204**
	30	24.7 (3.2)	15.3 (5.5)	Regime x Loading	**0.0211**

Table 5.11: Comparison of gross recruitment for each species subjected to two water regimes at three nutrient loadings using a Two-way ANOVA. Mean (Std. Dev.), *n* = 6-10.

		Water Regime		**ANOVA**	
Species	**Nutrient Loading**	**Static**	**Fluctuating**	Source	*P* value
C. gymnocaulos	**0**	47.3 (6.1)	39.7 (11.0)	Water Regime	0.1300
	10	63.3 (2.5)	56.0 (1.7)	Nutrient Loading	**<.0001**
	30	87.3 (14.0)	68.7 (6.7)	Regime x Loading	0.8040
P. australis	**0**	10.0 (3.5)	8.0 (7.0)	Water Regime	0.2720
	10	9.7 (1.12)	7.3 (3.1)	Nutrient Loading	0.9771
	30	13.3 (3.1)	5.0 (1.0)	Regime x Loading	0.4473
T. procerum	**0**	8.3 (2.3)	19.7 (10.3)	Water Regime	**0.0209**
	10	21.3 (3.1)	13.3 (5.5)	Nutrient Loading	0.3571
	30	17.0 (6.6)	10.0 (2.0)	Regime x Loading	**0.0128**
T. domingensis	**0**	13.7 (3.5)	23.0 (5.0)	Water Regime	**0.0109**
	10	18.3 (4.9)	18.0 (1.7)	Nutrient Loading	**0.0015**
	30	34.3 (3.1)	26.3 (6.7)	Regime x Loading	**0.0199**

5.4 Discussion

5.4.1 Species performance

Macrophyte species differ widely in their rates and forms of growth and in their physiology, and it is likely that the effect of water regime and of nutrient loading on individual species will differ (Schat 1984). The performance of each species increased with increased nutrient loading rates under a static water regime supporting the notion that anthropogenic nutrient loading into aquatic systems increases macrophyte production (Carr and Chambers 1998; Stevens *et al.* 2006), however, this effect was modified by a stochastic fluctuating regime (Grace 1988; Neill 1990). *C. gymnocaulos* (Table 5.2) had significantly increased plant performance with increased nutrient loading rates but this effect was significantly reduced under a fluctuating regime. Remarkably, under a fluctuating regime, *P. australis* (Table 5.3) had a significant reduction in performance with increased nutrient loading rates, whereas *T. domingensis* (Table 5.4) performance was significantly limited even with increased nutrient loading rates. *T. procerum* (Table 5.5) too had increased plant performance with increased nutrient loading rates but this effect was reduced under a fluctuating regime.

Neill (1990) found that nitrogen limited the growth of *Scolochloa festucacea* and *Typha glauca* and that water level effected growth and the degree of nitrogen limitation. Nitrogen limited the growth of *S. festucacea* more under intermediate flooded conditions (0-20cm) as opposed to deeply flooded conditions (20-40cm), whereas *T. glauca* had limited growth under deeply flooded conditions. Water depth placed a limit on how much increased growth was achieved in *T. glauca* with added nitrogen. Grace (1988) showed that nutrients enhanced *T. latifolia* in shallow to medium water depths while *T. domingensis* was enhanced in medium to deep depths. The influence of the water regime on the effects of nutrient loading on species performance were very much species specific. For *C. gymnocaulos* and *T. procerum* the effects of nutrient enrichment were largely independent of water regime (Gusewell *et al.* 2003), however, with *P. australis* and *T. domingensis* the effects of nutrient enrichment were dependent on the water regime (Grace 1988; Neill 1990).

Variations in hydrology may reduce the ability of fast growing species (i.e. *P. australis, T. domingensis* and *T. procerum*) to benefit from increased nutrient supply (Bollens *et al.* 2001). The partial drying of previously inundated sediment during draw-down may result in a reduction in the availability of N and P (Baldwin and Mitchell 2000) therefore limiting the effects of nutrient loading on plant performance. The re-wetting of desiccated sediments (re-flooding) will result in an initial flush of available N and P (Baldwin and Mitchell 2000), however, the plant productivity capabilities will be reduced (reduced photosynthetic canopy and availability of atmospheric CO_2) as an result to re-flooding (Siebentritt 2003). Uptake of nutrients by rice subjected to flush irrigation (wetting – drying cycles) was shown to be reduced compared to the normal flooding regime (Beyrouty *et al.* 1994). Gusewell *et al.* (2003) found that despite their reduced growth, periodically flooded plants were as nutrient limited as plants that were either constantly wet or periodically aerated. Reduced energy production in flooded plants might have reduced the plants ability to take up and transport nutrients (Schat 1984).

5.4.2 Morphological response - Biomass allocation

The morphological response (biomass allocation) of each species to nutrient loading rates and water regimes were largely as expected. A significantly greater proportion of each species biomass was allocated to the root tissue of those plants under lower nutrient loading rates (Tables 5.6-5.9) (Aerts and Chapin III 2000; Chapin III *et al.* 1987). But this allocation of biomass was significantly reduced in those plants subjected to a fluctuating regime. Plants subjected to a stochastic fluctuating regime allocated a significantly higher proportion of biomass to the above-ground shoot tissue, in a effort to maintain an emergent canopy, redeploying resources from the belowground parts (Tables 5.6-5.8) (Blanch *et al.* 1999a; Cooling 1996; Grace 1988; Grace 1989; Rea and Ganf 1994d; Waters and Shay 1990) except for *T. procerum* (Tables 5.9). In this effort to maintain their emergent canopy, those plants of *P. australis* and *T. domingensis* under higher nutrient loading rates (reduced nutrient up-take organ – root tissue) were in fact significantly reduced/limited in their performance due to this interaction of hydrology on nutrient availability, further reducing productivity capabilities. *T. procerum* on the other hand allocated a greater proportion of biomass to the root tissue of those plants subjected to a stochastic fluctuating regime while its allocation of biomass to the above-ground shoot tissue remained relatively uneffected by the water regime. This morphological response by *T. procerum* demonstrates that it is mainly limited by the nutrient loading rates and not the water regime (Table 5.9), suggesting that *T. procerum* accesses bicarbonate from the water column (Rea 1992) and is therefore uneffected by flooding events. These results support the observation that plant resources are allocated to the organ which acquires the resource in short supply (Aerts and Chapin III 2000; Chapin III *et al.* 1987).

5.4.3 Tagging study

The net recruitment by each species was similar to the outcomes of the individual species performance. Each species had an increased net recruitment with increased nutrient loading rates under a static water regime (Carr and Chambers 1998; Stevens *et al.* 2006) although not significant in *P. australis or T. procerum*. However, this effect was modified by a stochastic fluctuating regime (Table 5.10) (Grace 1988; Neill 1990). The net recruitment of *C. gymnocaulos* was reduced under a fluctuating regime. *P. australis* net recruitment was not only reduced under a fluctuating regime but was further reduced with increased nutrient loading rates but not significantly, whereas *T. domingensis* had limited net recruitment with increased nutrient loading rates. *T. procerum* had a negative net recruitment irrespective of nutrient loading rate under a fluctuating regime. The gross recruitment of *T. procerum* (Table 5.11) further illustrates that the water regime is the primary factor determining productivity, as it somehow caused a greater turnover rate of *T. procerum* leaves but as nutrient loading increases the turnover rate decreased. It is plausible that this increase in gross recruitment resulted in the greater proportion of biomass being allocated to the root tissue of those plants, increased recruitment requiring more resources (Aerts and Chapin III 2000; Chapin III *et al.* 1987). *T. procerum* was not limited by the acquisition of carbon (water depth) in this experiment (Rea 1992; Rea and Ganf 1994b), however, it was significantly limited/reduced by its increased turnover rates caused by a stochastic fluctuating water regime. Further illustrating that in fact the effects of nutrient enrichment on *T. procerum* were independent of water regime (Gusewell *et al.* 2003) but bearing in mind that water regime is the primary factor determining the productivity of this species.

5.4.4 Implications for flow restoration

The results of this pond experiment may be directly extrapolated to the field and used to predict the response of macrophyte to the imposition of environmental flows (restoration of fluctuating water regimes) along nutrient enriched reaches. The stochastic and stable water regimes used in this experiment are closely corresponding to the current (2002 as an example) and per-regulation (1970 as an example) water regimes of the EMLR. A once highly fluctuating water regime has now been replaced by a relatively stable water regime, particularly during the spring and early summer months when these species are likely to be highly active (Fig. 5.2).

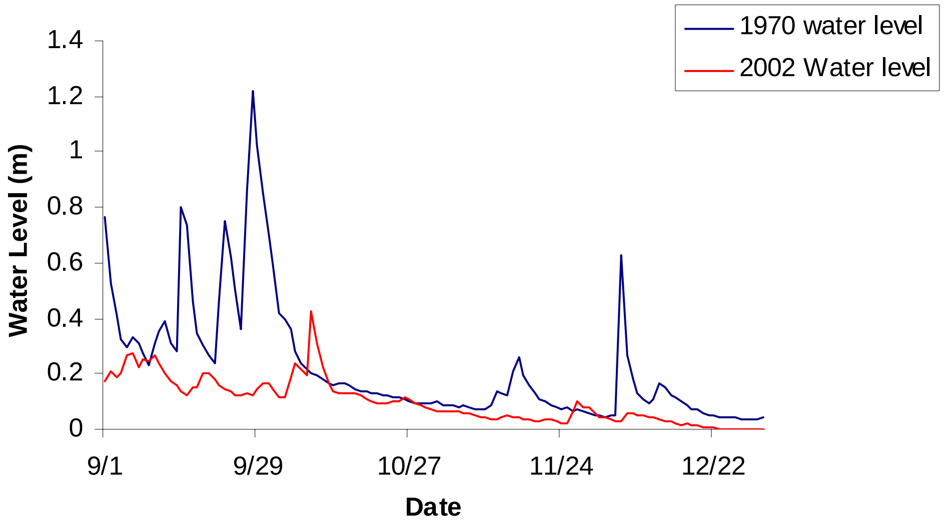

Figure 5.2: Comparison of variations in water levels on the Finniss River during spring/early summer at a location 4 km East of Yundi, ($35^{o}19'$ S, $138^{o}40'$ E) for the years 1970 and 2002 (pre and post regulation).

Increased nutrient loading does not outweigh the growth constraints of a fluctuating water regime. It may reduce the impact of a fluctuating regime on plant productivity (e.g. *C. gymnocaulos* and *T.procerum*) or even reduced/limit plant productivity (e.g. *P. australis* and *T. domingensis*). However, as a result of the effect of variations in hydrology on nutrient dynamics, the influence of water regime on the effects of nutrient loading is dependent upon the individual species and their elevation preference along the elevation gradient, which is predetermined by their growth form and physiology. For those species with higher elevation preferences, e.g. *C. gymnocaulos*, or low elevation preference, e.g. *T. procerum* the effects of nutrient loading are independent of water regime, whereas those species with an intermediate elevation preference, e.g. *P. australis* and *T. domingensis* the effects of nutrient loading are largely dependent on the water regime. Efforts to restore river health and ecological functioning must take into account the intrinsic interactions that take place between these different environmental factors and their effects on each individual species.

CHAPTER 6.

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6 Stream degradation results in a mismatch between consumers and their resources: the promotion of aquatic / riparian plant communities

6.1 Introduction

Information on the spatial extent of food webs that support stream and river consumers is essential for the management of lotic ecosystems (Finlay *et al.* 2002). However, the principal source of organic carbon supporting these lotic consumers appears to vary depending on the river type. In major tributaries of the Cooper River in an arid region of Queensland, algae were the major energy source supporting the consumers, especially snails, crustaceans and fish (Bunn and Davies 1999; Bunn *et al.* 2003). Feeding trials in the River Murray, Australia, suggested that riparian tree leaves may be the principal energy source for some benthic macroinvertebrates (Schulze and Walker 1997). In the Waikato region of New Zealand, food webs in the shaded, forested streams were clearly based on allochthonous material, whereas the carbon source in the unshaded pasture streams appeared to be a mixture of allochthonous and autochthonous material (Hicks 1997).

The use of stable isotopes is a powerful and effective tool for tracing this movement of energy and nutrients from autotrophs to consumers (Connolly *et al.* 2005). The stable isotope ratios of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) differ among autotrophs (Bouillon *et al.* 2002; Fry 1984) and these ratios, the isotopic signatures, are taken on by the consumers and reflected in their tissues at whatever trophic level they occur (Boon and Bunn 1994; Fry and Sherr 1984; Peterson 1999; Wada *et al.* 1991).

With the exception of some remote rivers in the arid zone (Walker *et al.* 1997) and the Northern Territory (Ganf and Rea 2006), most Australian floodplain rivers have been modified since European settlement. As a result, many have flipped from clear and macrophyte dominated systems, to turbid and plankton dominated systems (Harris 2001b; Scheffer *et al.* 2001), with significant alterations to riverine carbon cycles (Harris 1999a) as algal production may dominate these food webs. Flow regulations and other anthropogenic disturbances may magnify this autochthonous effect (Robertson *et al.* 1999). These changes will have, as yet, largely unquantified impacts on the dynamics of organic carbon cycles (Robertson *et al.* 1999) and food chain structure and function (Harris 1999a; Hicks 1997; Ward and Stanford 1983). This poses the questions of what are the principal energy sources supporting the lower trophic level consumers in modified riverine systems and do these energy sources alter across a gradient in catchment degradation? If there is a change in principal energy sources across a gradient in catchment degradation then what is the significance of these alterations for the higher trophic consumers.

A consequence of changing land use, river regulation and irrigation is that the floristic composition of rivers may alter. For example, Blanch et al. (1999b; 2000) showed that in the River Murray submerged macrophytes, with relatively low C : nutrient ratios were restricted to weir pools whereas emergent species with much higher C : nutrient ratios dominated the majority of river reaches. As many primary herbivores have C:N ratios of 5:1 (Evans-White *et al.* 2005) there is the possibility of a stoichiometric mismatch if their food source is restricted to carbon rich species. Similarly, Tibbetts and Molles (2005) compared nutrient ratios in cottonwoods in flood and non-flooded sites on the Rio Grande, U.S.A. and suggested that these may impose a food quality constraint on the detritivores. Ecological stoichiometry is a conceptual framework that may provide insight into the consequences of mismatches between the carbon: nutrient ratios of primary producers and their consumers (Frost *et al.* 2005).

The aim of this study was to determine whether or not aquatic macrophytes were a significant food source for macroinvertebrates of the shredder functional group across riverine reaches whose ecological condition varied from very poor to excellent. The excellent sites were wooded or forested and it was hypothesised that in these reaches allochthanous carbon sources would be the principal food source and aquatic macrophytes would play a minor role (Bunn 1993; Cummins *et al.* 1995; Hicks 1997; Vannote *et al.* 1980). It was also hypothesised that because the very poor sites were devoid of riparian vegetation and had few macrophytes, the role played by aquatic macrophytes in the food web would become redundant and be replaced by a nutritively inferior alternative.

The specific objectives were: i) to quantify the role of aquatic macrophytes in the diets of shredder communities, ii) to compare the role of aquatic macrophytes in the diets of shredder communities across gradients in catchment degradation (level of anthropogenic alteration), iii) determine if anthropogenic alterations of catchments have indeed altered food chain structure and function at the level of primary producers and their consumers, iv) determine the significance of altering food chain structure and possible knock-on effects for the higher trophic levels, and v) to assess which of the four conceptual riverine models (The River Continuum Concept (Vannote *et al.* 1980), the Serial Discontinuity Concept (Ward and Stanford 1983), the Flood Pulse Concept (Junk *et al.* 1989) and the Riverine Productivity Model (Thorp and Delong 1994; Thorp and Delong 2002)) or combinations of models best described the movement of energy and nutrient from primary to the secondary trophic levels in modified riverine systems.

6.2 Materials and Methods

6.2.1 Selection of Study sites

To reduce the effect of spatial variation (Boon and Bunn 1994) and to examine the effect of alterations to catchment primary production on carbon dynamics and food chain structure and function, nine sites were chosen along the Finniss River, South Australia (Fig. 6.1). The sites ranged in ecological condition from very poor to excellent (see Chapter 2), three representatives each of sites in excellent, average and very poor ecological condition were chosen.

Sites 40 (Ex. 1), 18 (Ex. 2) and 22 (Ex. 3) (see Chapter 2) had excellent total index condition scores (Jansen and Robertson 2001; Ladson *et al.* 1999) of 42, 41 and 40, respectively. Each of these sites was surrounded by extensive native vegetation, with no signs of agricultural development. Sites 48 (Av. 1), 17 (Av. 2) and 27 (Av. 3) had scores of 33, 34 and 31, respectively – average ecological condition. They had reduced canopy cover compared to the excellent sites and were subject to some grazing. Sites 36 (VP. 1), 44 (VP. 2) and 30 (VP. 3) had scores of 22, 19 and 16, respectively – very poor ecological condition. Each site had no canopy, understorey or riparian cover, and was subjected to intense grazing.

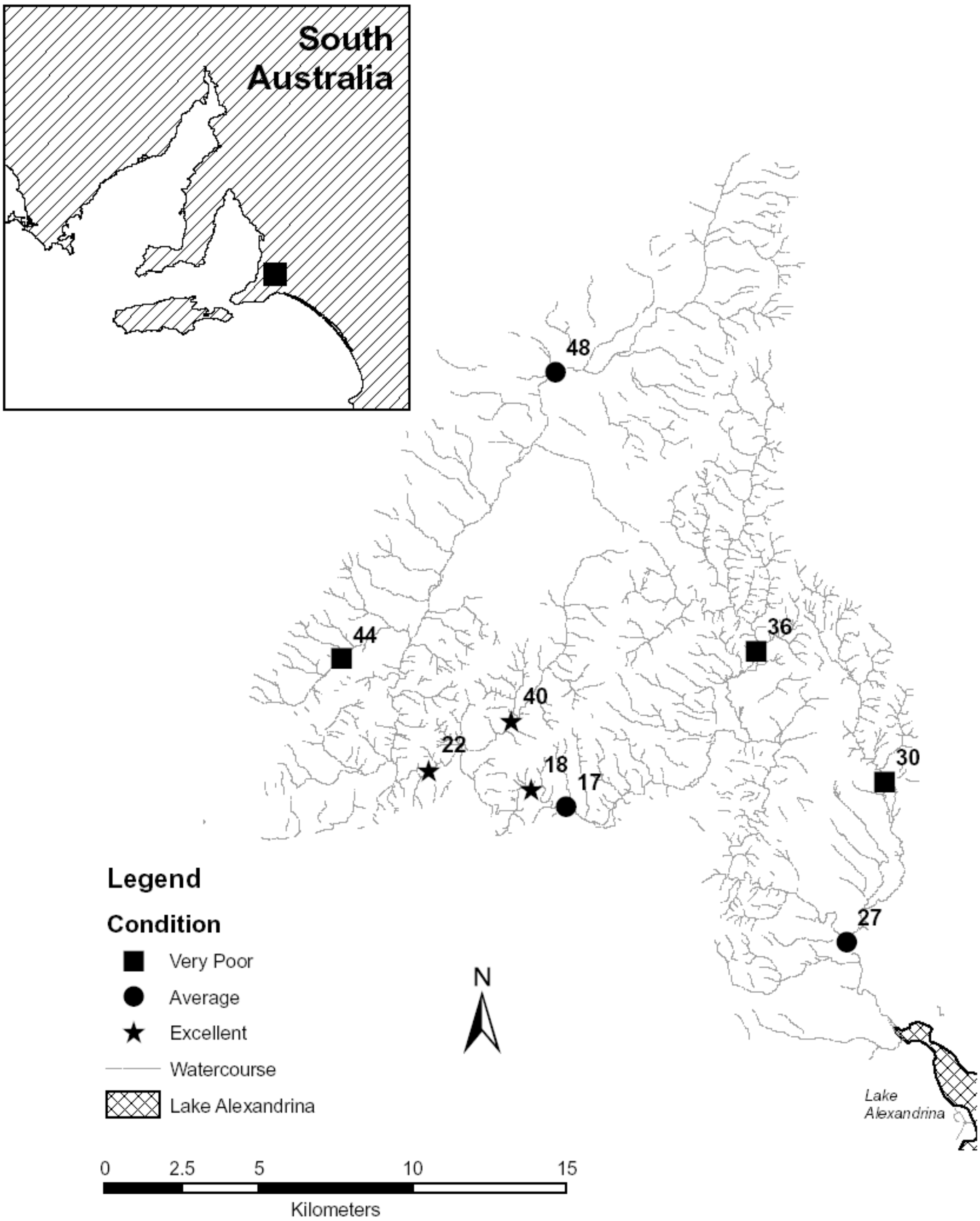

Figure 6.1: Map of the Finniss catchment indicating each of the study sites and their ecological condition.

6.2.2 Sampling protocol and collection of primary sources and consumers

A pilot study was undertaken on the 27th and 28th of March, 2005, in which three sites were sampled, sites Ex. 1, Av. 1 and VP. 1. A more extensive study took place between October 31st and November 2nd, 2005, during which nine sites were sampled. The protocol for the pilot study was to collect specimens of macroinvertebrates and of the three most dominant macrophytes species from each site (Table 6.1). This was used as an indication of the possible role, if any, aquatic macrophytes play in the nutrition of shredder communities. For the more extensive study, the protocol was to collect specimens of macroinvertebrates and all primary sources, both terrestrial and aquatic, in or at the waters edge, from each site (Table 6.2). Samples of each of the major primary sources of organic carbon were collected from each site by hand. Samples of macroinvertebrates were collected from each site using a kick-net (250 µm mesh) and immediately stored in 70% ethanol (Jardine *et al.* 2003). Three replicate samples of each source and consumer were collected from each site. Plant samples were refrigerated immediately and then frozen as soon as possible (same day) and stored for isotope analysis.

Table 6.1: Primary sources (three dominant macrophyte species) and consumers collected from three sites during the pilot study (27th and 28th of March, 2005).

Site	Ecological condition	Primary sources	Consumers (orders)
Ex. 1	Excellent	*Typha domingensis* *Triglochin procerum* *Persicaria decipiens*	Trichoptera Amphipoda
Av. 1	Average	*Typha domingensis* *Triglochin procerum* *Potamogeton crispus*	Trichoptera Amphipoda
VP. 1	Very Poor	*Phragmites australis* *Cyperus vaginatus* *Rorippa nasturtium-aquaticum*	Trichoptera Amphipoda

Table 6.2: All primary sources (terrestrial and aquatic) and consumers collected from nine sites during the second round of sampling (October 31st and November 2nd, 2005). CPOM: course particulate organic matter.

Site	Ecological condition	Primary sources	Consumers (orders)
Ex. 1	Excellent	*Typha domingensis*	Trichoptera
		Triglochin procerum	Amphipoda
		Persicaria decipiens	
		CPOM	
		Riparian leaves	
		Riparian grasses	
		Plantago major	
		Anagallis arvensis	
Ex. 2	Excellent	CPOM	Trichoptera
		Riparian grasses	Amphipoda
		Riparian leaves	
		Cyperus vaginatus	
		Juncus pallidus	
		Baumea juncea	
		Triglochin procerum	
Ex. 3	Excellent	CPOM	Trichoptera
		Myriophyllum simulans	Amphipoda
		Cyperus vaginatus	
		Juncus pallidus	
		Triglochin procerum	
		Riparian leaves	
		Riparian grasses	
		Crassula helmsii	
Av. 1	Average	*Callitriche stagnalis*	Trichoptera
		Ranunculus amphitrichus	Amphipoda
		Riparian leaves	
		Typha domingensis	
		CPOM	
		Potamogeton crispus	
		Triglochin procerum	
		Crassula helmsii	
Av. 2	Average	*Triglochin procerum*	Trichoptera
		Cyperus vaginatus	Amphipoda
		Riparian leaves	
		Crassula helmsii	
		Riparian grasses	
		CPOM	
Av. 3	Average	CPOM	Trichoptera
		Riparian leaves	Amphipoda
		Crassula helmsii	
		Typha domingensis	
		Cotula coronopifolia	
		Rorippa nasturtium-	

		aquaticum	
		Chara sp.	
VP. 1	Very Poor	CPOM	Trichoptera
		Filamentous Algae	Amphipoda
		Phragmites australis	
		Cyperus vaginatus	
		Riparian grasses	
		Rorippa nasturtium-aquaticum	
VP. 2	Very Poor	CPOM	Amphipoda
		Riparian grasses	
		Batrachium trichophyllum	
		Eleocharis pusilla	
		Callitriche stagnalis	
		Zantedeschia aethiopica	
VP. 3	Very Poor	CPOM	Amphipoda
		Callitriche stagnalis	
		Cotula coronopifolia	
		Cyperus vaginatus	
		Typha domingensis	
		Filamentous Algae 1	
		Filamentous Algae 2	

6.2.3 Sample preparation and analysis

All macroinvertebrates sampled were identified (Dean *et al.* 2004; Gooderham and Tsyrlin 2002; Hawking and Smith 1997) and separated into their functional feeding groups (Boulton and Brock 1999). Only those macroinvertebrates classified as shredders were analysed. The two orders of macroinvertebrates classified as shredders found at most sites were Trichoptera – *Triplectides* sp. and Amphipoda – *Austrogammarus* spp., *Paramelitidae* spp., *Corophiidae* spp., and *Neoniphargidae* spp.

All plant and animal material was washed in distilled water. Samples were oven-dried at 60°C for 36-48 h and then ground to a fine powder-like consistency using a mortar and pestle. Invertebrates classified as shredders were separated and pooled into two orders (Trichoptera and Amphipoda) and prepared whole, for each replicate for each site.

Dried, ground samples were oxidized at high temperatures and the resultant CO_2 and N_2 were analysed for percentage C, N and stable isotopes ratios with a Tracermass ion ratio mass spectrometer and Roboprep preparation system manufactured in 1997 by Europa PDZ, UK. Ratios of $^{13}C/^{12}C$ and $^{15}N/^{14}N$ were expressed as parts per thousands (‰)

difference between the sample and conventional standards (Vienna Pee Dee belemnite for C and atmospheric N_2 for N) (Gorokhova *et al.* 2005) where:

$$\delta X\ (‰) = (R_{sample} / R_{standard} - 1) \times 1000$$

Where $X = {}^{13}C$ or ${}^{15}N$ and $R = {}^{13}C/{}^{12}C$ or ${}^{15}N/{}^{14}N$.

Repeated analyses of homogeneous material yielded SD of 0.1‰ and 0.3‰ for $\delta^{13}C$ and $\delta^{15}N$ respectively.

6.2.4 Modelling feasible source mixtures to explain shredder nutrition

Mean $\delta^{13}C$ and $\delta^{15}N$ values were calculated for both the consumers and the primary sources collected from each of the study sites. To overcome the problem that not all primary sources (plant species) were represented at all sites (Table 6.2), the species were pooled into vegetation groups of similar life form (Table 6.3) and the mean $\delta^{13}C$ and $\delta^{15}N$ values calculated were pooled for each vegetation grouping across sites of the same ecological condition. This allowed for a comparison between sites of differing ecological condition even when there were different primary sources collected from each site.

Table 6.3: Plant species are grouped based on similar life forms. CPOM: course particulate organic matter.

Group	Species of similar life form
1	CPOM
2 (Riparian)	Riparian leaves, Riparian grasses, *Plantago major, Anagallis arvensis, Zantedeschia aethiopica*
3 (semi-emergent)	*Persicaria decipiens, Cotula coronopifolia, Rorippa nastuttium-aquaticum, Crassula helmsii, Callitriche stagnalis, Triglochin procerum*
4 (Emergent)	*Cyperus vaginatus, Juncus pallidus, Baumea juncea, Typha domingensis, Phragmites australis, Eleocharis pusilla*
5 (Submerged)	*Myriophyllum simulans, Ranunculus amphitrichus, Batrachium trichophyllum, Potamogeton crispus*
6 (Algal)	Filamentous Algae, *Chara* sp.

These pooled values were used in the isosource model of Phillips and Gregg (2003) to calculate feasible combinations of primary source material (vegetation groupings) that could explain the consumer signatures. This method examined all possible combinations of each primary source potential contribution (0 to 100%) in small increments (here 1%) when the number of primary sources per site were either 6 or 7, and 2% when the number of primary sources were 8 or more (Phillips and Gregg 2003). Combinations that added to within 0.01‰ of the consumer signature were considered feasible solutions (Connolly *et al.* 2005; Melville and Connolly 2003). As recommended by Phillips and Gregg (2003), results are reported as the distribution of feasible solutions for each primary source. The median contribution and the 1 and 99 percentile range is given, rather than the full range, which is sensitive to small numbers of observations on the tails of the distribution (Phillips and Gregg 2003). All feasible source mixture modelling is presented for each vegetation group across each level of ecological condition (Very Poor to Excellent), and individually for each site and its primary sources during the second sampling period.

To account for fractionation, a fractionation correction was used based on the most recently reported average fractionation increase of +0.3‰ for carbon isotopes and +2.2‰ for nitrogen isotopes per trophic level for consumers analysed whole, which were raised on plant and algal diets (McCutchan *et al.* 2003) in non-limited nutrient environments.

6.3 Results

6.3.1 Pilot study

Only the three dominant macrophyte species (sources) from each of three sites were analysed during the pilot study. It would therefore be misleading to use geometric or mixing model procedures to quantify the contributions of these food sources to the diets of Amphipoda and Trichoptera because not all possible food sources were collected and analysed. However, if fractionation corrections are put in place (Table 6.4), there is an overlap of both $\delta^{13}C$ and $\delta^{15}N$ values between two plant species and the consumers sampled. It appears that *R. nasturtium-aquaticum* is a contributor to the diets of both Amphipoda and Trichoptera at site VP. 1 and *P. crispus* is a contributor to the diets of Trichoptera at site Av. 1 (Table 6.4).

6.3.2 Modelled feasible source mixtures to explain shredder nutrition

In the riverine reaches with extensive agricultural development (VP. 1 – VP. 3) and with very little or no understorey and canopy cover, group 1 (CPOM) formed the main dietary component of Amphipoda (20–53%) (Table 6.5). The feasible contributions to Amphipoda nutrition from each of the individual primary sources modelled for each of the very degraded sites further support this observation (Table 6.7). It clearly shows CPOM to be the main dietary component of Amphipoda across sites of very poor ecological condition, with contributions of between 19 – 32% (VP. 1) to 49 – 65% (VP. 3). The balance of their diet appears to be generally distributed evenly across vegetation groups 2 to 6 (Table 6.5) depending on the species present at individual sites (Table 6.7). For Trichoptera (only recorded at VP. 1), group 6 formed the main dietary component (48 – 64%) followed by group 1 (2 – 22%) (Table 6.6). This observation is reflected in the contributions from each of the individual primary sources modelled (Table 6.7) at site VP. 1. The remaining aquatic and terrestrial plant species modelled played significantly reduced roles in the diet of Trichoptera.

Along reaches of average ecological condition, group 3 species were the major nutritive source for Amphipoda accounting for 65 – 97% of total intake (Table 6.5). This observation is further supported by modelling the feasible contributions of each individual primary source from each reach in average condition (Table 6.8). *C. stagnalis* (6-56%), *R. amphitrichus* (0-30%), *C. helmsii* (0-72%) and *T. procerum* (0-26%) form the main dietary components of Amphipoda at site Av. 1. At site Av. 2, *C. helmsii* and *T. procerum* (0-41% and 0-38% respectively) formed the main dietary components, while at site Av. 3, *C. coronopifolia, R. nasturtium-aquaticum* and *C. helmsii* (0-55%, 0-48% and 0-47%) formed the principal energy sources supporting Amphipoda. All of these species belong to vegetation group 3. Group 3 species were also the main source of nutrition for Trichoptera (47 – 91%) (Table 6.6) in each of these reaches (Table 6.8), except at site Av. 3 where the major dietary component for Trichoptera was *T. domingensis* (36-76%) (group 4), followed by group 3 species (Table 6.8).

In the riverine reaches of excellent ecological condition with extensive canopy and understorey cover, and no agricultural development, group 3 species again formed the main dietary components of Amphipoda (57 – 72%) (Table 6.5). However, the feasible contribution made by individual primary sources modelled for each of the excellent reaches does not support this observation (Table 6.9). Riparian grasses made up a considerable proportion of the Amphipoda diets at sites Ex. 1, Ex. 2 and Ex. 3 (18 – 64%, 39 – 46% and 0 – 68%, respectively) (Table 6.9) but these contributions are not reflected in group 2’s contribution to Amphipoda diet (Table 6.5). Similar observations were made for Trichoptera across the excellent sites (Table 6.6) but less pronounced (Table 6.9). In general, the results from the vegetation groupings and subsequent modelling (Table 6.6) hold true but are very much site specific (Table 6.9), i.e. the primary sources present and their availability. At site Ex. 1 group 4 (*T. domingensis*; 44-66%) were the main nutritional source followed by group 2 and then group 3. Group 2 (particularly Riparian grasses; 36 – 46%) made up the main dietary components followed closely by group 3 (*T. procerum* 23-38%) at site Ex. 2. And finally group 3 formed the main dietary components for Trichoptera at site Ex. 3, followed by groups 4 and 2 (Table 6.9).

6.3.3 C:N ratios found in primary sources and their primary consumers

The C:N ratio found in the primary sources varied considerably between sites of the same ecological condition and between sites of different ecological condition (Tables 6.10, 6.11, and 6.12). For example; CPOM ranged from 23.3 to 39.7 (Table 6.10) in sites of a very degraded ecological condition, from 24.7 to 47.0 (Table 6.11) in sites of average ecological condition, and from 43.1 to 59.4 (Table 6.12) in sites of excellent ecological condition. This was also true for primary producers; *C. stagnalis* had a C:N ratio of 7.6 at site Av. 1 (Table 6.11) and ratios of 10.6 and 11.9 at sites VP. 2 and VP. 3 (Table 6.10). *C. vaginatus* had a C:N ratio of 25.0 and 42.5 at sites VP. 1 and VP. 3 respectively (Table 6.10), a ratio of 27.4 at site Av. 2 (Table 6.11), and a ratio of 50.1 at site Ex. 2 (Table 6.12). The primary consumers, however, were very much homeostatic in their C:N ratios, regardless of the ecological condition of the site. Amphipoda ranged from 4.5 to 5.0 and Trichoptera from 4.7 to 5.7 between sites of the same and different ecological conditions (Tables 6.10, 6.11, and 6.12).

In general the mean C:N ratio for each of the vegetation groupings shows that group 3 had the lowest C:N ratio while group 1 had the highest across each level of ecological condition (Fig. 6.2).

Table 6.4: Corrected mean δ^{13}C and δ^{15}N values of dominant macrophytes (primary sources) and mean δ^{13}C and δ^{15}N values of primary consumers collected from three sites during first sampling period. Standard deviations in brackets.

Site & Date	**Isotope**	**Corrected Primary Sources**			**Consumers**	
		C. vaginatus	*R. nasturtium-aquaticum*	*P. australis*	Trichoptera	Amphipoda
VP. 1 March 05	δ^{13}C	-27.4 (0.5)	-29.4 (0.8)	-27.3 (0.6)	-29.4 (3.2)	-28.4 (1.4)
	δ^{15}N	10.6 (0.8)	8.1 (0.2)	11.0 (0.2)	7.8 (0.0)	8.1 (0.4)
		T. procerum	*P. crispus*	*T. domingensis*		
Av. 1 March 05	δ^{13}C	-24.2 (0.5)	-29.8 (0.4)	-27.0 (1.1)	-30.5 (0.8)	-28.7 (1.1)
	δ^{15}N	10.3 (0.6)	6.7 (0.8)	10.5 (0.3)	7.8 (0.4)	8.2 (0.4)
		P. decipiens	*T. procerum*	*T. domingensis*		
Ex. 1 March 05	δ^{13}C	-30.0 (0.3)	-27.3 (0.5)	-29.4 (0.3)	-25.1 (0.9)	-26.8 (0.9)
	δ^{15}N	9.1 (0.2)	10.0 (0.1)	5.9 (0.1)	6.3 (0.2)	8.3 (0.0)

Table 6.5: Distribution of feasible contributions to Amphipoda nutrition presented for each vegetation grouping across each level of ecological condition (Excellent to Very Poor). Ranges: 1 and 99 percentiles. Median in brackets.

Vegetation groupings	**Ecological Condition**		
	Excellent	Average	Very Poor
Group 1	0 – 13% (4%)	0 – 5% (1%)	20 – 53% (38%)
Group 2	2 – 25% (8%)	0 – 3% (1%)	0 – 31% (8%)
Group 3	57 – 72% (67%)	65 – 97% (88%)	0 – 49% (14%)
Group 4	0 – 27% (8%)	0 – 24% (6%)	0 – 48% (13%)
Group 5	7 – 12% (11%)	0 – 11% (4%)	0 – 29% (8%)
Group 6		0 – 2% (0%)	0 – 23% (11%)

Table 6.6: Distribution of feasible contributions to Trichoptera nutrition presented for each vegetation grouping across each level of ecological condition (Excellent to Very Poor). Ranges: 1 and 99 percentiles. Median in brackets.

Vegetation groupings	**Ecological Condition**		
	Excellent	Average	Very Poor
Group 1	0 – 27% (10%)	0 – 8% (3%)	2 – 22% (13%)
Group 2	0 – 28% (11%)	0 – 5% (1%)	0 – 19% (5%)
Group 3	31 – 64% (48%)	47 – 91% (78%)	0 – 35% (9%)
Group 4	1 – 59% (25%)	0 – 34% (10%)	0 – 28% (7%)
Group 5	0 – 6% (4%)	0 – 17% (7%)	0 – 17% (4%)
Group 6		0 – 3% (0%)	48 – 64% (57%)

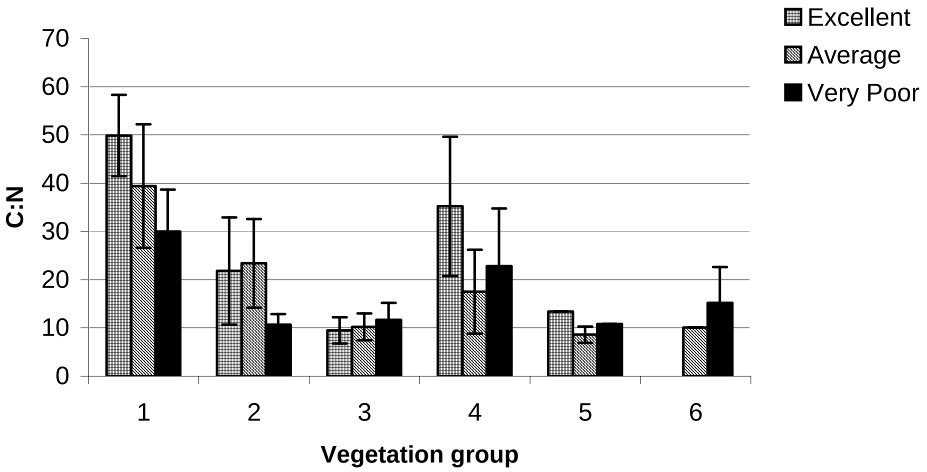

Figure 6.2: Mean C:N ratios for each of the vegetation groupings across each level of ecological condition (Excellent to Very Poor).

Table 6.7: Distribution of feasible contributions to shredder nutrition from primary sources collected from sites of very poor ecological condition based on δ^{13}C and δ^{15}N values. Ranges: 1 and 99 percentiles. Median in brackets. CPOM: course particulate organic matter.

Site	**Consumer**	**Primary Sources**					
		CPOM	Riparian Grasses	*C. vaginatus*	*P. australis*	*R. nasturtium-aquaticum*	Filamentous Algae
VP. 1	Amphipoda	19 – 32% (24%)	0 – 47% (12%)	0 – 39% (10%)	0 – 36% (9%)	0 – 41% (10%)	17 – 33% (25%)
	Trichoptera	32 –36% (33%)	0 – 14% (3%)	0 – 11% (3%)	0 – 9% (2%)	0 – 12% (3%)	50 – 54% (52%)
		CPOM	Riparian Grasses	*E. pusilla*	*C. stagnalis*	*Z. aethiopica*	*B. trichophyllum*
VP. 2	Amphipoda	11 – 46% (36%)	0 – 27% (7%)	0 – 57% (15%)	0 – 23% (6%)	20 – 29% (25%)	0 – 26% (7%)
		CPOM	*C. coronopifolia*	*C. vaginatus*	*C. stagnalis*	Filamentous Algae 1.	Filamentous Algae 2.
VP. 3	Amphipoda	49 – 65% (61%)	0 – 18% (4%)	0 – 9% (2%)	0 – 18% (4%)	2 – 19% (13%)	0 – 44% (10%)

Table 6.8: Distribution of feasible contributions to shredder nutrition from primary sources collected from sites of average ecological condition based on $\delta^{13}C$ and $\delta^{15}N$ values. Ranges: 1 and 99 percentiles. Median in brackets. CPOM: course particulate organic matter.

Site	**Consumer**	**Primary Sources**							
Av. 1		CPOM	Riparian Leaves	*C. stagnalis*	*R. amphitrichus*	*C. helmsii*	*T. procerum*	*T. domingensis*	*P. crispus*
	Amphipoda	0 –22% (4%)	0 – 16% (2%)	6 – 56% (36%)	0 – 30% (10%)	0 – 72% (16%)	0 – 26% (6%)	0 – 30% (6%)	0 – 24% (10%)
	Trichoptera	0 – 22% (4%)	0 – 16% (4%)	0 – 36% (16%)	0 – 56% (18%)	0 – 50% (14%)	0 – 28% (6%)	0 – 30% (6%)	0 – 44% (24%)
Av. 2		CPOM	Riparian Leaves	Riparian Grasses	*C. vaginatus*	*C. helmsii*	*T. procerum*		
	Amphipoda	0 – 43% (15%)	0 – 27% (10%)	21 – 33% (16%)	0 – 48% (13%)	0 – 41% (18%)	0 – 38% (20%)		
	Trichoptera	0 – 20% (8%)	0 – 12% (5%)	9 – 20% (14%)	0 –76% (21%)	0 – 64% (22%)	0 – 60% (20%)		
Av. 3		CPOM	Riparian Leaves	*C. coronopifolia*	*R. nasturtium-aquaticum*	*C. helmsii*	Chara sp.	*T. domingensis*	
	Amphipoda	0 – 37% (12%)	0 – 21% (7%)	0 –55% (17%)	0 – 48% (17%)	0 – 47% (13%)	0 – 15% (5%)	0 – 53% (17%)	
	Trichoptera	0 – 28% (12%)	0 – 11% (3%)	0 – 30% (8%)	0 – 28% (8%)	0 – 26% (6%)	0 – 6% (1%)	36 – 76% (57%)	

Table 6.9: Distribution of feasible contributions to shredder nutrition from primary sources collected from sites of excellent ecological condition based on δ^{13}C and δ^{15}N values. Ranges: 1 and 99 percentiles. Median in brackets. CPOM: course particulate organic matter.

Site	**Consumer**	**Primary Sources**							
		CPOM	Riparian Leaves	Riparian Grasses	*T. procerum*	*A. arvensis*	*P. major*	*T. domingensis*	*P. decipiens*
Ex. 1	Amphipoda	0 – 12% (2%)	0 – 12% (2%)	18 – 64% (50%)	0 – 26% (8%)	0 – 62% (14%)	0 – 14% (4%)	0 – 18% (4%)	0 – 28% (8%)
	Trichoptera	0 – 32% (10%)	0 – 32% (16%)	0 – 6% (0%)	0 – 16% (4%)	0 – 8% (2%)	0 – 20% (4%)	44 – 66% (56%)	0 – 18% (4%)
		CPOM	Riparian Leaves	Riparian Grasses	*T. procerum*	*C. vaginatus*	*J. pallidus*	*B. juncea*	
Ex. 2	Amphipoda	0 – 9% (2%)	0 – 7% (1%)	39- 46% (43%)	33 – 43% (39%)	0 – 19% (4%)	0- 19% (4%)	0 – 16% (3%)	
	Trichoptera	0 – 12% (2%)	0 – 9% (2%)	36 – 46% (42%)	23 – 38% (32%)	0 – 27% (6%)	0 – 27% (6%)	0 – 22% (5%)	
		CPOM	Riparian Leaves	Riparian Grasses	*T. procerum*	*C. vaginatus*	*J. pallidus*	*C. helmsii*	*M. simulans*
Ex. 3	Amphipoda	0 –22% (4%)	0 –16% (4%)	0 – 68% (18%)	0 – 52% (14%)	0 – 26% (6%)	0 – 60% (12%)	0 – 52% (24%)	0 – 18% (4%)
	Trichoptera	0 – 22% (4%)	0 – 16% (4%)	0 – 66% (16%)	0 – 50% (12%)	0 – 26% (6%)	0 – 58% (12%)	0 – 54% (24%)	0 – 20% (6%)

Table 6.10: Mean C:N ratios of consumers and primary sources collected from sites of very poor ecological condition. CPOM: course particulate organic matter.

Site	**Consumer**		**Primary Sources**					
VP. 1	Amphipoda	Trichoptera	CPOM	Riparian Grasses	*C. vaginatus*	*P. australis*	*R. nasturtium-aquaticum*	Filamentous Algae
	4.8	5.4	23.3	9.3	25.0	11.9	7.9	7.7
VP. 2	Amphipoda		CPOM	Riparian Grasses	*E. pusilla*	*C. stagnalis*	*Z. aethiopica*	*B. trichophyllum*
	4.9		26.7	9.4	18.8	10.6	13.1	10.8
VP. 3	Amphipoda		CPOM	*C. coronopifolia*	*C. vaginatus*	*C. stagnalis*	Filamentous Algae 1.	Filamentous Algae 2.
	5.0		39.7	16.3	42.5	11.9	15.3	22.5

Table 6.11: Mean C:N ratios of consumers and primary sources collected from sites of average ecological condition. CPOM: course particulate organic matter.

Site	**Consumer**		**Primary Sources**							
Av. 1	Amphipoda	Trichoptera	CPOM	Riparian Leaves	*C. stagnalis*	*R. amphitrichus*	*C. helmsii*	*T. procerum*	*T. domingensis*	*P. crispus*
	5.0	4.7	24.7	34.9	7.6	9.8	11.4	7.8	11.0	7.3
Av. 2	Amphipoda	Trichoptera	CPOM	Riparian Leaves	Riparian Grasses	*C. vaginatus*	*C. helmsii*	*T. procerum*		
	4.7	5.7	47.0	17.5	14.6	27.4	14.9	9.1		
Av. 3	Amphipoda	Trichoptera	CPOM	Riparian Leaves	*C. coronopifolia*	*R. nasturtium-aquaticum*	*C. helmsii*	Chara sp.	*T. domingensis*	
	4.8	5.4	46.6	26.7	12.0	6.9	11.8	10.1	14.0	

Table 6.12: Mean C:N ratios of consumers and primary sources collected from sites of excellent ecological condition. CPOM: course particulate organic matter.

Site	Consumer		Primary Sources							
Ex. 1	Amphipoda	Trichoptera	CPOM	Riparian Leaves	Riparian Grasses	*T. procerum*	*A. arvensis*	*P. major*	*T. domingensis*	*P. decipiens*
	4.7	4.9	47.4	18.4	15.4	7.1	12.7	21.0	15.1	8.5
Ex. 2	Amphipoda	Trichoptera	CPOM	Riparian Leaves	Riparian Grasses	*T. procerum*	*C. vaginatus*	*J. pallidus*	*B. juncea*	
	4.5	5.0	59.4	29.2	21.8	8.7	50.1	44.0	48.8	
Ex. 3	Amphipoda	Trichoptera	CPOM	Riparian Leaves	Riparian Grasses	*T. procerum*	*C. vaginatus*	*J. pallidus*	*C. helmsii*	*M. simulans*
	4.6	5.7	43.1	45.2	10.6	8.8	25.3	27.7	14.3	13.4

6.4 Discussion

In undisturbed forested riverine(Lyte and Poff 2004) reaches with little to no anthropogenic impact, riparian vegetation has a controlling influence on ecosystem function by reducing solar radiation and therefore limiting in-stream primary production (Boston and Hill 1991; Cummins *et al.* 1995). As a result, food webs in most forested/wooded streams are thought to be largely dependent on terrestrial allochthonous material (Bunn 1993; Cummins *et al.* 1995; Hicks 1997; Vannote *et al.* 1980). However, in this study emergent macrophytes (local in-stream primary production) were found to be the major energy sources supporting the local shredder communities along forested riverine reaches (Tables 6.5 & 6.6).

Reaches subjected to a reduction in shading (limited clearance and grazing by livestock) and increased solar radiation, together with increased nutrient inputs due to anthropogenic developments in the catchments often result in increased in-stream primary production (submerged and emergent macrophytes) (Brookes 1994; Bunn *et al.* 1998). It is reasonable to assume that the increased in-stream primary productivity (abundance and diversity of submerged and emergent macrophytes) would play an even greater role in the nutrition of local shredder communities. Shredder communities found in these reaches have an even greater nutritional dependence on succulent semi-emergent macrophytes in comparison to those found in reaches of excellent ecological condition (Tables 6.5 & 6.6).

Those reaches subjected to extensive clearance and anthropogenic developments have resulted in changes to their fluvial geomorphology, bank erosion, leading to river channelisation (Amoros and Bornette 2002). This has resulted in significant alterations to catchment primary production and hence to riverine carbon cycles (Walker *et al.* 1997), which has altered food chain structure and function (Harris 1999b; Hicks 1997; Ward and Stanford 1983). The major energy sources supporting the local shredder communities found in these degraded reaches have switched from emergent aquatic plant species to CPOM and filamentous algae (Tables 6.5 & 6.6).

6.4.1 Conceptual model of the flow of nutrients through riverine ecosystems

The RPM (Thorp and Delong 1994; Thorp and Delong 2002; Thorp *et al.* 1998) is the most appropriate model to use for this study in explaining the flow of energy and nutrients from primary producers to primary consumers (shredders) in riverine ecosystems subjected to limited/minimal disturbance. It emphasises the importance of local autochthonous autotrophic production (riparian and aquatic plant species) near the banks where benthic species tend to aggregate. Other recognised conceptual riverine models accentuate the importance of nutrients derived from either headwater streams (RCC (Vannote *et al.* 1980), SDC (Ward and Stanford 1983)) or seasonal floodplain pulses (FPC (Junk *et al.* 1989)), and downplay the role of local in-stream primary production. However, in riverine ecosystems of this study that are subjected to extensive anthropogenic modifications leading to a state of poor ecological condition, the RCC (Vannote *et al.* 1980) and the RPM are the most appropriate models to use. In these modified systems CPOM imported from further up the catchment is one of the principle energy sources supporting the shredder communities, probably due the lack of other available food sources. The in-stream primary production has also flipped from aquatic macrophytes to filamentous algae (Harris 2001b; Scheffer *et al.* 2001), which also plays a significant role in the nutrition of shredders.

6.4.2 Nutritional constraints as a result of anthropogenic alterations

The factors that influence the nutrient ratios in the leaves of primary producers and leaf litter (CPOM) are not consistent. Large variations in the C: nutrient ratios of autotrophs occur within and between ecosystems (Elser *et al.* 2000a). The C:N ratio found in the primary sources varied considerably within sites of the same ecological condition and between sites of differing ecological condition (Tables 6.10, 6.11, and 6.12). Reasons for this discrepancy have been attributed to differences in resorption efficiency, nutrient availability, and plant homeostatic regulation (Aerts 1996; Gusewell 2004). However, regardless of the ecological condition of a site and across a broad range of food qualities and physiochemical environmental conditions (Cross *et al.* 2005), the primary invertebrate consumers were relatively homeostatic in their C:N ratios (Tables 6.10, 6.11 and 6.12) and this is in accordance with other studies (Cross *et al.* 2005; Cross *et al.* 2003; Elser *et al.* 2000b; Frost *et al.* 2003).

The elemental composition of autotrophs is often out of balance with the nutritional demands of herbivorous animals (Elser *et al.* 2000a). Aquatic macrophytes tend to be carbon-rich due to a requirement for a carbon-based strengthening frame whereas most herbivores and decomposers (animals, bacteria and fungi) found in these aquatic systems have a much lower C: nutrient ratio (Elser *et al.* 2000a). This was the case for the shredder communities in this study (Tables 6.10, 6.11 and 6.12). This suggests that elemental imbalances between food resources and consumer requirements may be common in these systems (Cross *et al.* 2005). Many consumers selectively feed on high energy (high C) or high nutritive food resources or a specific combination thereof (Plath and Boersma 2001). Both Amphipoda and Trichoptera selectively fed on vegetation group 3 across sites of average to excellent ecological condition (Tables 6.5 and 6.6), depending on availability, as this vegetation group contained the lowest C:N ratio (Fig. 6.2) and therefore the highest nutritional content. In degraded riverine reaches there is limited food resources available, hence vegetation group 1 (CPOM) formed the main dietary components of Amphipoda even though it had the highest C:N ratio. At site VP. 1, vegetation group 6 (filamentous algae) was the main dietary component of Trichoptera due to its availability and its low C:N ratio in comparison to the other primary sources available (Table 6.10). The imbalanced consumer-resource nutrient ratios in these degraded riverine reaches are likely to impose constraints on the growth and reproduction of their aquatic shredder communities with probable knock-on effects at higher trophic levels (Brookes *et al.* 2005; Cross *et al.* 2003; Frost and Elser 2002; Frost *et al.* 2002; Plath and Boersma 2001; Tibbets and Molles 2005; Tuchman *et al.* 2002; Tuchman *et al.* 2003).

The concept of a stoichiometric resource optima (Elser *et al.* 2005) predicts that primary consumers may respond positively or negatively to low C: nutrient ratios in food resources depending on the elemental requirements of the consumers and their physiological responses (e.g. ingestion and assimilation) to increases in food nutrient concentrations. Anthropogenic alterations and modifications in catchments leading to increased nutrient inputs, outputs and retention times within aquatic ecosystems can alter the stoichiometric relationships between consumer and food resources, which will have profound consequences for riverine carbon cycles and on aquatic food-web structure and function (Frost *et al.* 2005; Harris 1999b; Harris 2001b; Hicks 1997; Scheffer *et al.* 2001; Walker *et al.* 1997; Ward and Stanford 1983).

CHAPTER 7.

7 General Discussion

7.1 Restoration potential

For environmental flows to be ecologically successful in promoting aquatic / riparian plant communities, flows must be allocated to reaches with sufficient physical habitat remaining and land management practices in place (Chapter 2) (Boulton 1999; Jansen and Robertson 2001; Ladson *et al.* 1999; Rapport *et al.* 1998b; Robertson 1997; Robertson and Rowling 2000). The extent of the physical habitat remaining will be a function of the bank / channel morphology, which will be determined by the bank stability and aquatic wood debris present (Boulton 1999; Jansen and Robertson 2001; Ladson *et al.* 1999). However, fencing, grazing and width of riparian vegetation are a direct function of the immediate and surrounding land management practices and these factors will have a substantial bearing on the bank morphology, and hence the physical habitat availability (Allan 2004; Allan *et al.* 1997; Baattrup-Pedersen *et al.* 2005; Bunn 1993; Molles *et al.* 1998; Robertson 1997; Robertson and Rowling 2000; Walker *et al.* 1997).

Biggs *et al.* (2001) found that enhanced habitat heterogeneity in the restored reaches of the River Cole in the U.K. was unrelated to the observed increase in macrophyte richness. Instead macrophyte richness and composition was related to the shallower waters and lower banks of the new stream channel compared to the prerestoration channel, increased physical habitat availability (Biggs *et al.* 2001). In the western part of Jutland, Denmark, wide banks were associated with numerous species occurring both on the banks and in the streams (Pedersen *et al.* 2006). Wide and shallow stream banks retain more moisture than narrow, steep banks – channelised systems, thereby improving the conditions for wetland/riparian species (Baattrup-Pedersen *et al.* 2005; Clarke and Wharton 2000). Bank morphology is important for the composition and richness of the communities in the stream channel (Pedersen *et al.* 2006). Channelised streams are often deeply incised, which increases the channel capacity and flow velocity (Brookes 1994) which may reduce macrophyte establishment, colonisation and overall species richness (Riis and Biggs 2003; Riis *et al.* 2004). In addition, incision of the streambed leads to a lowering of the stream level and consequently a lowering of the water table in the riparian area. Thereby, both the longitudinal and lateral hydrological connectivity are effected by channelisation (Amoros and Bornette 2002), and both the structure and function of the ecosystem are likely to be severely effected (Baattrup-Pedersen *et al.* 2005). This was found in the regulated Green River and the free flowing Yampa River in north-western Colorado, USA (Merritt and Cooper 2000), where vegetation patterns reflect a dichotomy in moisture conditions across the floodplain. There will be a change in species composition which reflects the creation of more moist bank habitat, as was the case in the Gudenå River in Denmark (Baattrup-Pedersen *et al.* 2000).

Successful re-establishment of diverse aquatic / riparian plant communities is dependent on the species present before stream restoration work, as well as on the potential for species recruitment (Baattrup-Pedersen *et al.* 2000). Other studies have demonstrated successful reestablishment of macrophytes communities in restored streams (Biggs *et al.* 2001; Henry and Amoros 1996).

The plant communities of ephemeral systems at any one time reflect local conditions rather than longer term evolutionary events (Brock and Rogers 1998). Human induced alterations to the water regime and catchment land use in temporary systems, such as those studied, make each system more permanently wet or dry which is likely to reduce or alter species richness (Pedersen *et al.* 2006; Thompson 1992b) and hence change the seed bank composition and dynamics (Brock and Casanova 1997; Poiani and Johnson 1989). This was demonstrated in this study, not only by the high proportion of terrestrial species present (63% of all species recorded), but more so by the relatively high proportion of exotic (both aquatic and terrestrial) species present in the seed bank of each catchment. However, seed banks do provide a source of potential aquatic / riparian species (Baker 1989) and the seed banks in the EMLR do have the potential to germinate and establish given the right conditions (Brock and Rogers 1998; Poiani and Johnson 1989; Thompson and Grime 1979; Warwick and Brock 2003). A seed bank study in a northern Everglades marsh, in Florida, USA, focusing on hydrologic restoration to remedy an artificially shortened hydro period found that flooding inhibited the germination of all species except *T. domingensis* (Smith *et al.* 2002). They also found the assay communities' bore little resemblance to vegetation in currently undisturbed or historic wetlands of the northern Everglades. Moreover, rehydration may encourage the spread of undesirable hydrophytes such as *T. domingensis*

(Smith *et al.* 2002). Given the potential for undesirable exotics to recruit from the seed bank and displace immature native species upon the imposition of environmental flows, intensive weed control by management during the initial establishment years is strongly recommended (Budelsky and Galatowitsch 2000). The goal of a well-planned restoration should be to establish dense stands of native vegetation before aggressive perennials can pre-empt the sites (Galatowitsch *et al.* 1999). Well-established native vegetation has a greater chance of excluding subsequent invasions (Johnstone 1986).

7.2 Installation of environmental flows and their implications

Rivers and their floodplains need their natural water regime in all of its spatial and temporal variability to maintain natural ecological integrity and long-term evolutionary potential (Bunn and Arthington 2002; Poff *et al.* 1997; Puckridge *et al.* 1998; Walker *et al.* 1995). Variability in flow quantity, quality, timing and duration are often critical to maintain river ecosystems. Depending on the climate in which the system is situated, average river discharge may be one of the least essential elements of natural water regime (Dyson *et al.* 2003). This is particularly relevant for countries with drier climates that typically see seasonal flooding, followed by periods of drought (Dyson *et al.* 2003). In ephemeral systems such as those investigated, the promotion of aquatic and riparian plant communities may be achieved by using environment flows to extend the ‘wet period’. It is this ‘wet period’ that has been significantly reduced in recent times (Fig. 1.3, Chapter 1). For example, in the upper Finniss flow regulations have potentially reduced the median summer flows by 72% and median winter flows by 7% (Savadamuthu 2003). Though summer flows constitute only 2-3% of the annual flows, they are critical to the water dependent ecosystems as autumn/early winter is the period when the ecosystems are likely to be highly stressed (Savadamuthu 2003).

It is plausible that the timing of the environmental flows (Dyson *et al.* 2003), particularly when the system is highly stressed, would restore some of its ecological health and functioning, rather than greater volumes of flows when the system is not as highly stressed, such as winter (Fig. 1.2, Chapter 1). The application of environmental flows in the EMLR will be constrained to the amount of available water in local farm dams. The estimated storage capacity of farm dams in the upper Finniss catchment for example is 5,822ML. To extend the anthropogenically shortened ‘wet period’ in this region would only require approximately 14% of the total volume of water stored in those farm dams (Fig. 7.1). To raise the water level by 5cm requires an additional 10ML of water per day (Savadamuthu, 2003).

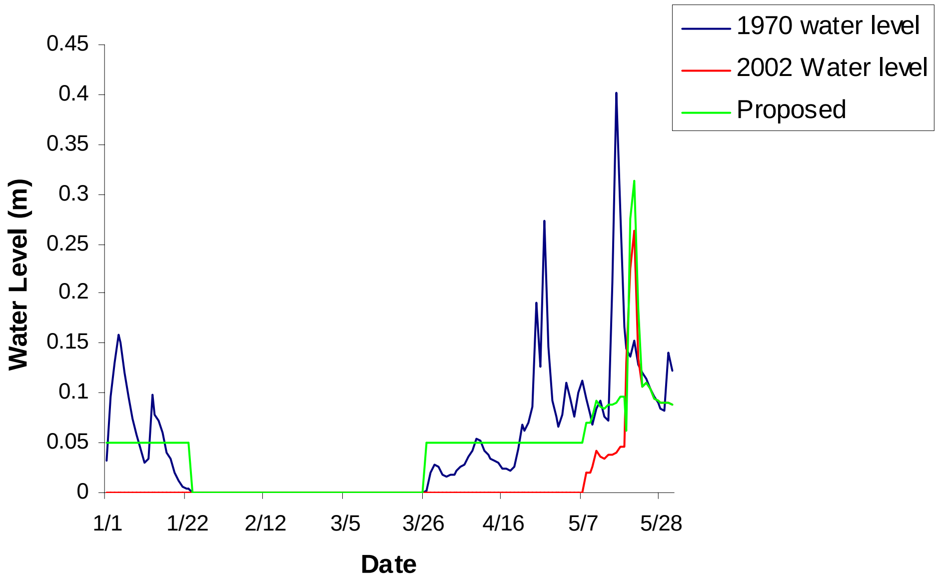

Figure 7.1: Comparison of variations in water levels on the Finniss River between the years 1970 and 2002, and the proposed water level for the future through the imposition of environmental flows.

Although this proposed increase in water levels through the imposition of environmental flows allows for minimal variation in the water level outside that of the present norm (2002 water levels with an increase of 5cm per day for a duration 80 days) it results in a significantly longer ‘wet period’ (65 days per annam) (Fig. 7.1). This would require substantially less environmental flow prescriptions in comparison to other river systems, such as those studied in Queensland and the Northern Territory or even the River Murray, South Australia, where 66 – 90% of their natural flow regimes are required to prevent further degradation (Arthington and Pusey 2003).

The re-introduction of variable stream flow regimes is proposed as a possible management tool to solve problems caused by flow regulations (Arthington and Pusey 2003; Bunn and Arthington 2002; Lake 2005; Leyer 2005; Poff *et al.* 1997; Puckridge *et al.* 1998; Richter *et al.* 1997; Rosenberg *et al.* 2000; Tharme 2003). Blanch *et al.* (2000) suggest that reinstating greater amplitude of weir pool water levels, more frequent shallow flooding, and longer periods of inundation would be beneficial for many plant species, promoting diversity by restoring a wider range of water regimes. Bearing in mind the estimated total storage capacity of farm dams in the EMLR (e.g. 5,822ML in the upper Finniss catchment) there is potential for the re-introduction of a more variable water regime (Chapter 4). However, given the current drought conditions in South Australia this is unlikely as a management technique, but that is not to say, that the present conditions will not change in the future allowing more water to be made available for environmental flows.

7.3 Ecological benefits of restoring and promoting aquatic plant communities

Macrophytes increase habitat and diversity by providing shelter, nursing habitats and substrate for epiphytes, invertebrates and fish (O'Hare and Murphy 1999). Changes in macrophyte composition and diversity have been shown to effect the distribution and abundance of macroinvertebrates and fish in lowland streams (Armitage *et al.* 2001; Langler and Smidth 2001). It is plausible that these alterations in the distribution and abundance of macroinvertebrates and fish in lowland streams is as a result of an imbalanced consumer-resource nutrient ratios found in those altered riverine reaches (Chapter 6). These imbalanced consumer-resource nutrient ratios are likely to impose constraints on the growth and reproduction of their aquatic macroinvertebrate communities, hence their distribution and abundance, with probable knock-on effects at higher trophic levels (Brookes *et al.* 2005; Cross *et al.* 2003; Frost and Elser 2002; Frost *et al.* 2002; Plath and Boersma 2001; Tibbets and Molles 2005; Tuchman *et al.* 2002; Tuchman *et al.* 2003). It is not too far removed to believe that the imposition of environmental flows would promote the germination and establishment of aquatic macrophyte species, along with the extant vegetation. This in turn may reduce the imbalanced consumer-resource nutrient ratios that occur in these altered systems and also reinstating other ecological functions and services which macrophytes provide higher trophic organisms (Ehrenfeld 2000; Giller 2005).

7.4 Conclusions

There have been significant attempts around the world to restore degraded river and stream systems with great success (Bernhardt *et al.* 2005; Giller 2005; Lepori *et al.* 2005; Malakoff 2004; Moerke and Lamberti 2004; Nakamura *et al.* 2006; Palmer *et al.* 2005). Environmental flows are a valid restoration method given the damage that regulation to natural flow regimes have caused (Dyson *et al.* 2003; Tharme 2003), however, the imposition of flows alone is not sufficient to restore these degraded systems. This study supports the contention that hydrologic restoration must be accompanied by some level of active vegetation management (Budelsky and Galatowitsch 2000) and that the reference restoration condition cannot be attained passively (Giller 2005).

The installation of environmental flows to restore and promote aquatic / riparian plant communities, which in turn would benefit higher trophic organisms, is a viable and realistic management option along selected reaches. Although catchment scale restoration is preferable to the selected reach scale approach (Lake 2005; Moerke and Lamberti 2004), this may not be an option given the logistics and constraints involved (Moerke and Lamberti 2004). Likewise, focusing solely on in-stream manipulations of water regimes may not be the best solution if streams have been degraded by catchment activities (Kauffman *et al.* 1997). The implementation of environmental flows should be accompanied by other catchment wide macro-restoration projects in order to achieve the full ecological potential and success of flows (Lake 2005). Such projects of restoration are desirable and preferable but will require partnerships to be formed between resource managers and scientists, with other stakeholders possibly involved (Kauffman *et al.* 1997; Lake 2005; Moerke and Lamberti 2004).

7.5 Future considerations

The challenges ahead for freshwater ecosystem management are far from over. Long-term rainfall records for these catchments indicate an overall decreasing trend in annual rainfall and/or delay of rainfall in the month of June (Savadamuthu 2003). Similar trends of decreasing annual and June rainfall were observed in studies of the Barossa Valley, the Onkaparinga and Marne catchments, South Australia (Savadamuthu 2003). On a global scale the prediction of impacts of climate change on river restorations as their flow regimes change in response to rising temperatures, altered rainfall distributions, increasing evaporation rates and overall greater water stress is daunting. Climate change will result in the competition for environmental water allocations becoming more difficult under future climatic and hydrological scenarios (Arthington and Pusey 2003). This is something, which management and scientists need to focus on now, rather than the future after these changes have already occurred.

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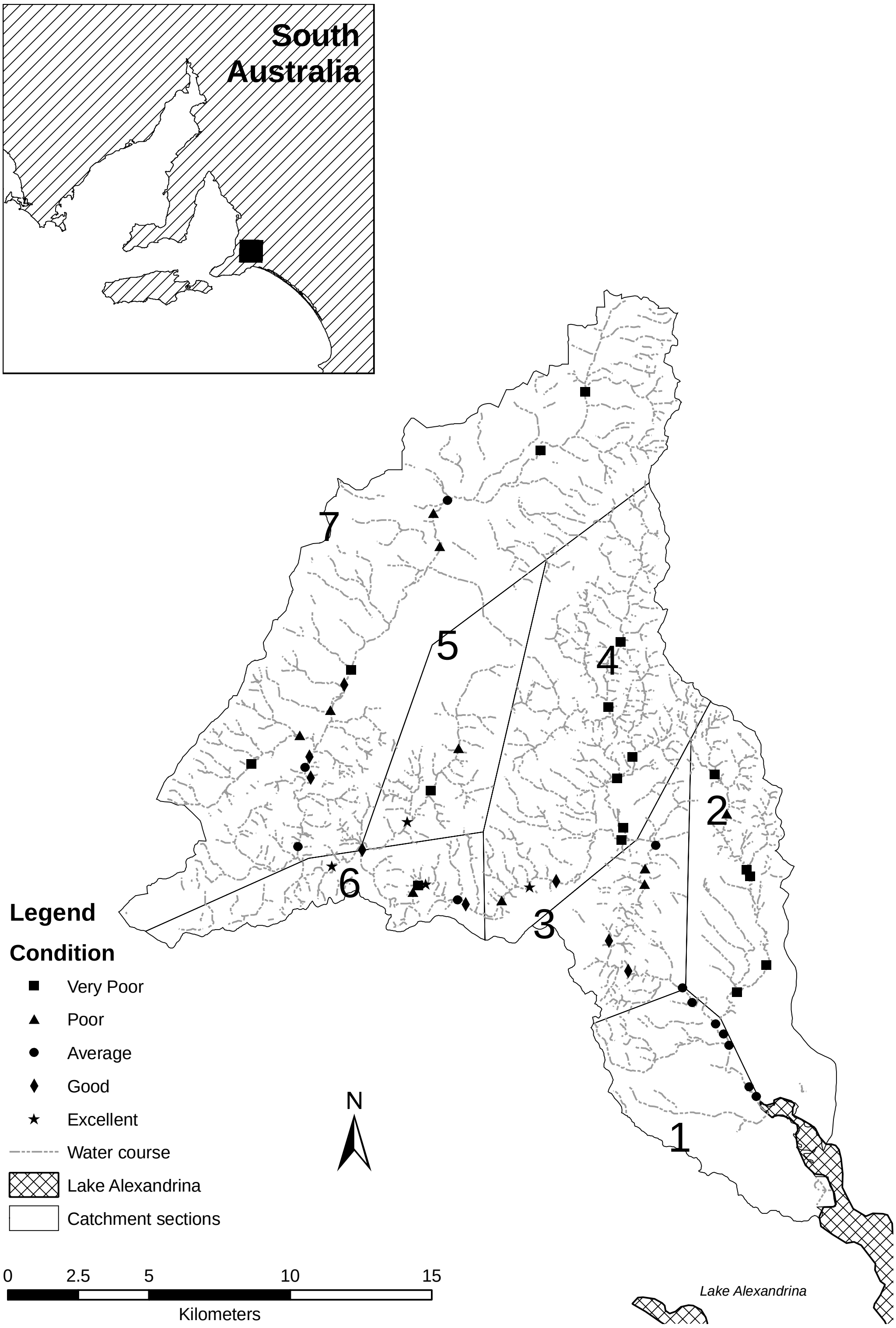
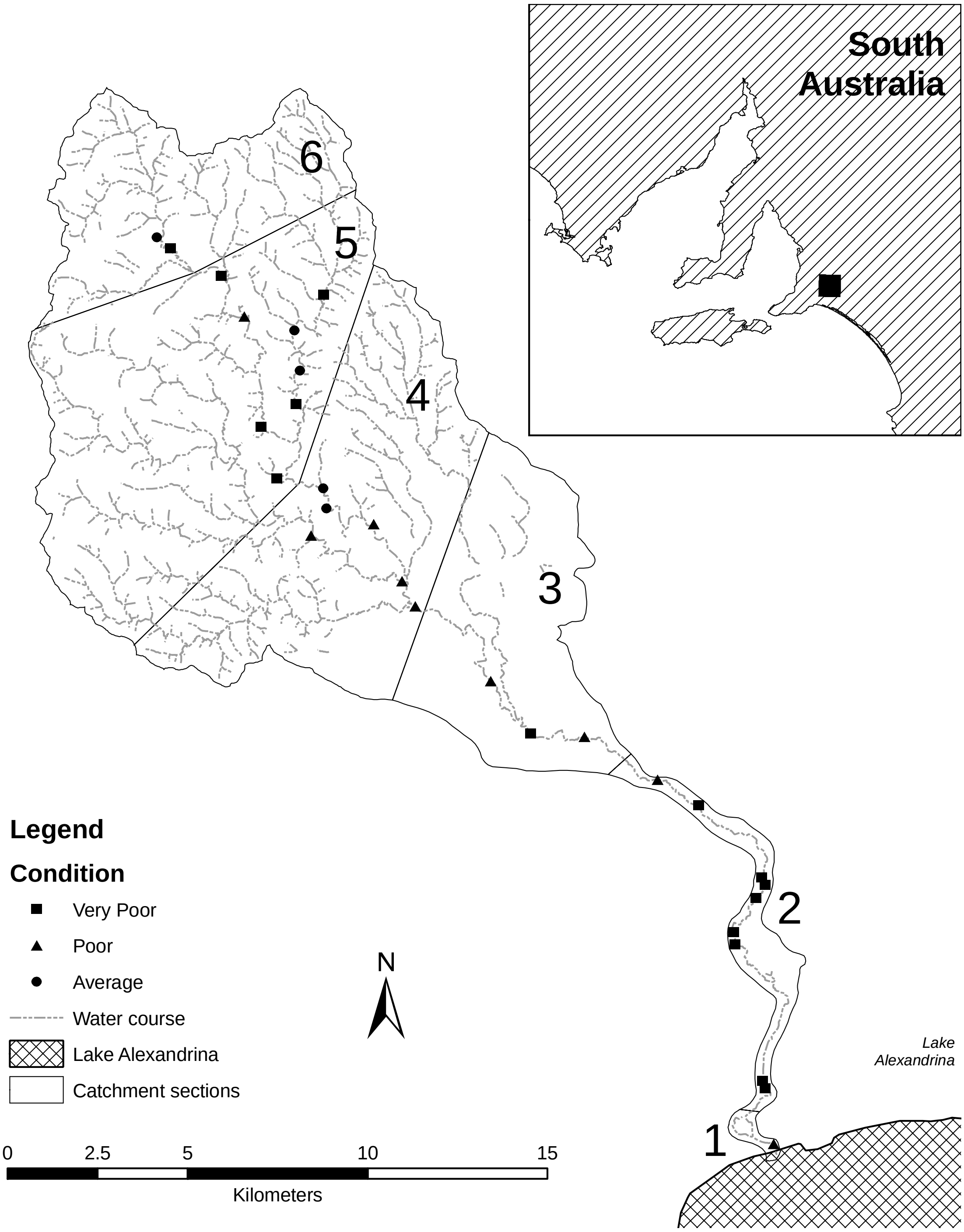
9 Appendices

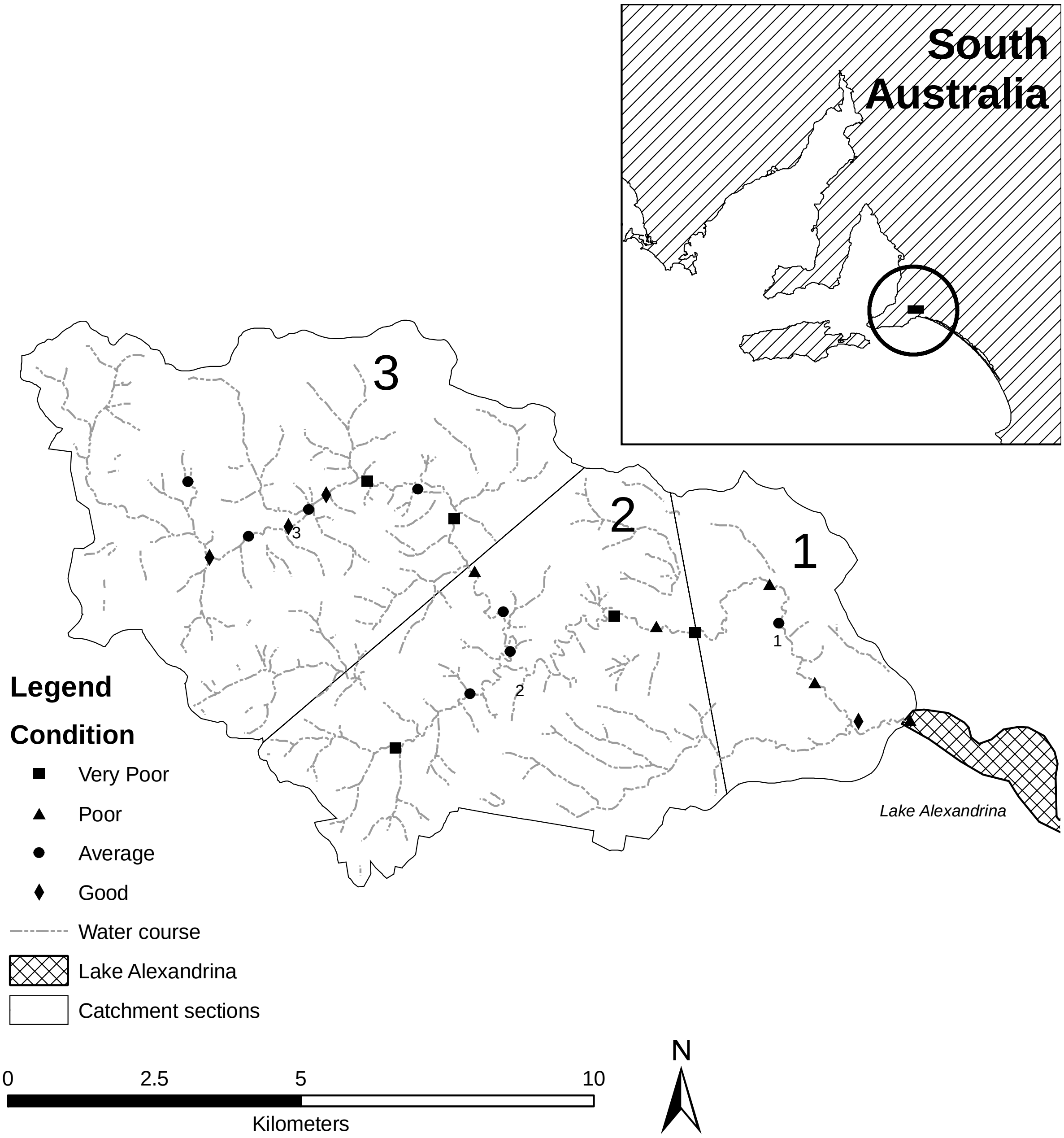
9.1 Appendix 1



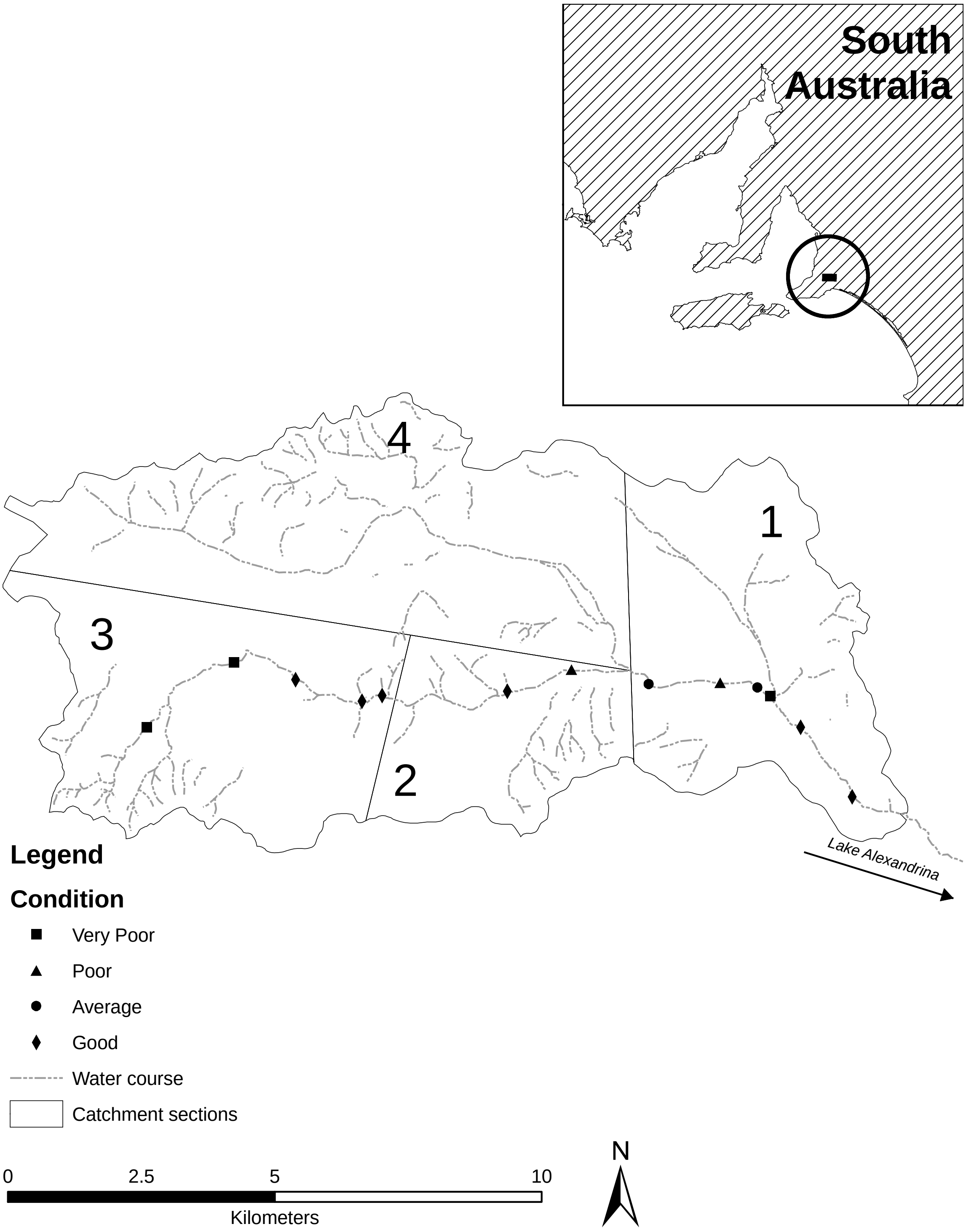
Surveyed reaches along the Finniss Catchment indicating their ecological condition (Chapter2) and the seed bank catchment sections (Chapter 3).



Surveyed reaches along the Angas catchment indicated their ecological condition (Chapter2) and the seed bank catchment sections (Chapter 3).



Surveyed reaches along Currency creek catchment indicating their ecological condition (Chapter2) and the seed bank catchment sections (Chapter 3).



Surveyed reaches along Tookayerta creek catchment indicating their ecological condition (Chapter2) and the seed bank catchment sections (Chapter 3).

9.2 Appendix 2

The species recorded in each catchment (1 indicates presence) during the ecological condition surveys. Functional classifications were either terrestrial or aquatic/riparian. Bold indicates presence recorded in the seed bank (Chapter 3).

Catchments:	**Finniss**	**Angas**	**Currency**	**Tookayerta**
Species:				
Oxalis pes-carpe (Terrestrial)	1	1	1	1
Cyperus vaginatus (Aqu/Rip)	**1**	**1**	**1**	
Pasture grasses (Terrestrial)	1	1	1	1
Phragmites australis (Aqu/Rip)	1	1	1	1
Isolepis nodosa (Aqu/Rip)	1	1	1	1
Rumex (Terrestrial)	1	1	1	1
Senecio (Terrestrial)	1	1	1	1
Juncus usitatus (Aqu/Rip)	1	1	1	1
Triglochin procerum (Aqu/Rip)	1	1	1	1
Hydrocotyle verticillate (Aqu/Rip)	1	1		
Mallee (Terrestrial)	1	1	1	1
Isolepis fluitans (Aqu/Rip)	**1**	**1**	**1**	**1**
Rubus fruticostus (Terrestrial)	1	1	1	1
Persicaria decipiens (Aqu/Rip)	1	1	**1**	**1**
Acacia (Terrestrial)	1	1	1	1
Eucalyptus camaldulensis (Aqu/Rip)	1	1	1	1
Melaleuca (Aqu/Rip)	1	1	1	1
Callistemon (Aqu/Rip)	1	1	1	1
Typha domingensis (Aqu/Rip)	**1**	**1**	1	**1**
Trifolium (Terrestrial)	1		1	1
Rosa (Terrestrial)	1	1	1	1
Cyperus gymnocalus (Aqu/Rip)	1	1	1	
Plantago lanceolata (Terrestrial)	1	1	1	1
Foeniculum vulgare (Terrestrial)	1	1	1	1
Zantedeschia aethiopica (Aqu/Rip)	1	1		1
Teline monspessulana (Terrestrial)	1	1	1	1
Baumea juncea (Aqu/Rip)	1	1	1	1
Cyperus eragrostis (Aqu/Rip)	1	**1**	1	1
Juncus pallidus (Aqu/Rip)	1	1	1	1
Potamogeton ochreatus (Aqu/Rip)	1		1	

Pteridium esculentum (Terrestrial)	1		1	1
Salix (Aqu/Rip)	1	1	1	1
Lepidosperma longitudinale (Aqu/Rip)			1	
Gahnia sieberiana (Aqu/Rip)			1	1
Crassula helmsii (Aqu/Rip)	**1**	**1**	**1**	1
Myriophyllum (Aqu/Rip)	1			
Gratiola peruviana (Aqu/Rip)	1	**1**	**1**	1
Carex appressa (Aqu/Rip)	1	1	1	1
Ranunculus inundatus (Aqu/Rip)	1			
Cotula coronopifolia (Aqu/Rip)	**1**	**1**	**1**	
Callitriche stagnalis (Aqu/Rip)	**1**	**1**	**1**	**1**
Medicago (Terrestrial)	1	1	1	1
Rorippa nasturtium-aquaticum (Aqu/Rip)	1	**1**	1	1
Schoenoplectus pungens (Aqu/Rip)	1	1		
Azolla (Aqu/Rip)	1	1	1	1
Baumea ribinosa (Aqu/Rip)	1	1	1	
Isolepis inundata (Aqu/Rip)	1			
Schoenoplectus validus (Aqu/Rip)	1	1	1	
Phalaris (Terrestrial)	1			
Anagallis arvensis (Terrestrial)	1	1	1	
Tetragonia tetragonioides (Terrestrial)	1	1		
Batrachium trichophyllum (Aqu/Rip)	1	1		
Baumea articulate (Aqu/Rip)	1		1	1
Ulex europaeus (Terrestrial)	1	1		
Eleocharis acuta (Aqu/Rip)		1		1
Ceratophyllum demersum (Aqu/Rip)		1		
Halosarcia (Aqu/Rip)		1		
Bolboschoenus caldwelli (Aqu/Rip)		1		
Potamogeton drummondi (Aqu/Rip)		1		
Potamogeton crispus (Aqu/Rip)		1		
Spirodella polyrrhiza (Aqu/Rip)		1	1	1
Cladium procerum (Aqu/Rip)		1	1	
Mimulus gracilis (Aqu/Rip)		1		
Juncus microcephalus (Aqu/Rip)			1	1
Juncus articulatus (Aqu/Rip)			1	
Gahnia filum (Aqu/Rip)				1
Lycopus australis (Aqu/Rip)				1
Mentha australis (Aqu/Rip)				1

Blechnum (Aqu/Rip)	1